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The postcranial skeletal anatomy of the therocephalian *Regisaurus* (Therapsida: Regisauridae) and its utilization for biostratigraphic correlation

Heidi Fourie* & Bruce S. Rubidge

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

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The postcranial morphology of the therocephalian genus *Regisaurus* from the *Lystrosaurus* Assemblage Zone of South Africa is described. The remarkably complete state of preservation of the vertebral column has, for the first time, provided a full vertebral count for a therocephalian and demonstrates that it is possible to differentiate between cervical, thoracic, lumbar, sacral and caudal vertebrae. It is demonstrated that some postcranial elements can be used to identify particular therocephalian groups and will be of use in biostratigraphic studies in areas where cranial remains have not been found. A slender scapula, low scapular ridge, shallow scapular depression, short and broad interclavicle, oval sternum, and a small obturator foramen are characteristics of therocephalians known from the *Cistecephalus, Dicynodon* and *Lystrosaurus* assemblage zones of the Beaufort Group of South Africa.

Keywords: Therapsida, Therocephalia, *Regisaurus,* postcranium.

INTRODUCTION

Therocephalians form a significant component of the therapsid faunas from the Karoo of South Africa, and together with dicynodonts are the therapsid clade that have the longest stratigraphic range in the rocks of the Karoo Supergroup. They also have a wide geographic range being known from Permian and Triassic rocks of southern and eastern Africa (Boonstra 1935, 1969; Drysdall & Kitching 1963; Kitching 1977; Keyser & Brink 1979), China (Li & Cheng 1995), Russia (Tatarinov 1974), and Antarctica (Colbert & Kitching1981). Many therocephalian taxa from South Africa have been described, and although several relatively recent descriptions on the cranial morphology are known (e.g. van den Heever 1987; 1994; Durand 1991; Hillenius 1992, 1994), studies on the postcranium of this important group have lagged behind. This paper describes a unique and almost completely preserved therocephalian skeleton (BP/1/3973). The presence of a long and high lacrimal; jugal meets the postorbital posteriorly and makes up the ventral portion of the postorbital bar; parietal present on dorsal part of occipital surface; upper dental formula of I6 C1 PC10; absence of precanines; palatal teeth on pterygoid boss; and apparent absence of a pineal foramen enables us to identify the specimen as *Regisaurus* (Mendrez 1975). Mendrez (1972) described the holotype of *Regisaurus* (BP/1/5394) on cranial morphology alone even though isolated elements of the hind limb, pelvic and pectoral girdles, and vertebral fragments are preserved. Kemp (1978) described the ilium and hind limb of the same specimen and made conclusions on the stance and gait of the genus.

MATERIAL

BP/1/3973 was collected by J.W. Kitching in 1964 from the *Lystrosaurus* Assemblage Zone on the farm Nooitgedacht, Bethulie, South Africa. *Proterosuchus* and *Lystrosaurus* are co-occurring genera from the same horizon at this locality, whereas *Dicynodon* (=*Daptocephalus*) and *Moschorhinus* are recorded from stratigraphically lower levels (Kitching 1977).

The specimen was preserved in a single calcareous nodule and was exposed by mechanical preparation using compressed air-driven engravers fitted with tungsten carbide tips. Because of the uniquely complete nature of the specimen great care was taken to preserve the original bone surface. For comparative purposes several therocephalian specimens that have postcranial elements preserved were studied in various museum collections (Table 1).

POSTCRANIAL DESCRIPTION

The skeleton of BP/1/3973 is almost complete, lacking only the right manus, left pes, left femur, left ilium and portion of the left tibia and right tibia and fibula. Parts of the pelvic girdle were disarticulated prior to fossilization and are preserved on the left side of the body close to the distal tibia and fibula (Figs 1B, 2B). As the holotype preserves only parts of the ilium and hind limb and elements of the shoulder girdle, specimen BP/1/3973 has much to contribute to our understanding of therocephalian postcranial anatomy. In the following description the ‘in life’ dorsal, ventral, lateral, and medial orientation of the different bones is assumed.

Vertebrae (Fig. 3)

A remarkable feature of BP/1/3973 is that, apart from the most distal caudals, the entire vertebral column is preserved in articulation. It is thus possible, for the first time, to accurately document the vertebral count of 32, excluding the caudals, for *Regisaurus.* A list of vertebral counts for a variety of therocephalian genera is provided (Table 2).

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*Author for correspondence. Present address: Transvaal Museum, P.O. Box 413, Pretoria, 0001 South Africa. E-mail: hfourie@nfi.co.za

Table 1. List of therocephalian specimens used for comparative purposes.

Specimen No.	Genus	Assemblage Zone	Description
UCMP V 42667	*Cynariognathus platyrhinus*	*Tapinocephalus*	Cys (1967)
SAM 4321	*Blattoidealestes gracilis*	*Tapinocephalus*	Boonstra (1954)
SAM 12185	*Zinnosaurus (Lycosuchus)*	*Tapinocephalus*	Boonstra (1964)
SAM/K 7809	*Glanosuchus macrops*	*Tapinocephalus*	Fourie (2001)
SAM 4004	*Macroscelesaurus janseni*	(Gemsbokfontein)	Haughton (1918)
?	*Pristerognathus baini*	*Tapinocephalus*	Broom (1936)
SAM 6004	*Macroscelesaurus*	*Pristerognathus*	Haughton, 1918
TM 1608	*Silpholestes jackae*	*Tropidostoma*	Broom (1948)
RC 104	*Ictidosuchoides intermedius*	*Cistecephalus*	Broom (1938)
UCMP V 40467	*Mirotenthes*	*Cistecephalus*	Attridge (1956)
AMNH 5529	*Ictidosuchus primaevus*	(near Pearston)	Broom (1901)
BP/1/182	*Aneugomphius*	*Dicynodon*	Brink (1958)
BMNH R5694/5755	*Whaitsia*	*Dicynodon*	Boonstra (1934)
BP/1/2294	*Ictidosuchops intermedius*	*Dicynodon*	Not described
BP/1/3155	*Ictidosuchops intermedius*	*Tropidostoma*	Not described
BP/1/1341	*Scaloposaurus constrictus*	*Lystrosaurus*	Not described
BP/1/2710	*Tetracynodon darti*	*Lystrosaurus*	Sigogneau (1963)
BP/1/3849	*Olivieria parringtoni*	*Lystrosaurus*	Brink (1965)
BP/1/3973	*Regisaurus*	*Lystrosaurus*	Fourie (2001)
BP/1/5394	*Regisaurus jacobi*	*Lystrosaurus*	Kemp (1978)
SAM K 1392	*Zorillodontops gracilis*	*Lystrosaurus*	Cluver (1969)
AMNH 9550	*Ericiolacerta parva*	Fremouw Formation, Antarctica	Colbert & Kitching (1981)
DMSW R377/ MZC 7369	*Ericiolacerta parva*	*Lystrosaurus*	Watson (1931)
UMZC T 837	Baurioid	*Lystrosaurus*	Kemp (1986)
BP/1/1180	*Bauria cynops*	*Cynognathus*	Not described
AMNH 5622	*Bauria cynops*	*Cynognathus*	Broom (1937), Boonstra (1938), Schaeffer (1941)
V 4786	*Ordosia*	Er-Ma-Ying Formation	Lianhai (1979)
BMNH 4095	*Bauria cynops*	*Cynognathus*	Watson (1931)
NMQR 3189	*Bauria cynops*	*Cynognathus*	King (1996), Fourie (2001)
?	Bauriamorph	*Cynognathus*	Watson (1931)

Specimen BP/1/3973 preserves six articulated cervical vertebrae (including the atlas). A proatlas is not preserved and of the atlas, only the left transverse process is preserved. The axis is the largest of the cervical vertebrae and is easily distinguishable from the rest as it has the widest neural process which, in dorsal view, is triangular with rounded sides. The area below the neural spine (neural arch) is broadly rectangular in outline when viewed dorsally, with the enlarged prezygapophyses comprising the anterior rounded corners and the smaller postzygapophyses situated posterolaterally. The dorsal surface between the left and right prezygapophyses and left and right postzygapophyses is concave. Dorsally, the prezygapophysis is oval with a convex articulation surface, whereas the postzygapophysis has the same shape, but a concave articulation facet. Ventrally the prezygapophysis is concave and dips laterally towards the transverse process. The rectangular transverse process is placed closer to the prezygapophysis than to the postzygapophyses and at a lower level (Fig. 3A). In lateral view the anteroposteriorly expanded neural spine rises vertically, slightly overhanging the neural arch. It is broadly rectangular with concave anterior and posterior sides and slopes ventrolaterally towards the transverse process. An oval

Table 2. Table of vertebral counts of different therocephalian genera from both the literature and personal observation. The final row provides a summary of the range of recorded vertebral counts for well-preserved therocephalian specimens.

Specimen	Total (excl. caudal)	Presacral	Cervical	Thoracic	Lumbar	Sacral	Caudal
Glanosuchus, SAM/K7809	>28–29	27–28	5–6	>16	6	>1	>4
Macroscelesaurus, SAM4004	>30	27	7	>15	>5	3	
Cynariognathus, UCMPV42667	>30	27	7	>15	5	3	14
Mirotenthes, UCMPV3695	>10–11	>7	7			3–4	14
Aneugomphius, BP/1/182	>29	>25	>5	14–16	6–7	4	>3
Zorillodontops, SAMK1392	>15	>15–17	6–7	>5–6	>4		
Regisaurus, BP/1/3973	>32	28	6	17	5	4	>4
Scaloposaurus, BP/1/1341	>26	>24–25	6	>13	5–6	3–4	>2
Ericiolacerta, MZC7369	>19	>17–18	6–7	8	>3	3	>2
Baurioid, UMZCT837	>28	>19–21	14–15	5–6	3	>9–10	
All Therocephalia	28–32	27–28	6–7	15–17	5–6	3–4	>9

> = counts may be larger as the table is based on preserved material only.

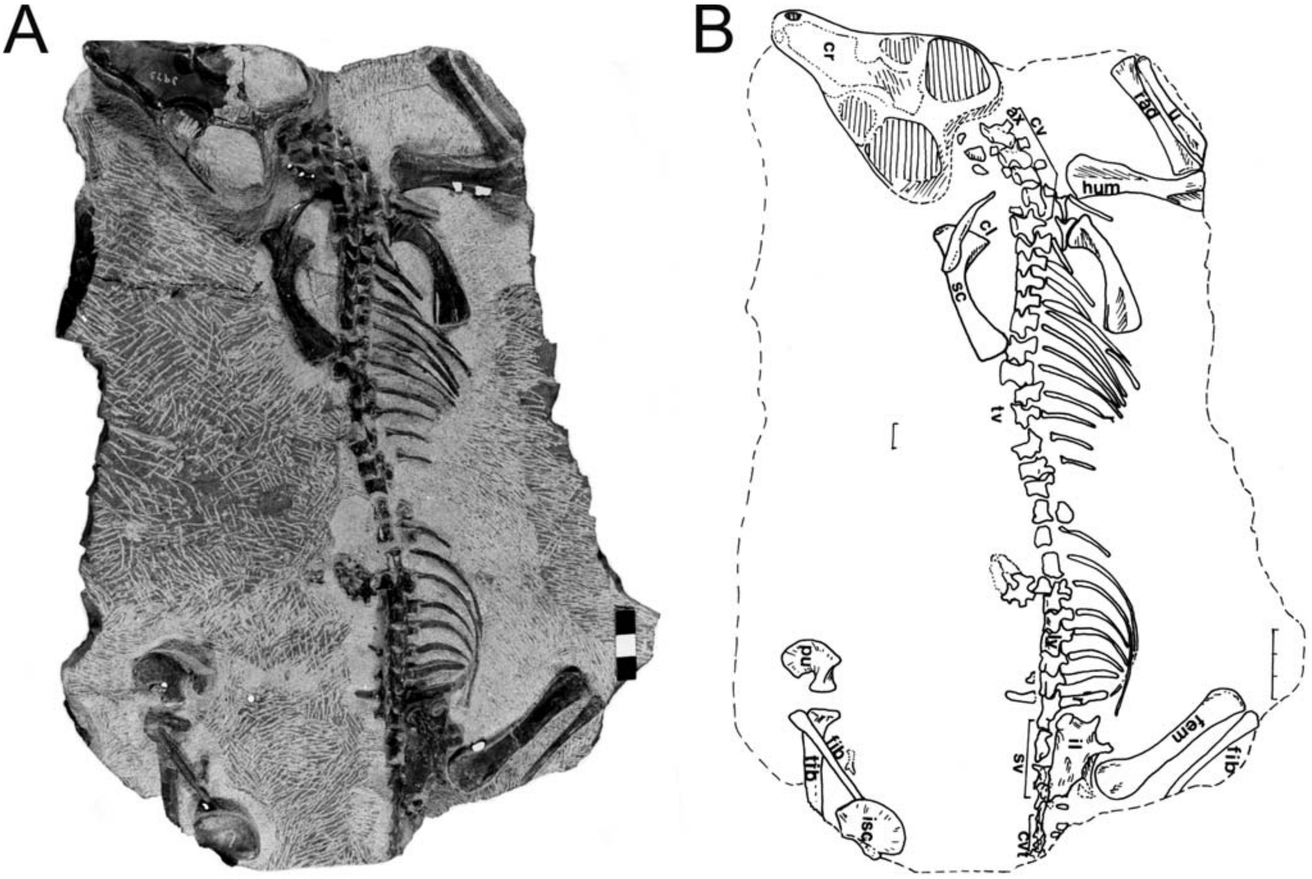

Figure 1. Dorsal view of *Regisaurus* sp. (BP/1/3973). Scale bar = 10 mm.

facet, which is thickened for the articulation with the tuberculum of the rib, is situated on the lateral extremity of the transverse process. The spindle-shaped amphicoelous centrum thins toward the middle.

The remaining four cervical vertebrae (Fig. 3B) have the same general shape as the axis, except that the neural spine is not anteroposteriorly expanded. The sixth cervical has a slightly wider neural spine than those of the preceding four vertebrae, but is not as wide as that of the axis.

As in all therocephalian genera the 17 thoracic vertebrae

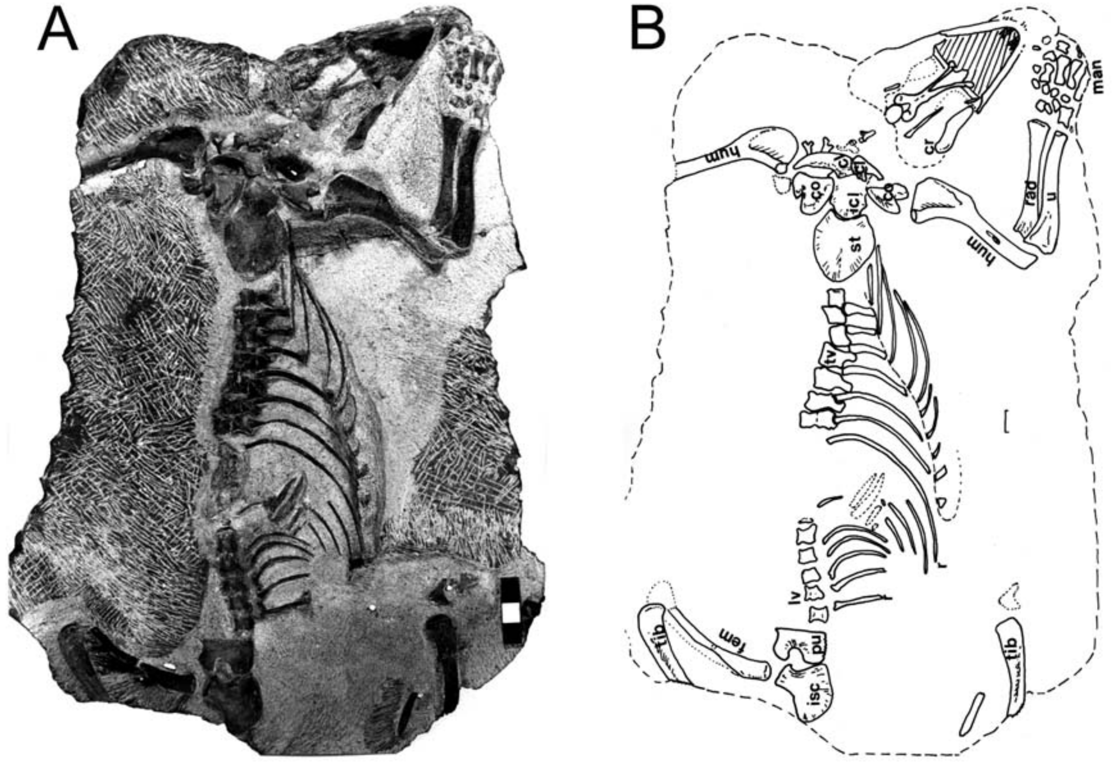

Figure 2. Ventral view of *Regisaurus* sp. (BP/1/3973). Scale bar = 10 mm.

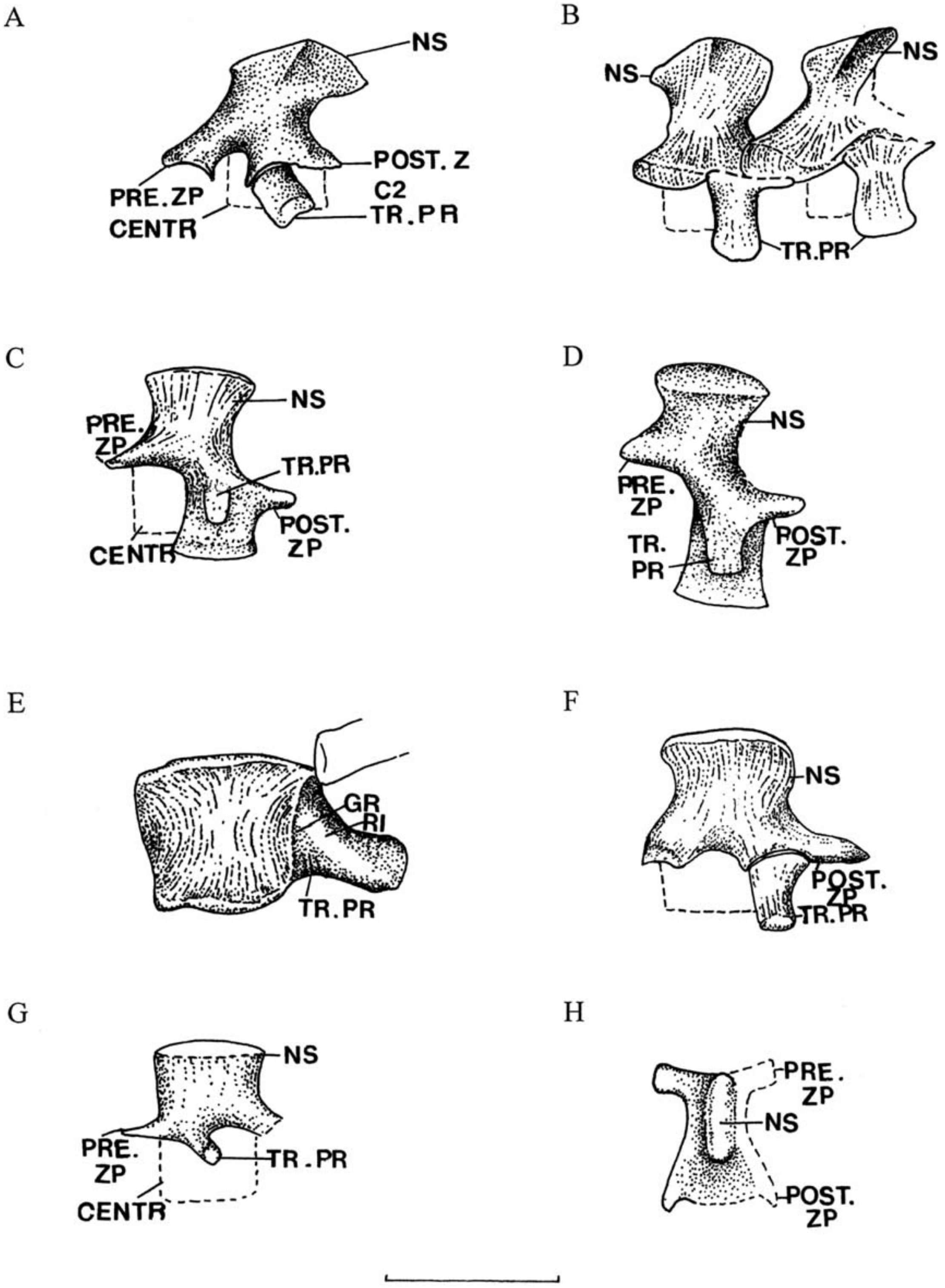

Figure 3. Vertebrae of *Regisaurus* sp. (BP/1/3973): **A**, axis (lateral view); **B**, cervical C3, C4 (lateral view); **C**, thoracic T1 (lateral view); **D**, thoracic T10 (lateral view); **E**, thoracic T 10 centrum showing groove (ventral view); **F**, lumbar L4 (lateral view); **G**, sacral S3 (lateral view); **H**, sacral S3 (dorsal view). Scale bar = 10 mm.

of BP/1/3973 (Fig. 3C,D) are similar in shape to the cervical vertebrae, but differ in that they are more lightly built. In ventral view the transverse process of each of the 17 thoracic vertebrae is broadly triangular with the apex extending posterolaterally and ventrally to contact its corresponding rib. The anterior border of the process is straight while the posterior one is slightly concave. A ridge is present on the anteroventral edge of the transverse process and has an elongated groove extending parallel to it (Fig. 3E). The transverse process was not ossified to the centrum, as can be seen clearly in T11 and T12 (Fig. 3B), suggesting this was a young individual.

The five lumbar vertebrae have the same general shape as those of the cervical and thoracic regions. In lateral view, the neural spines of the lumbar vertebrae are longer than those of the thoracic vertebrae whereas the transverse processes are shorter, more robust and wider (Fig. 3F). In these vertebrae the transverse processes point laterally

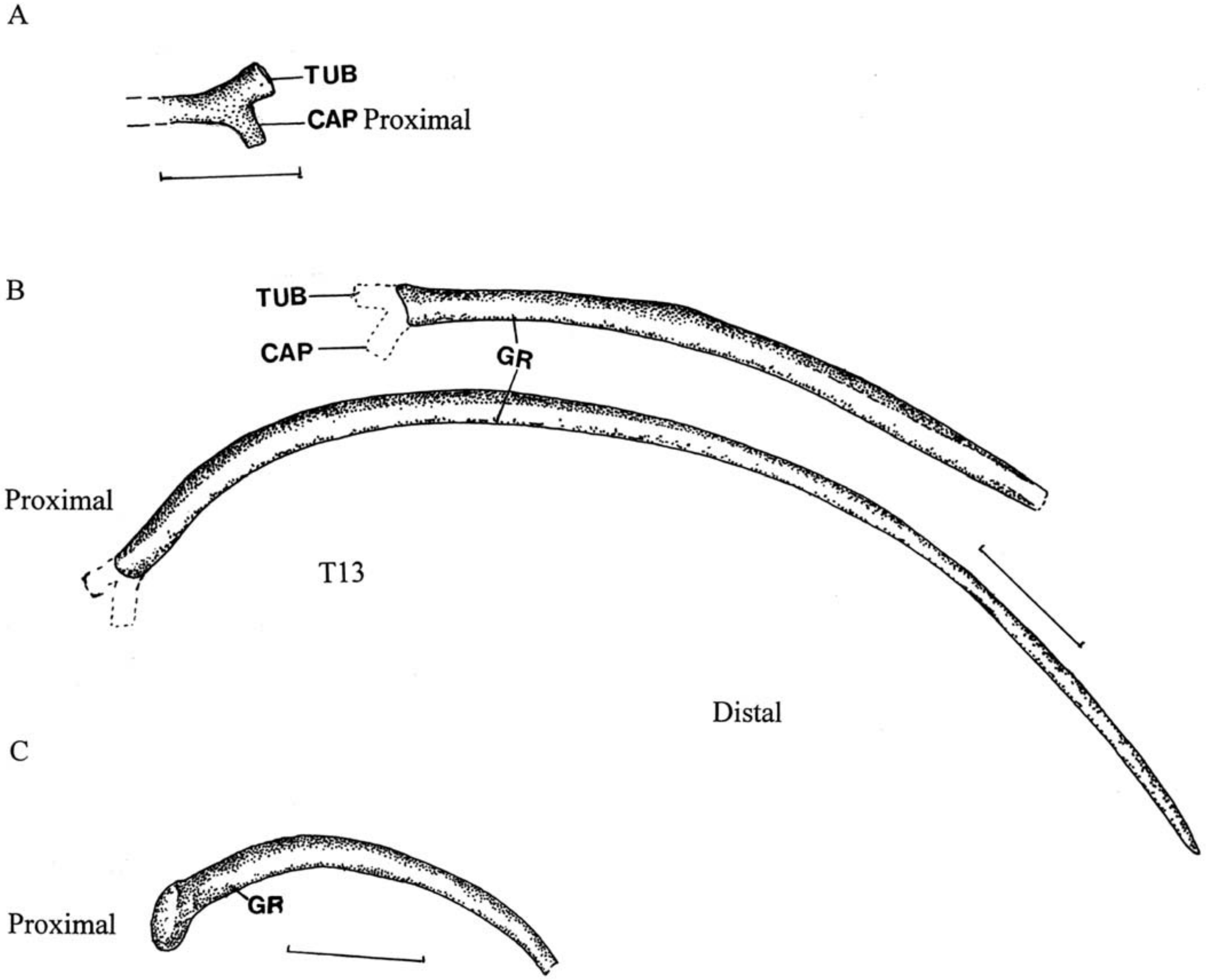

Figure 4. Ribs of *Regisaurus* sp. (BP/1/3973): **A**, cervical, proximal end; **B**, thoracic T5 and T13 (posterior view); **C**, Lumbar L3 (posterior view). Scale bars = 10 mm.

rather than posterolaterally as in the cervical and thoracic vertebrae.

In general shape the four sacrals are similar to the other vertebrae, but each has a shorter and thinner neural spine, and a shorter transverse process (Fig. 3G,H). In dorsal view the transverse process is rectangular with a rounded upper surface and is fused to its corresponding sacral rib.

Only the anteriormost four caudal vertebrae are preserved. Although they are similar in shape, they are much smaller than the other vertebrae and decrease in size posteriorly. The transverse processes slope ventrally and are short, thick and rounded dorsally with a concave contact area for the ribs at their distal extremity. These vertebrae have low neural spines which decrease in size posteriorly. As the last caudal vertebrae of all therocephalians, where they are preserved, comprise only centra, it is expected that in BP/1/3973 caudal neural spines, transverse processes and ribs disappear posteriorly.

Ribs (Fig. 4)

Although the rib cage of specimen BP/1/3973 was flattened in the fossilization process many of the ribs are preserved (Fig. 1). In the cervical region most of the ribs are broken, but two well-preserved ribs demonstrate that the cervical ribs have a short, thin, and slightly curved shaft with a dichocephalous head. The tuberculum is wider and more stocky than the capitulum (Fig. 4A), which in turn is longer and thinner. The articulation facet of the tuberculum for the transverse process (diapophysis) is slightly flattened compared to that of the capitulum for the centrum (parapophysis) which is rounded. A groove which lines up with the groove on the transverse process extends from the tuberculum to the distal end of the rib. These ribs, which are very short, did not contact the sternum.

The dichocephalous thoracic ribs of BP/1/3973, which are attached to the sternum, are longer and more slender than the cervical ribs and a broad sheet of bone joins the tuberculum and capitulum. The proximal part of the rib is wider than the distal end and flattened anteroposteriorly. As in the cervical ribs, a groove (Fig. 4B, GR) extends on the posterior side of the rib from the tuberculum to the distal end. The flattened rib shaft curves away ventrally from the vertebral column for a short distance and straightens towards the distal end to meet the sternal segment. In BP/1/3973 12 sternal segments are visible in

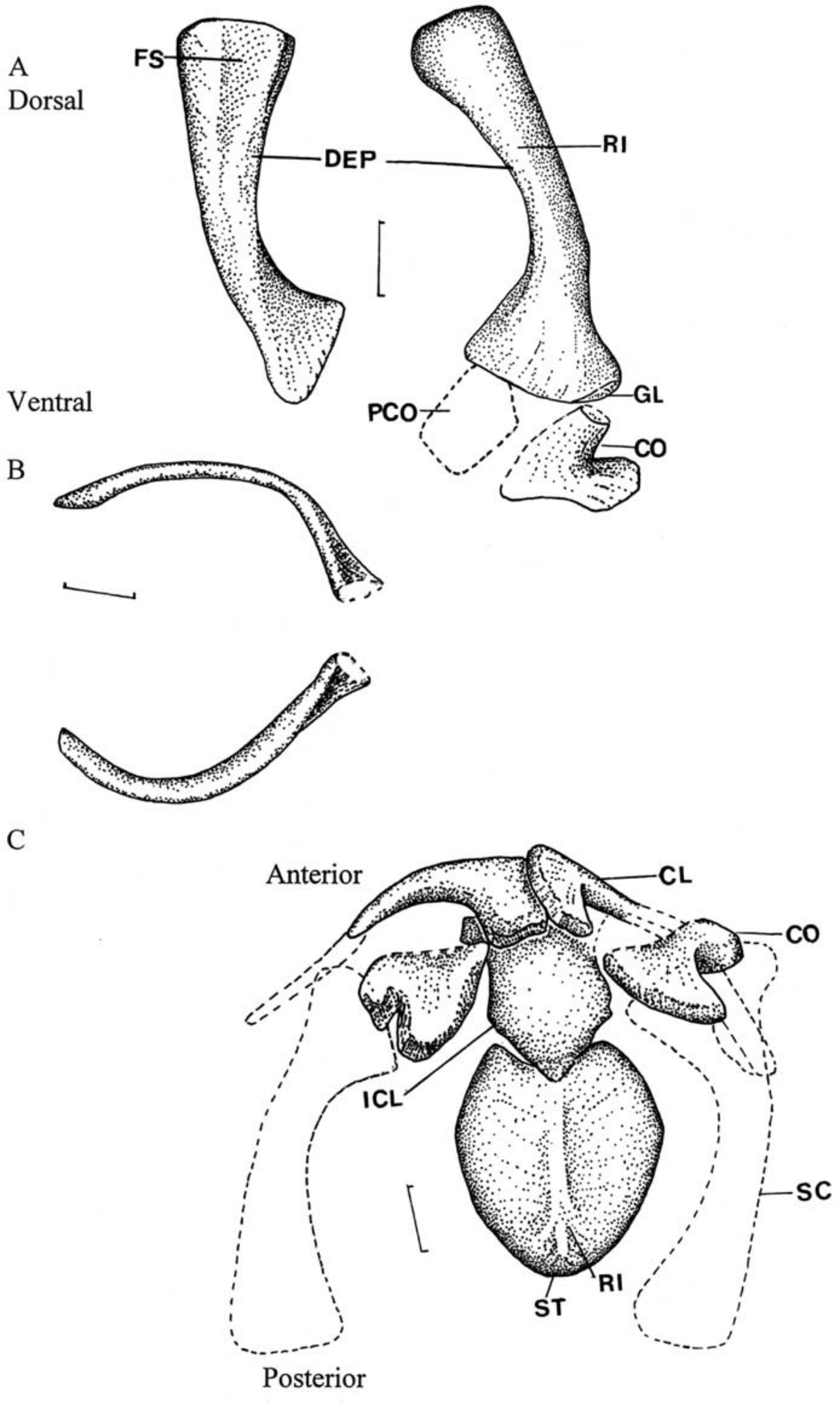

Figure 5. Pectoral girdle of *Regisaurus* sp. (BP/1/3973): **A**, scapula and coracoid (lateral view); **B**, claviculae (dorsal view); **C**, ventral view showing coracoids, interclavicle and sternum. Scale bars = 10 mm.

ventral view. These are attached to the sternum and decrease in length posteriorly. Rib 14 is the longest, and from this point the ribs become progressively shorter both anteriorly and posteriorly.

Lumbar ribs, which are much shorter and broader than the thoracic ribs, are fused to the vertebrae and decrease in size posteriorly. These dorsally rounded ribs are all single-headed (Fig. 4C) and are expanded both dorso-ventrally and anteroposteriorly with the proximal end being the widest. The first three lumbar ribs curve ventrally (the third less than the first) and the last two are straight. Distally the shafts of all the lumbar ribs have a rounded end.

In dorsal view the caudal ribs are rectangular and much shorter than those of the lumbar region. These single headed ribs are fused to the vertebrae and curve ventrally. The distal end is blunt.

Pectoral girdle (Fig. 5)

The interclavicle of BP/1/3973 (Fig. 5C), visible in ventral view, is situated between the coracoids, clavicles and sternum and is a broad flat circular bone. A posteromedial ridge is present as seen in *Ericiolacerta* (Watson 1931). Both clavicles, which are 55 mm long, are preserved but the right one lacks the distal end. In ventral view the rectangular proximal end of the left clavicle is displaced over the right, and they both overlie the interclavicle. Dorsally the oval end fits loosely against the bottom third of the scapula. Both procoracoids and coracoids are preserved, but they are displaced in such a way that the procoracoids are tilted and not much of them are visible. The large oval sternum is ossified with a longitudinal median ridge extending down the ventral side of the thin plate. Both humeri, which are robust bones, are preserved in a sprawling position and are articulated distally with the lower leg.

The scapula of only the holotype (BP/1/5394) has the ventral portion preserved and so the complete scapula of BP/1/3973 affords the best description. This bone, which is approximately 80 mm in length, is the largest element of the pectoral girdle (Fig. 5B). Both scapulae of BP/1/3973 are tilted so that the lateral surface is exposed on the dorsal side of the specimen. It is a curved bone which is flattened lateromedially and has slightly expanded proximal and distal ends. In lateral view the dorsal end is expanded anteroposteriorly. The entire flattened lateral surface has striations extending from the proximal to the distal end of the shaft. From the dorsal end, the scapula narrows towards the middle of the bone where the shaft is semi-circular in cross-section. The lateral surface has a median ridge that extends dorsoventrally (Fig. 5B, RI) on the shaft to terminate on the glenoid facet. Ventrolaterally the bone surface is flat and only slightly rounded in the glenoid area. The glenoid facet is concave and oval. The ventral end of the scapula is much more expanded anteroposteriorly than on the dorsal end and it flares further posteriorly towards the glenoid facet than towards the anterior side. The extreme ventral surface of the bone is curved downwards. An area above the glenoid facet is striated towards the shaft in a dorsal direction. Striations are present on the medial depressed surface in a dorsal direction, both striated areas terminating on the shaft. These striations extend in an anteromedial and posteromedial direction. The medial surface of the scapula curves posteroventrally to overlie the thoracic ribs. As in all therocephalians in which the scapula is known, this bone lacks an acromion process.

The presence of an ossified cleithrum in therocephalians is uncertain, and has been described in only a few genera (Boonstra 1964; Watson 1931) as a very small splint of bone attached to the anterior edge and outer surface of the upper end of the scapula as seen in *Scymnosaurus* and *Pristerognathus,* The lack of a cleithrum in BP/1/3973 and the absence of facets on the anterior edge of the scapula of suggests that an ossified cleithrum may not have been present.

The coracoid (Fig. 5C) is blade-like and the surface is almost flat. It has a smooth contact with the sternum and a sutural contact with the procoracoid. The dorsal edge is unattached forming the concave glenoid facet. The blade surface is slightly convex with striations that extend from the glenoid towards the medial edge.

In ventral view the thin sternum is oval with an indentation at the anterior end to accommodate the overlapping interclavicle (Fig. 5C). A prominent midline ridge which increases posteriorly in height extends from the centre of the bone towards the posteriormost edge to end pointed. On either side of this ridge is a slightly depressed area. Striations extend in a flaring pattern from the centre of the sternum outwards towards the edge.

Forelimb (Figs 6 & 7)

The humerus of BP/1/3973 is a robust and relatively long bone (Fig. 6) with the deltopectoral crest situated proximally and the double condyle at the opposite end. The bone is twisted such that the deltopectoral crest was oriented vertically in life, while the distal end of the humerus had a horizontal orientation. A marked triangular recess between the ente- and ectepicondyles on the dorsal side of the humerus served as the fossa for the olecranon, while a small lip at the distal end of the fossa prevented the olecranon from dislocating.

The deltopectoral crest is expanded dorsoventrally, but narrows towards the circular short shaft. The proximal extremity of the caput humerus curves outwards towards the glenoid. Long proximodistally oriented striations on the anterior side of the deltopectoral crest are interpreted as muscle scars.

In ventral view (Fig. 6D) the proximal end of the deltopectoral crest curves posteriorly and has a thin rounded edge. A small oval elongated entepicondylar foramen is present close to the distal end where the ente- and ectepicondyles have a concave triangular recess in which the entepicondylar foramen is situated. No ectepicondylar foramen is present as is the situation in *Mirotenthes* (Attridge 1956), *Cynariognathus* (Cys 1967), Regisauridae (Kemp 1986), Scylacosauridae (Boonstra 1964), *Silpholestes* (Broom 1948) and *Whaitsia* (Boonstra 1934). The presence of this foramen in *Bauria* (NMQR 3189) indicates that this feature is variable in therocephalians or only present in the more derived forms.

The sigmoid curved ulna of BP/1/3973 is long and thin with an expanded olecranon process at the proximal end (Fig. 7A,B). It is blunt distally where it has an ovoid articulation facet for the ulnare. In anterior view the proximal end is lateromedially expanded with a longitudinal groove (Fig. 7A) which extends half-way down the bone. The shaft is thin and flattened. The ulna exhibits a weak olecranon process (Fig. 7B). Posteroventral to the olecranon process is a triangular depression area with the apex pointing distally (Fig. 7B, DEP). The ulna and radius cross to some degree with the proximal ulna positioned medial to the radius.

The radius (Fig. 7) is an elongated bone with a relatively thin shaft and lateromedially expanded ends, with the proximal end much broader than the distal. The proximal articulating facet is slightly concave on the anterior side where it articulates with the entepicondyle of the humerus. Both the proximal and distal extremities are oval and concave. An incipient ridge (Fig. 8B, RI) extends on the posterior side of the bone from a position two-thirds down the length of the radius to the distal end. In *Bauria*

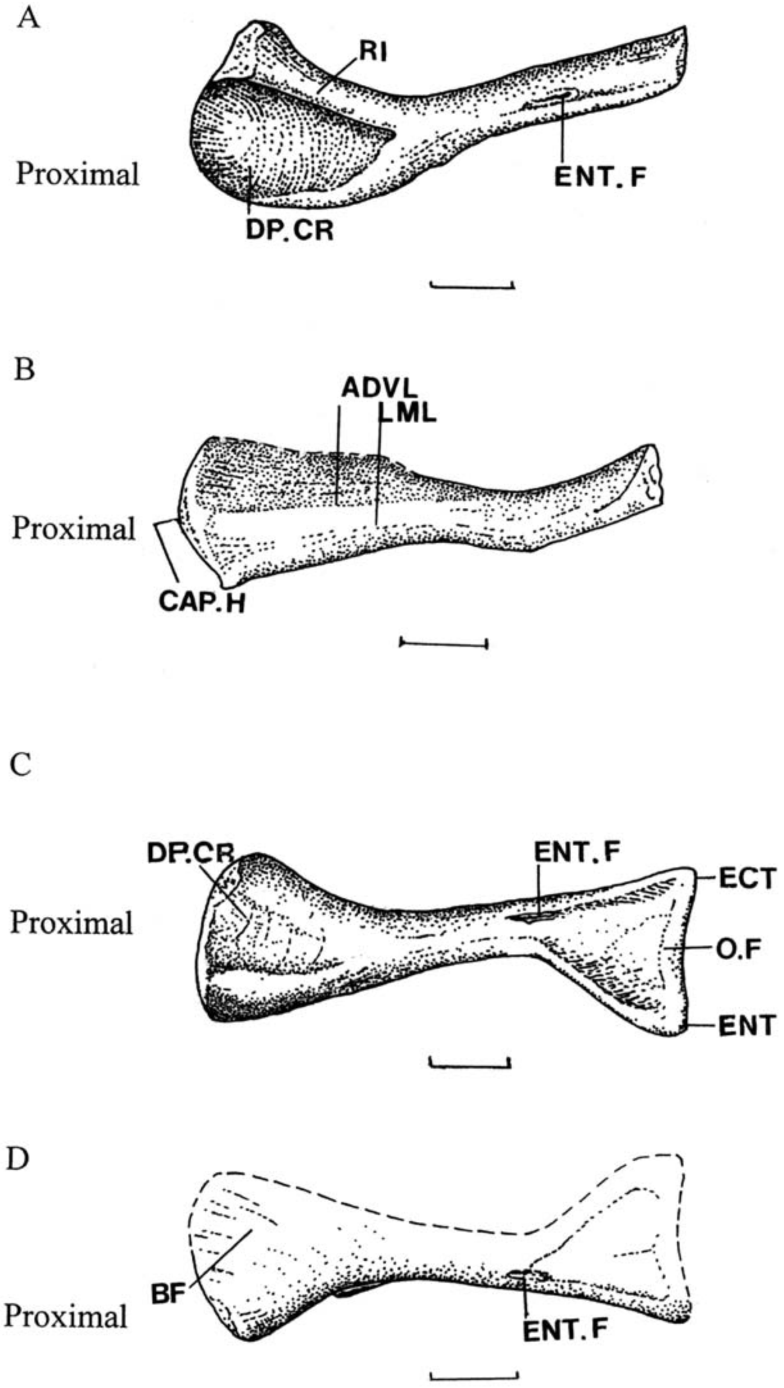

Figure 6. Left humerus of *Regisaurus* sp. (BP/1/3973): **A**, posterior view; **B**, anterior view; **C**, dorsal view; **D**, ventral view. Scale bars = 10 mm.

(NMQR 3189) there is a ridge on the anterior surface.

The carpals are remarkably well preserved with the ulnare, radiale, pisiforme, intermedium, one centrale and three distals being preserved in articulation (Fig. 7C). These bones are present in two rows with the radiale, ulnare, intermedium, pisiforme and the centrale at the proximal end of the wrist, and the distals in the second row. The ulnare is the largest of the carpal bones and is dorsoventrally flattened and rectangular. It has a round proximal facet for articulation with the distal end of the ulna. As in all therocephalians the ulnare is hour-glass shaped in dorsal view with expanded ends. A distinct groove is present between the ulnare and centrale 1 on the dorsal side while the ventral surface of the ulnare has a longitudinal groove. The flattened proximal end has its lateral edge truncated into an articular facet for the pisiforme. Centrale 1 articulates with the medial surface of the ulnare while the fused distals 4 and 5 articulate with the distal side of the ulnare.

The radiale is the second largest wrist bone and articulates with the radius. This quadrangular bone is positioned at the distal end of the radius. Both medial and lateral sides are straight with the anterior and posterior ends rounded and a central concavity is present on the dorsal surface. The posteriorly situated radial articular surface is broad and slightly convex, while anteriorly, centrale 1 articulates with the radiale in a concave facet as in all therocephalians where this bone is preserved.

Both the pisiforme and intermedium are small bones, the rounded pisiforme being present on the lateral side of

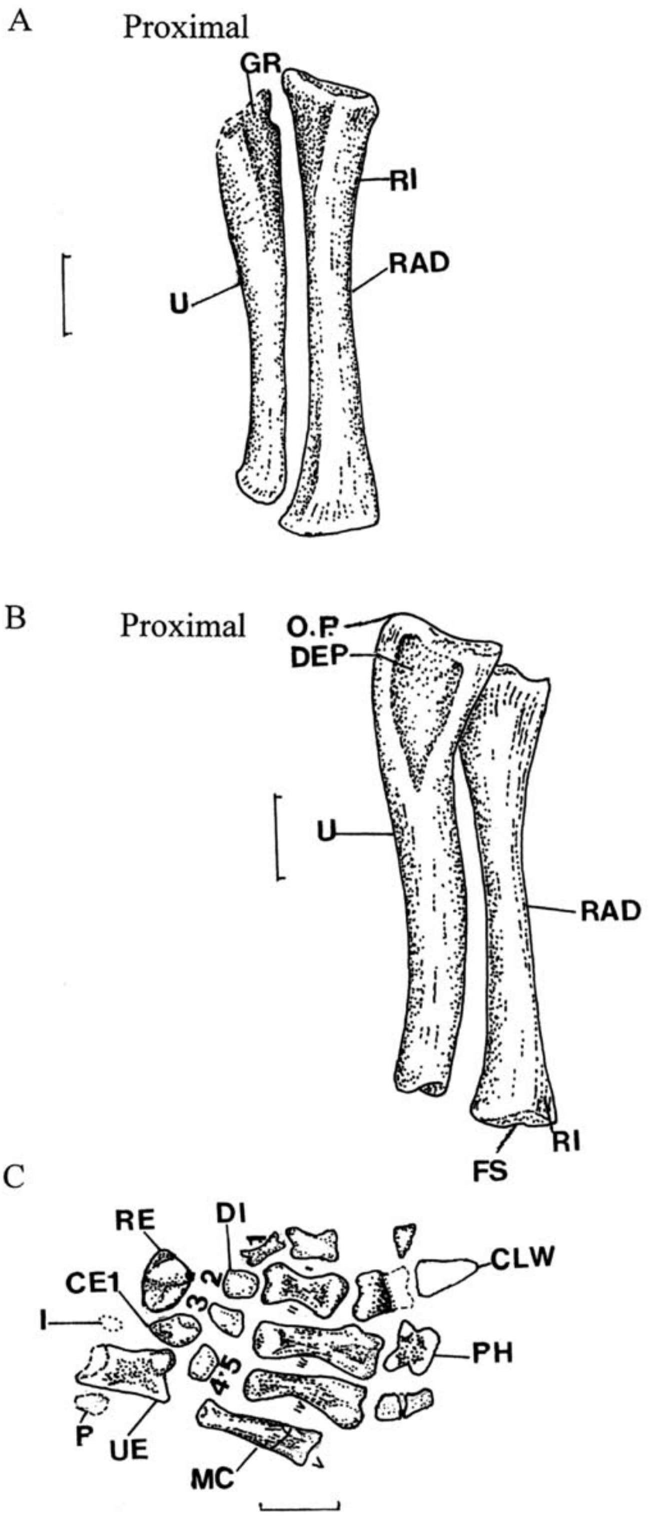

Figure 7. Distal forelimb of *Regisaurus* sp. (BP/1/3973): **A**, radius and ulna (anterior view); **B**, radius and ulna (posterior view); **C**, manus (ventral view). Scale bars = 10 mm.

the wrist next to the ulnare, and the oval intermedium between the ulnare and radiale. Only one centrale is preserved in this specimen and is situated between the ulnare and the radiale. Three distal carpals are preserved, as distals 4 and 5 are fused and distal 1 is absent. These are relatively small quadrangular bones and are positioned at the proximal end of their corresponding metacarpal and the displaced fused distal 4 and 5 is situated above metacarpals 4 and 5.

A single, almost circular centrale is rounded posteriorly with a depression present close to the ulnare and a ridge on the opposite side. There is a slight concavity close to where distal 1 is supposed to be preserved between the radiale and distal 2. Distal 2 is squarish with rounded corners and is situated close to metacarpal II. The dorsal surface is convex. Distal 3 is round with a convex dorsal surface and articulates with metacarpal III. Fused distal 4 and 5 is a small bean-shaped bone situated on the proximal ends of metacarpals IV and V and has a round posterior edge.

All five metacarpals are preserved and are the longest bones of the hand (Fig. 7C). They are elongated with a long, thin, rounded shaft, and expanded ends. Metacarpal I, the smallest, has been slightly displaced towards the radiale. It is relatively short with a rounded dorsal surface and constricted towards the middle to have an hour-glass shape. The proximal articulating surface is concave while the distal surface is rounded to form double condyles. The more laterally positioned metacarpals are larger with Metacarpal IV being the longest and Metacarpal III longer than V. Distally all the metacarpals are more expanded laterally than medially.

Only four phalanges are preserved of which two are terminal. The proximal phalanges are almost square in outline with a slight narrowing in the middle, and double condyles at the ends. Unguals are triangular, ventrally curved, forming blunt pointed claws.

Pelvic girdle (Fig. 8)

All components of the right pelvis of BP/1/3973 are preserved almost in articulation. As is evident from both this specimen and the holotype, the ilium (Fig. 8A) is a large antero-posteriorly elongated bone with a slightly expanded blade. It has an almost vertical orientation in the body parallel to the sacral vertebrae. One posterior and two anterior processes are present on the blade, and the acetabulum is situated ventrolaterally. The blade is relatively large with striations on the lateral surface extending from the dorsal edge towards the acetabulum. Dorsally the blade is flat and thin and slopes postero-ventrally as well as anteroposteriorly. The acetabulum is a concave facet forming a lunate surface with a large prominent capping supra-acetabular buttress (Fig. 8A, SAB) with rounded, ridged edges as described in the holotype (Kemp 1978). Anterior to the acetabulum the blade curves anteriorly to form the thin and pointed ventral anterior process. The dorsal anterior process is larger and rounded. A slight triangular depression (Fig. 8A, DEP) is present between the two anterior processes on the medial surface. As in the holotype (Kemp 1978) two distinctive larger depressions are visible on the lateral surface of the blade, one between the anterior processes and one just below the ventral anterior process. At the posterodorsal side of the acetabulum, just posterior to the buttress, is the supra-acetabular notch.

In ventral view the pubis is roughly rectangular with a prominent posterior indentation which forms the anterior margin of the obturator foramen which is situated between the pubis and the ischium. A slightly concave

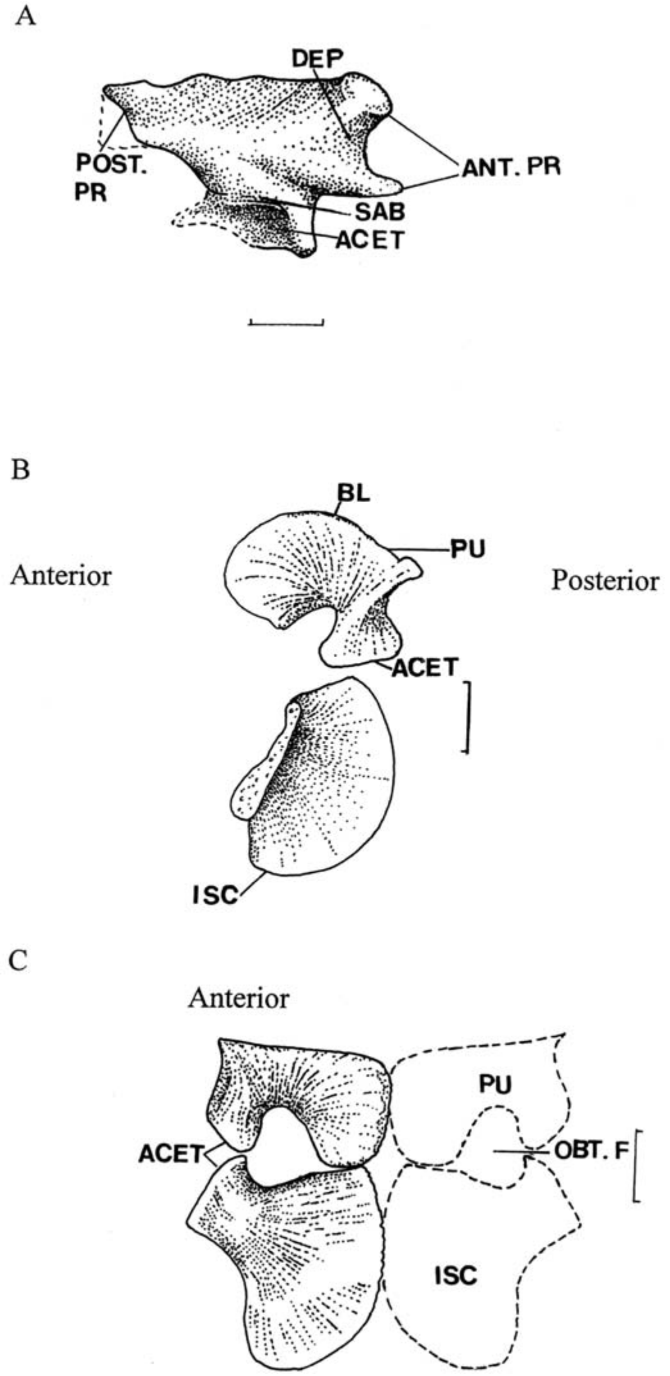

Figure 8. Pelvic girdle of *Regisaurus* sp. (BP/1/3973): **A**, right ilium (lateral view); **B**, left pubis and ischium (dorsal view); **C**, pubis and ischium (ventral view). Scale bars = 10 mm.

acetabular portion of the pubis is less developed than that of the ischium. The dorsal surface of the pubis is convex while the ventral side is concave.

The ischium has a mushroom-shaped outline (Fig. 8B,C) when viewed from the ventral side. It has a relatively large, thin blade with marked striations fanning out from the centre. The flared blade surface is convex ventrally and concave dorsally, and meets its counterpart medially in a slightly convex symphysis. The acetabular facet is slightly concave.

Hind limb (Figs 9 & 10)

The left hind limb of BP/1/3973 is not well preserved but the right limb is reasonably complete and articulated with the pelvis. The distal end of the leg, including the ankle and pes, is missing. Unidentifiable elements of the left pes are scattered in the matrix.

As the left hind limb of the holtype is particularly well preserved (Kemp 1978) this description will refer to the holotype in areas where BP/1/3973 is not well preserved.

The femur is an elongated bone with a slight sigmoid curvature in dorsal view and both proximal and distal ends are expanded (Fig. 9). In dorsal view the rounded caput femoris is anteroposteriorly expanded. Elongated striations extend from the proximal end down the shaft which is dorsoventrally flattened with the posterior side thinner than the anterior side. A prominent posteriorly positioned trochanter major (external trochanter) is present immediately behind the head. The trochanter minor (internal trochanter) is situated anteriorly opposite the trochanter major and is positioned further from the proximal edge of the bone than the trochanter major as in the holotype (BP/1/5394).

As in the holotype, distal to the major and minor trochanters the shaft is circular in cross-section and ends distally in a double condyle. On the dorsal surface there is a triangular depression, the patella groove, between the condyles (Fig. 9D, PAT.GR). The internal trochanter is visible on the ventral side of the proximal end of the femur just below the caput femoris and slopes towards the shaft. It is smaller than the trochanter major and the same size as the trochanter minor. An oval fossa is situated anterior to the internal trochanter, whereas a slight depression is placed posteriorly (Fig. 9C, DEP). Proximally to the internal trochanter is a deep fossa that can also be seen in posterior view.

Only the proximal portions of the left and right tibiae are preserved in BP/1/3973. The tibia is an elongated lateromedially flattened bone with striations extending down the shaft as in the holotype (BP/1/5394). In lateral view the proximal end is rounded and expanded further posteriorly than anteriorly. As has been reported for *Bauria* (King 1996) a shallow longitudinal groove is present on the posterior side of the proximal end of the shaft (Fig. 10B, GR). Medially the shaft is rounded and has an elongated short ridge (Fig. 10A, RI). No cnemial crest is present on the shaft (Kemp 1978). Stretching from the proximal end, the lateral face has a broad, flat fossa which terminates about two centimetres from the ventral end of the bone as a distinct groove (Kemp 1978). Distally the tibia is only slightly expanded, with its astragalar face slightly concave as seen in *Bauria* (Schaeffer, 1941). Kemp (1978) described the tibia of the holotype as flattened lateromedially with the articulation surface for the astragalus as flat, apart from the notch for the fibula, which is circular in outline.

The fibula is a long, straight and slender bone which is slightly expanded proximally (Fig. 10C,D). It is slightly bowed such that it is gently concave towards the tibia. The shaft is ovoid in cross-section, being slightly flattened on the anterior and posterior sides as in the holotype (Kemp 1978). Kemp described the distal end as even more flattened and terminating in an oval-shaped, distally-facing facet for the articulation with the calcaneum.

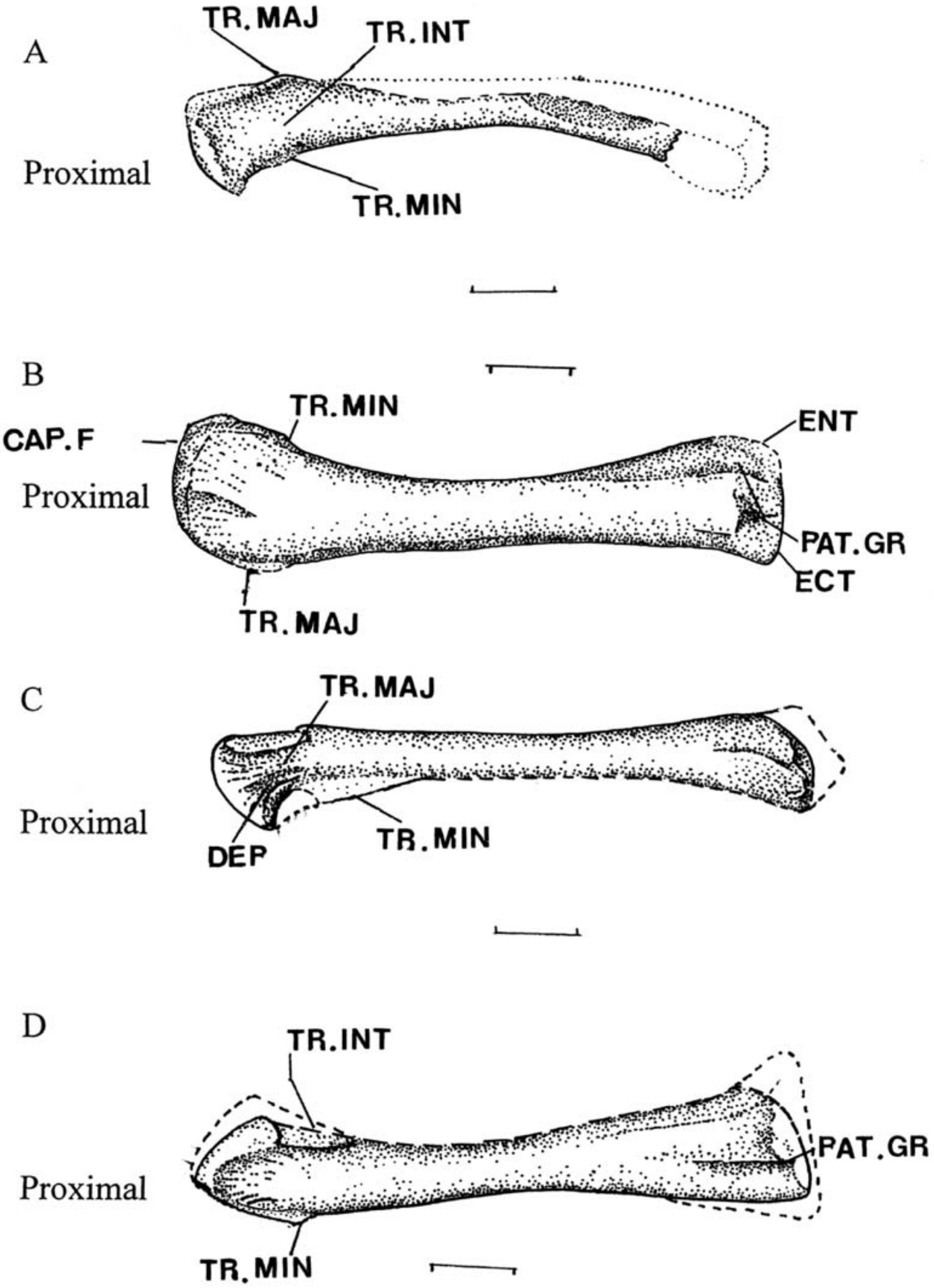

Figure 9. Right femur of *Regisaurus* sp. (BP/1/3973): **A**, ventral view, **B**, dorsal view, **C**, posterior view, **D**, anterior view. Scale bars = 10 mm.

DISCUSSION

The remarkably complete state of preservation of *Regisaurus* (BP/1/3973) has enabled, for the first time, the description of the postcranial anatomy of an almost complete skeleton of a therocephalian. Because this specimen preserves a complete vertebral column, except for some distal caudals, it has been possible to compare the vertebral morphology of *Regisaurus* with that of other therocephalian genera based on both personal observation and literature studies. This description has determined that *Regisaurus* has six cervical, 17 thoracic, five lumbar, and four sacral vertebrae. This figure differs from previous descriptions for a variety of therocephalian genera (Table 2), but most of these are based on incomplete specimens.

In the literature vertebrae have been described for the following therocephalian genera; *Cynariognathus* (Cys 1967), *Pristerognathus* (Broom 1936), *Macroscelesaurus* (Haughton 1918), *Ictidosuchoides* (Broom 1938), *Mirotenthes* (Attridge 1956), *Glanosuchus* (Fourie 2001), *Silpholestes* (Broom 1948), *Zorillodontops* (Cluver 1969), *Tetracynodon* (Sigogneau 1963), *Aneugomphius* (Brink 1958), *Ictidosuchus* (Broom 1901), *Ericiolacerta* (Watson 1931; Colbert & Kitching 1981), *Olivieria* (Brink 1965), *Regisaurus* (Kemp 1978), a baurioid (Kemp 1986), *Ordosia* (Lianhai 1979), a bauriamorph (Watson 1931) and *Bauria* (King 1996; Fourie 2001).

Cervical vertebrae of all therocephalians, as in other therapsids, can be morphologically separated into the pro-atlas, atlas, axis and remaining cervical vertebrae. The difference in the morphology of different cervical vertebrae in *Regisaurus* is characterized by the morphology of the

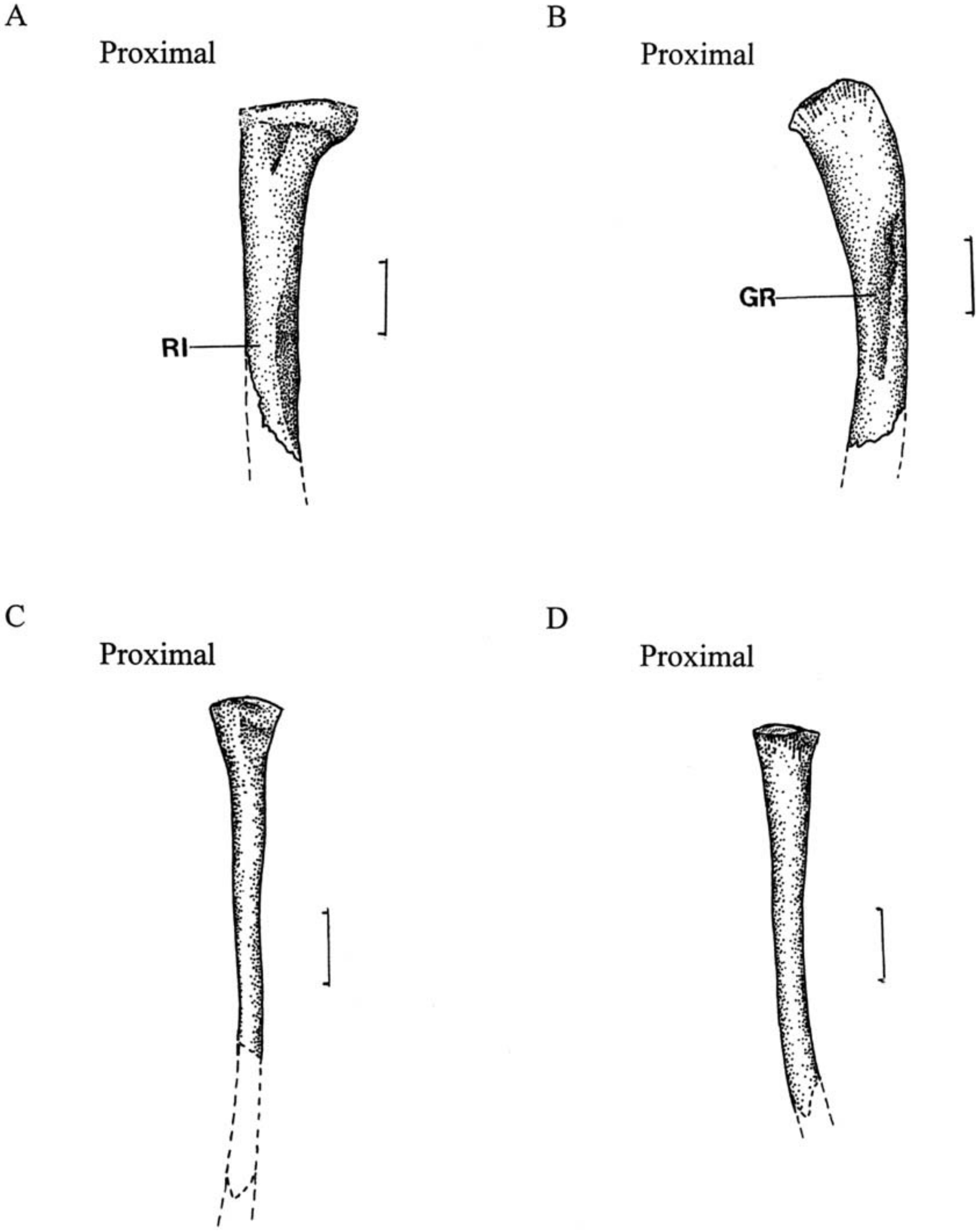

Figure 10. Proximal tibia and fibula of *Regisaurus* sp. (BP/1/3973): **A**, left tibia (anterior view); **B**, left tibia (posterior view); **C**, left fibula (lateral view); **D**, right fibula (medial view). Scale bars = 10 mm.

neural spine as the last cervical has a more anteroposteriorly expanded neural spine than the rest of the cervicals, but even this is not as expanded as the neural spine of the axis. No intercentra are present in the cervical region of *Regisaurus* as in *Cynariognathus* (Cys 1967), *Macroscelesaurus* (Haughton 1918) and *Aneugomphius* (Brink 1958). They have however been recorded between the cervical vertebrae in the Chinese genus *Ordosia* (Hou Lianhai 1979). Kemp (1986) reported poor ossification of the ends of the centra of an unidentified baurioid and considered this as an indication of the presence of unossified intercentra between the atlas and axis.

Thoracic vertebrae of *Regisaurus* have the same anatomy as the preceding cervical vertebrae, but are more lightly built with longer, thinner transverse processes that extend posterolaterally rather than laterally. The lumbar vertebrae are characterized by wider neural spines and short, wide transverse processes. Sacral and caudal vertebrae have thin neural spines with short ribs. The sacral vertebrae have higher neural spines when compared to the caudal vertebrae, but vertebrae from both these regions are characterized by having fused holocephalous ribs which are grooved on the posterior side.

None of the specimens studied have a fully preserved caudal series but it is evident that *Regisaurus,* as in all therocephalians, must have had a short stocky tail with many small and short vertebrae as has been reported for *Glanosuchus* (Fourie 2001), *Silpholestes* (Broom 1948), *Mirotenthes* (Attridge 1956), *Cynariognathus* (Cys 1967) and *Aneugomphius* (Brink 1958), *Ictidosuchoides* (Broom 1938), *Ericiolacerta* (Watson 1931; Colbert & Kitching 1981) and an unidentified bauroid (Kemp 1986). King (1996) described remnants of haemal arches on the caudal vertebrae of *Bauria* (NMQR 3189), but these have more recently been interpreted as remnants of the neural spines of the dorsal vertebrae (Fourie 2001).

Ribs in most therocephalian specimens are not well preserved and have been described for *Cynariognathus* (Cys 1967), *Macroscelesaurus* (Haughton 1918), *Zorillodontops* (Cluver 1969), *Mirotenthes* (Attridge 1956), *Glanosuchus* (Fourie 2001), *Silpholestes* (Broom 1948), *Tetracynodon* (Sigogneau 1963), *Aneugomphius* (Brink 1958), *Olivieria* (Brink 1965), *Ericiolacerta* Watson 1931; Colbert & Kitching 1981), *Bauria* (King 1996; Fourie 2001) and a baurioid (Kemp 1986). In *Regisaurus* the ribs from the different regions of the body all have differing morphologies. By far the longest ribs are those of the thoracic region which also have their sternal segments preserved. The only other therocephalian which has sternal segments preserved is *Olivieria* (BP/1/3849), while they were considered to have been cartilaginous in *Mirotenthes* (Attridge 1956). The cervical and thoracic ribs are of *Regisaurus* as in other therocephalians where they are described (see above) are dichocephalous whereas the lumbar, sacral and caudal ribs are holocephalous.

The pectoral girdle has been preserved in skeletons of the following therocephalian genera: *Cynariognathus* (Cys 1967), *Pristerognathus* (Broom 1936), *Macroscelesaurus* (Haughton 1918), *Silpholestes* (Broom 1948), *Zinnosaurus* (Boonstra 1964), *Glanosuchus* (Fourie 2001), *Zorillodontops* (Cluver 1969), *Ictidosuchus* (Broom 1901), *Ictidosuchoides* (Broom 1938), *Aneugomphius* (Brink 1958), *Regisaurus* (Kemp 1978), *Ordosia* (Lianhai 1979), *Tetracynodon* (Sigogneau 1963), *Mirotenthes* (Attridge 1956), *Ericiolacerta* (Watson 1931), *Olivieria* (Brink 1965), *Bauria* (King 1996; Fourie 2001) and a baurioid (Kemp 1986). All of these descriptions are based on incomplete material, while BP/1/3973 affords the opportunity to describe a completely articulated pectoral girdle and forelimb for the first time. There are significant differences in the pectoral girdle of different therocephalian genera and it is apparent that three definite scapular shapes are present. Scylacosaurids and lycosuchids have a short and broad scapula, while *Ictidosuchops, Mirotenthes, Aneugomphius, Ictidosuchus, Tetracynodon, Zorillodontops, Olivieria* and *Regisaurus* have a less broad scapula, while that of *Bauria* and *Ordosia* is delicate and narrow. The scapula of *Bauria* is diagnostic in that a prominent lateral ridge is present on the blade surface with a deep depression positioned next to it (King 1996, fig. 5). The ridge on the scapular blade is present although remarkably reduced in the *Tapinocephalus* Assemblage Zone therocephalians (Boonstra 1964) while an acromion process of the scapula is not present in any therocephalian genus.

The cleithrum of therocephalians is splint-like and has been described in *Pristerognathus* (Broom 1936), *Bauria* (Watson 1931) and *Ericiolacerta* (Watson 1931), but appears to have been absent in *Cynariognathus* (Cys 1967), *Mirotenthes* (Attridge 1956), *Regisaurus* (BP/1/3973), a baurioid (Kemp 1986) and *Bauria* (King 1996). The scapular facet of the glenoid in all therocephalians is oval, facing posteriorly and laterally, with the procoracoid either forming a part of the glenoid as in *Cynariognathus* (Cys 1967) or taking no part in the formation of the glenoid as in *Zinnosaurus* (Boonstra 1964), *Macroscelesaurus* (Haughton 1918), *Ericiolacerta* (Watson 1931), *Mirotenthes* (Attridge 1956), *Ictidosuchus* (Broom 1901), *Regisaurus* (Kemp 1978) and a baurioid (Kemp 1986). The procarocoid of *Regisaurus* is an irregular quadrangular bone and has a long, broad articulation with the scapula. The presence of a procoracoid foramen has variously been reported on the procoracoid–coracoid suture in *Ericiolacerta* (Watson 1931), *Tetracynodon* (Sigogneau 1963), and a baurioid (Kemp 1986), *Macroscelesaurus* (Haughton 1918); on the procoracoid–scapula suture in *Bauria* (Watson 1931); and in the procoracoid in *Zinnosaurus* (Boonstra 1964), *Cynariognathus* (Cys 1967), *Mirotenthes* (Attridge 1956), *Ictidosuchus* (Broom 1901) and *Regisaurus.*

An ossified sternum has been reported only in more derived therocephalians such as *Regisaurus* (BP/1/3973), *Ictidosuchoides* (Broom 1938), *Tetracynodon* (Sigogneau 1963), *Olivieria* (Brink 1965), *Ericiolacerta* (Watson 1931), and in a baurioid (Kemp 1986; Watson 1931). As a sternum is not preserved in any of the early therocephalians, Boonstra (1964) concluded that scylacosaurids did not have an ossified sternum. In the South African Karoo record the earliest therocephalian to have a sternum is a specimen of *Ictidosuchoides* from the *Cistecephalus* Assemblage Zone (Broom 1938).

Another variable feature in different therocephalian genera is the morphology of the interclavicle. Taxa from the lowermost biozones of the Beaufort Group (scylacosaurids) have a long thin interclavicle (*Zinnosaurus, Cynariognathus*) (Boonstra 1964; Cys 1967), while *Regisaurus* (BP/1/3973), *Ictidosuchoides* (Broom 1938), *Aneugomphius* (Brink 1958) and *Olivieria* (Brink 1965), which occur in the younger biozones, have a clavicle which is short and broad. Some of the most derived forms from the *Lystrosaurus* Assemblage Zone (e.g. *Ericiolacerta*) have a cruciform interclavicle (Watson 1931).

The forelimbs of the following therocephalian genera have been described to varying degrees in the literature; *Cynariognathus* (Cys 1967), *Macroscelesaurus* (Haughton 1918), *Pristerognathus* (Broom 1936), *Zinnosaurus* (Boonstra 1964), *Ictidosuchoides* (Broom 1938), *Zorillodontops* (Cluver 1969), *Mirotenthes* (Attridge 1956), *Glanosuchus* (Fourie 2001), *Silpholestes* (Broom 1948), *Tetracynodon* (Sigogneau 1963), *Ictidosuchus* (Broom 1901), *Whaitsia* (Boonstra 1934), *Aneugomphius* (Brink 1958), *Ericiolacerta* (Watson 1931), *Olivieria* (Brink 1965), *Ordosia* (Lianhai 1979), a bauriamorph (Watson 1931), *Bauria* (King 1996; Fourie 2001) and a baurioid (Kemp 1986). Forelimbs of different therocephalian genera are all very similar in morphology, but they do vary in degree of robustness. A short and robust humerus with a very short shaft is present in the scylacosaurids (Boonstra 1964) and *Macroscelesaurus* (Haughton 1918). In contrast the humerus of *Regisaurus* is long and slender, as is that of *Whaitsia* (Boonstra 1934), *Aneugomphius* (Brink 1958), *Tetracynodon* (Sigogneau 1963), *Zorrilodontops* (Cluver 1969) and

Olivieria Brink 1965), while a very slender humerus is present in *Ericiolacerta* (Watson 1931), *Bauria* (King 1996) and the baurioids (Kemp 1986). Most therocephalian genera lack an ectepicondylar foramen, with *Bauria* being the only exception (King 1996). The ulna of all therocephalians is characterized by the presence of an anterior groove extending down the proximal end towards the shaft. In posterior view the ulna has a proximal triangular depression below the olecranon process. This process is weakly developed and in life probably extended further as a cartilaginous structure (Kemp 1986). The radius is characterized, in posterior view, by a short distal ridge in all therocephalian genera and an anterior depression is present at the proximal end, which, in *Bauria* is particularly deep (Fourie 2001).

In the manus of all therocephalians, the radiale is rectangular or oval and the ulnare is hour-glass shaped. Both the intermedium and pisiforme are very small and because of their small size are preserved in very few specimens. Centrale 1 is larger than centrale 2 and the former is distinguished by its L-shape in comparison with the rectangular centrale 2. Distals 4 and 5 are fused in all therocephalian specimens where they are preserved. The metacarpals are wide proximally while the distal end is expanded more distolaterally and Metacarpal IV is always the longest.

Therocephalian genera for which the pelvic girdles have been described are *Cynariognathus* (Cys 1967), *Zinnosaurus* (Boonstra 1964), *Pristerognathus* (Broom 1936), *Macroscelesaurus* (Haughton 1918), *Glanosuchus* (Fourie 2001), *Zorillodontops* (Cluver 1969), *Silpholestes* (Broom 1948), *Mirotenthes* (Attridge 1956), *Aneugomphius* (Brink 1958), *Regisaurus* (Kemp 1978), *Ericiolacerta* (Watson 1931; Colbert & Kitching 1981), *Ordosia* (Lianhai 1979), *Bauria* (King 1996; Fourie 2001), and an unidentified baurioid (Kemp 1986). The iliac blade of all therocephalians is a thin flat bone which is expanded anteroposteriorly with a straight dorsal border and two anterior processes, a character found only in the Therocephalia, but is not very prominent in scylacosaurids (Boonstra 1964). Two distinctive large depressions are present on the lateral surface of the iliac blade above and below the ventral anterior process (Kemp 1978). A supra-acetabular buttress is present on the ilium above the acetabulum in all therocephalians and has a medial supra-acetabular notch. Depressions for attachment of the sacral ribs are present medially on the surface of the blade. The contribution of the ischium to the acetabulum is larger than that of the pubis and is slightly concave. An apparent phylogenetic trend is found with the pubic foramen present in the pubis (*Glanosuchus, Zinnosaurus*) or between the counterparts of the pubis (*Regisaurus*) (BP/1/3973) with a small obturator foramen (e.g. in *Zorillodontops, Regisaurus, Aneugomphius*), and a large obturator foramen (e.g. in *Ericiolacerta, Bauria,* baurioid).

Hind limb morphology has been described for *Cynariognathus* (Cys 1967), *Blattoidealestes* (Boonstra 1954), *Macroscelesaurus* (Haughton 1918), *Zinnosaurus* (Boonstra 1964), *Pristerognathus* (Broom 1936), *Glanosuchus* (Fourie 2001), *Silpholestes* (Broom 1948), *Ictidosuchus* (Broom 1901), *Ictidosuchoides* (Broom 1938), *Tetracynodon* (Sigogneau 1963), *Mirotenthes* (Attridge 1956), *Aneugomphius* (Brink 1958), *Regisaurus* (Kemp 1978), *Ericiolacerta* (Watson 1931; Colbert & Kitching 1981), *Bauria* (Boonstra 1938; Schaeffer 1941; King 1996; Fourie 2001) and a baurioid (Kemp 1986).

The morphology of the femur, which is a long and massive bone with a gentle sigmoid shape, is very similar in all therocephalians. Three trochanters are present, but in derived forms such as *Bauria,* the trochanters are not distinct as the bone is straighter with a less prominent proximal end. The tibia is long, slightly curved with a flattened shaft and an expanded proximal end. Medially it has a distinct groove with a prominent ridge next to it. The slender, gently curved fibula is probably the thinnest long bone in the body with the least distinguishable characters, except for slightly expanded proximal and distal ends and a medial groove on the shaft.

CONCLUSIONS

This description is the first on the complete postcranial anatomy of the therocephalian *Regisaurus.* Because the described specimen is so well preserved it has demonstrated the possibility of identifying therocephalian groups from certain isolated postcranial elements. This could have useful application for biostratigraphic work in areas where no diagnostic skulls have been discovered.

The following suite of postcranial characters are diagnostic of *Regisaurus* when taken together: procoracoid foramen which is positioned in procoracoid only; slender scapula with a low ridge and shallow depression alongside the ridge; ossified sternum; interclavicle which is short, broad and almost square; very small obturator foramen which is less than half the length of the contact between the pubis and ischium; slender humerus and femur with clearly defined shaft and proximal and distal ends.

In the pelvic girdle of all therocephalians the ilium, ischium and pubis all meet in the acetabulum. The life-orientation of the ilium was vertical while the pubis and ischium were medially inclined. The latter two bones are firmly attached at the midline symphysis and form a pubo-ischiadic plate. In comparison with other therapsids the ilium of all therocephalians is unique in having two anterior processes.

In the hind limb of all therocephalians three trochanters are present on the proximal femur. The proximal ends of both the tibia and fibula have large areas of articulation with the femur, but do not appear to have contact with each other medially. The heel process on the calcaneum of the pes is present only in the more derived forms such as *Bauria* (King 1996).

Comparison of different therocephalian genera reveals a decrease in body size with younger stratigraphic age, and with this decrease in size the long bones become slender and acquire a well-defined shaft.

Specimen BP/1/3973 is unique as it has an almost complete (save for a few distal caudals) articulated vertebral column and has enabled the determination of accurate vertebral counts for the first time in a therocephalian genus. Furthermore, the articulated preservation of the limbs and their associated girdles has enabled a full description of these elements and facilitated deductions as to the stance and gait of the genus which is the subject of a future paper.

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ABBREVIATIONS

Anatomical

ACET	Acetabulum
ADVL	Anterior dorsoventral line
ANT.PR	Anterior process
AS	Astragalus
AX	Axis
BL	Blade
CA	Calcaneum
CAP	Capitulum
CAP.H	Caput humerus
CAP.F	Caput femorus
CC	Cnemial crest
CE1	Centrale 1
CE2	Centrale 2
CENTR	Centrum
CL	Clavicle
CO	Coracoid
CR	Cranium
CV	Cervical vertebra
CVT	Caudal vertebra
DEP	Depression
DI	Distal
DP.CR	Deltopectoral crest
ECT	Ectepicondyle
ECT.F	Ectepicondylar foramen
ENT	Entepicondyle
ENT.F	Entepicondylar foramen
F	Facet
FEM	Femur
FIB	Fibula
GL	Glenoid
GR	Groove
HUM	Humerus
I	Intermedium
ICL	Interclavicle
IL	Ilium
ISC	Ischium
LML	Lateromedial line
LV	Lumbar vertebrae
MAN	Manus
MC	Metacarpal
N.C	Neural canal
N.P	Neural process
N.S	Neural spine
OBT.F	Obturator foramen
O.F	Olecranon fossa
O.P	Olecranon process
P	Pisiforme
PAT.GR	Patella groove
PES	Pes
PH	Phalange
POST.PR	Posterior process
POST.ZP	Postzygapophysis
PRE.ZP	Prezygapophysis
PU	Pubis
R	Rib
RAD	Radius
RE	Radiale
SAB	Supra-acetabular buttress
SAN	Supra-acetabular notch
SC	Scapula
ST	Sternum
SV	Sacral vertebra
TIB	Tibia
TR.INT	Trochanter internal
TR.PR	Transverse process
TR.MAJ	Trochanter major
TR.MIN	Trochanter minor
TUB	Tuberculum
TV	Thoracic vertebra
U	Ulna
UE	Ulnare

Institutional

AMNH	American Museum of Natural History, New York, U.S.A.
BMNH	Natural History Museum, London, United Kingdom.
BP	Bernard Price Institute for Palaeontological Research, University of Witwatersrand, Johannesburg, South Africa.
CUMZ	University Museum of Zoology, Cambridge, United Kingdom.
DMSW R/ MZCD	M.S. Watson Collections, Cambridge, United Kingdom.
IVPP V	Institute for Vertebrate Palaeontology, Peking, China.
NMQR	National Museum, Bloemfontein, South Africa.
RC	Rubidge Collection, Wellwood, Graaff-Reinet, South Africa.
SAM	Iziko Museums, Cape Town, South Africa.
TM	Northern Flagship Institution, Pretoria, South Africa.
UCMP	University of California Museum, California, U.S.A.

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A non-mammaliaform cynodont from the Upper Triassic of South Africa: a therapsid Lazarus taxon?

Fernando Abdala[1*], Ross Damiani[2], Adam Yates[1] & Johann Neveling[3]

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

[2]*Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, D-70191, Stuttgart, Germany*

[3]*Council for Geoscience, Private Bag X112, Pretoria, 0001 South Africa*

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The tetrapod record of the 'Stormberg Group', including the Lower Elliot Formation, in the South African Karoo is widely dominated by archosaurian reptiles, contrasting with the therapsid dominion of the subjacent Beaufort Group. The only therapsids represented by skeletal remains in the Upper Triassic Lower Elliot Formation are the large traversodontid cynodont *Scalenodontoides macrodontes* and the recently described tritheledontid cynodont *Elliotherium kersteni.* Here we present a fragmentary lower jaw that provides evidence of a third type of cynodont for the Upper Triassic of South Africa. The fossil is tentatively assigned to the Diademodontidae. The latter representative of this family is known from the Late Anisian, and its tentative record in the Norian Lower Elliot Formation, if confirmed, will represent a case of Lazarus taxon. Thus, Diademodontidae apparently disappeared from the fossil record by the end of the Anisian and then reappeared in the Norian of South Africa, a stratigraphic interval of some 21 million years. This new cynodont record, together with the recently described Tritheledontidae, show that cynodonts are now the second most diverse tetrapod group in the Lower Elliot fauna.

Keywords: Lower Elliot Formation, Karoo Basin, Lazarus taxon, Diademodontidae.

INTRODUCTION

The South African Karoo Basin preserves the most comprehensive record of non-mammaliaform therapsids in the world. The oldest representatives of this group and their subsequent diversification are recorded in the Permian and Triassic rocks of this basin over a time span of approximately 32 million years (Hancox & Rubidge 2001; Rubidge & Sidor 2001). Among the groups that evolved during this time are the cynodonts, which first appeared near the end of the Permian, approximately 252 millions years ago, and include Mammalia as their living descendants.

Cynodonts were an important component of the vertebrate faunas of the Early Triassic *Lystrosaurus* Assemblage Zone (AZ) and the overlying Early to Middle Triassic *Cynognathus* AZ of the Beaufort Group (Rubidge 1995; Hancox & Rubidge 2001). The *Cynognathus* AZ, the uppermost faunal assemblage of the Beaufort Group, encompasses the strata of the Burgersdorp Formation (Hancox & Rubidge 2001) and is informally subdivided into three faunas (Hancox *et al.* 1995; Damiani & Hancox 2003), namely subzone A (late Olenekian), subzone B (early Anisian), and subzone C (late Anisian). Seven cynodont taxa are known from the *Cynognathus* AZ, with the large-bodied herbivorous/omnivorous *Diademodon tetragonus* Seeley, 1894, the only known representative of the Diademodontidae, being one of the most common. *Diademodon* is the most abundant cynodont of the subzone B fauna, but in subzone C it has a scanty record (Abdala *et al.* 2005), and apparently became extinct by the end of Beaufort Group sedimentation in the early Middle Triassic.

The South African tetrapod record resumes in the Upper Triassic (Norian) Lower Elliot Formation of the 'Stormberg Group', and is highlighted by a marked faunal turnover when compared to that of the Beaufort Group. The Lower Elliot Formation is dominated by archosaurian reptiles (especially dinosaurs) whereas the only named therapsids are the traversodontid cynodont *Scalenodontoides macrodontes* Crompton & Ellenberger, 1957, and the new tritheledontid cynodont *Elliotherium kersteni* Sidor & Hancox, 2006. Here we describe a partial lower jaw from the Lower Elliot Formation that provides evidence of a third cynodont from the Upper Triassic of South Africa. The mandible is tentatively assigned to the Diademodontidae and represents by far the youngest record of that group.

GEOLOGICAL SETTING

The Elliot Formation is a fluvial redbed sequence, with some aeolian input towards the top (Visser & Botha 1980; Smith & Kitching 1997; Bordy *et al.* 2004a). It is dominated by red floodplain siltstones with minor channel and splay sandstones. Kitching & Raath (1984) were the first to recognize different subunits in the Elliot Formation, establishing two biozones and a tripartite lithostratigraphic subdivision. Bordy *et al.* (2004a,b,c) replaced this tripartite system with a two-fold lithostratigraphic subdivision that corresponds to the biostratigraphic subdivision. Argillaceous rocks of the two intervals differ little, although pedogenic horizons are more prevalent in the Upper Elliot Formation (Smith & Kitching 1997; Bordy *et al.* 2004a).

The lower jaw fragment, BP/1/5724, comes from the farm Edelweiss 698 (29°06'37.3014"S, 27°19'16.5"W) in the Ladybrand District, eastern Free State Province, South Africa (Fig. 1). The sauropod *Antetonitrus ingenipes* Yates & Kitching, 2003, some remains of other dinosaurs, most likely *Melanorosaurus,* and fragmentary temnospondyl

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[*] Author for correspondence. E-mail: fernando.abdala@wits.ac.za

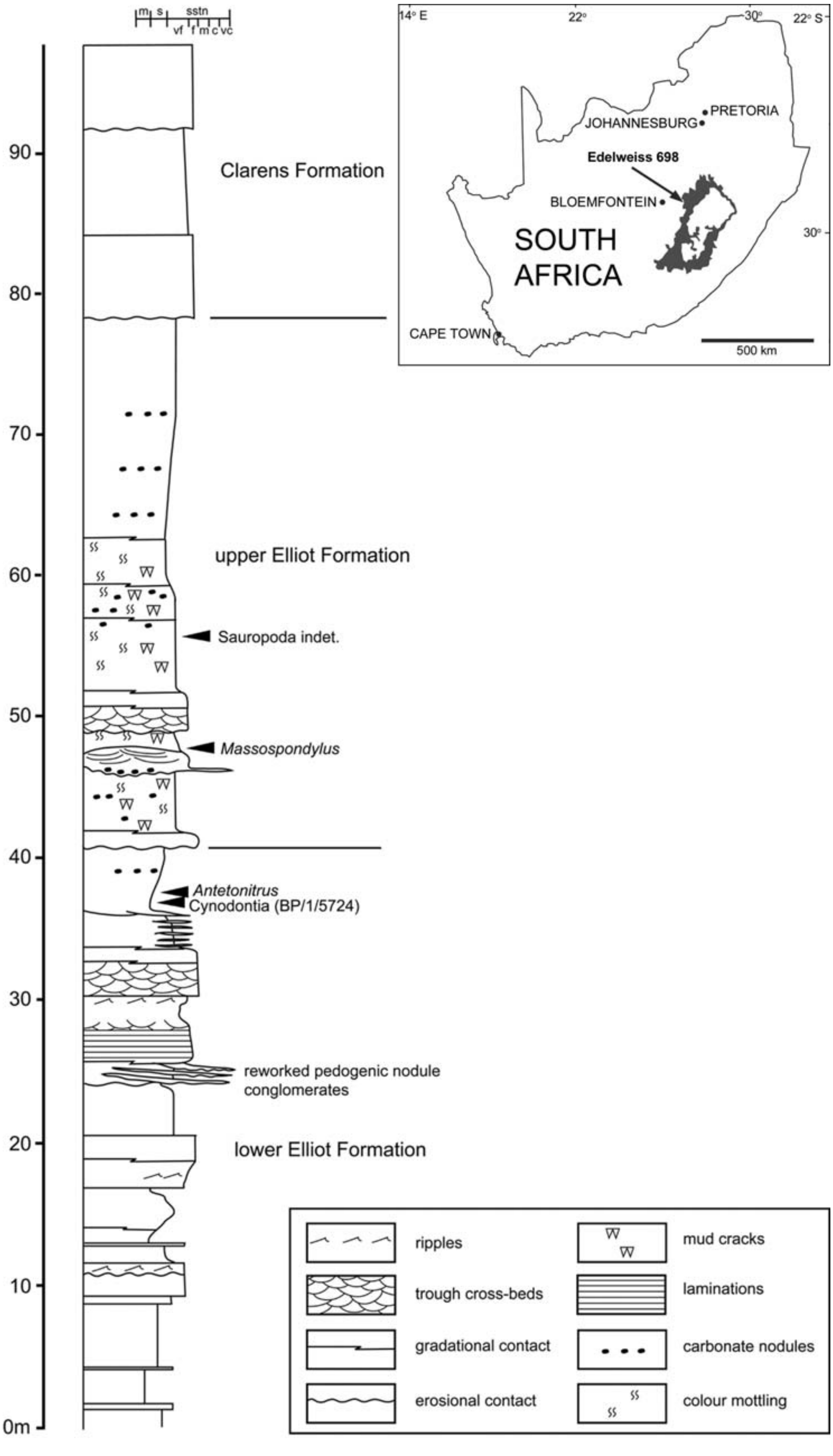

Figure 1. Stratigraphic section through the Elliot Formation at Edelweiss 698, Ladybrand District, Free State Province, South Africa, with fossil occurrences indicated. Note that the base of the Elliot Formation is not exposed at the locality. Inset, map of South Africa shows location of Edelweiss 698 and aerial extent of the 'Stormberg' Group.

remains are also known from this locality. Vegetation covering on hill slopes at Edelweiss largely confines the exposures of the Elliot Formation to a saddle between two low hills. Red siltstones predominate the lithology, with greenish and reddish-grey channel sandstones (2–10 m thick) more prevalent in the lower half of the section (Fig. 1). Argillaceous rocks in this part of the sequence consist of massive mudstone and siltstone packages, with rare and poorly developed calcareous pedogenic horizons with occasional greenish-grey mottling. In the upper half of the section channel sandstones are comparatively scarce, but there is a marked increase in grain size of the argillaceous rocks towards the top of the Formation. Well-developed pedogenic horizons, characterized by calcareous nodules, rhizocretions, desiccation cracks, and purple to reddish-grey mottling, occur extensively. We interpret the tripartite paleosol between 52–63 m to be the local expression of the *Tritylodon* Acme Zone (Kitching & Raath 1984; Smith & Kitching 1997).

BP/1/5724 was collected immediately above the thick channel deposit between 25–36 m in the lower half of the section (Fig. 1). The lenticular shape and lateral accretion surfaces at the base of this channel sandstone is consistent with the narrow, fixed, and meandering channels interpreted for the Lower Elliot Formation (Bordy *et al.* 2004c), as opposed to the lateral sandsheets and ephemeral fluvial deposition of the Upper Elliot Formation (Bordy *et al.* 2004a,b). Overall, the nature of the channel sandstones, the paucity of well-developed pedogenic horizons, and the stratigraphic position of the *Tritylodon* Acme Zone in relation to BP/1/5724, suggests that the latter is placed in the Lower Elliot Formation. This is fully consistent with biostratigraphic data: remains of *Melanorosaurus* were recovered from the same level as BP/1/5724, which indicates that the horizon pertains to the '*Euskelosaurus*' Range Zone (*Melanorosaurus* Range Zone of Yates 2004) of the Lower Elliot Formation. A review of the vertebrate and ichnological evidence suggests a Norian age for the Lower Elliot Formation (Lucas & Hancox 2001; Knoll 2004). Lucas & Hancox (2001) cautioned that the biostratigraphic correlations of this unit were not strong, but the suggested age is reinforced by the close relationship between *Elliotherium kersteni* and *Chaliminia musteloides* from the Norian Los Colorados Formation of Argentina (Sidor & Hancox 2006).

DESCRIPTION

BP/1/5724 consists of a portion of a right lower jaw that preserves the posterior portion of the horizontal ramus of the dentary, including several teeth, and the beginning of the coronoid process (Fig. 2). The jaw fragment corresponds to a medium-sized animal with a skull length of approximately 200 mm. The ramus is dorsoventrally deep but narrow from side to side and somewhat broader in its dorsal region than ventrally. The dorsal margin of the jaw is distinctly convex laterally in cross-section.

The labial surface (Fig. 2a) of the jaw is rather flat throughout except dorsally, where it forms a gently curving shelf that accommodates the dental arcade. There is no evidence of the lateral crest of the dentary. Two distinct bone fibre orientations are visible on this surface: a dorsal region in which the fibres are oriented parallel to the direction of the coronoid process, and a less extensive, ventral region at the base of the jaw in which the fibres are oriented posteroventrally, towards the angle of the dentary.

The lingual surface (Fig. 2b) is slightly convex and there is a well-developed trough for the postdentary bones separating the dorsal and ventrally directed fibres of the dentary. The postdentary elements are not preserved with the exception of a small splint of bone anteriorly that is probably part of the splenial. Close to the dorsal margin of the dentary, where the coronoid process begins to rise, is a scar which we interpret as the facet for articulation of the coronoid bone.

The tooth arcade is displaced slightly toward the lingual side of the jaw. Ten tooth alveoli are preserved, four of which retain broken teeth with the remaining alveoli being filled with matrix (Fig. 2c). The postcanines display thecodont implantation and have a single root, as is evident in the section at the anterior end of the jaw and from dissection of the lingual surface of the tooth-bearing fourth alveolus (Fig. 2b). The four broken teeth retain no vestiges of the original crown morphology. Remnants of the external enamel of the crown are observed in the mesial and distal margins of the fourth postcanine. The preserved bases of the postcanine crowns are slightly ovoid to circular in cross-section. The most striking aspect of the dental arcade is the position of the alveoli of the last four postcanines, which are located on the ascending margin of the coronoid process and appear slightly enlarged anteroposteriorly.

DISCUSSION

Taxonomic affinities of BP/1/5724

Specimen BP/1/5724 represents a new therapsid record for the Lower Elliot Formation, clearly distinct from *Scalenodontoides macrodontes* or *Elliotherium kersteni.* The overall configuration of the dentary, the thecodont implantation of the postcanines, and the presence of a postdentary trough are together indicative of therapsid affinities, while the marked depth of the postdentary trough and the prominent coronoid process provide compelling evidence that the specimen is a cynodont. The comparatively small size of the teeth and the circular crown bases of the preserved teeth indicate that they are plainly different from those of *Scalenodontoides* (Hopson 1984, fig. 1C). In addition, the latter feature precludes placement of BP/1/5724 in either Traversodontidae, which have quadrangular lower postcanines, or Trirachodontidae with ovoid/ellipsoid lower postcanines (Crompton 1955, fig. 5), although not the probainognathian *Aleodon.* Both the circular bases of the teeth and their single roots exclude the Tritylodontidae (Ginsburg 1962: fig. 3; Cui & Sun 1987) a group of cynodonts that are particularly well represented in the Upper Elliot Formation (Smith & Kitching 1997). By contrast, both of these characters are shared with the Diademodontidae.

The most intriguing feature of BP/1/5724 is the presence of alveoli on the ascending margin of the coronoid process. In some cynodonts such as *Probainognathus* and *Chiniquodon* (Romer 1969, 1970), the postcanine series ends in front of the coronoid process. Observations of other cynodonts show that the last lower postcanines continue behind the coronoid process and are often partially (e.g. *Thrinaxodon,* BMNH R511, R511a; *Cynognathus,* Broili & Schröder 1934) or totally (e.g. *Exaeretodon,* Bonaparte 1962; *Aleodon,* UMCZ T906) concealed when viewed laterally. In *Diademodon* the condition is somewhat

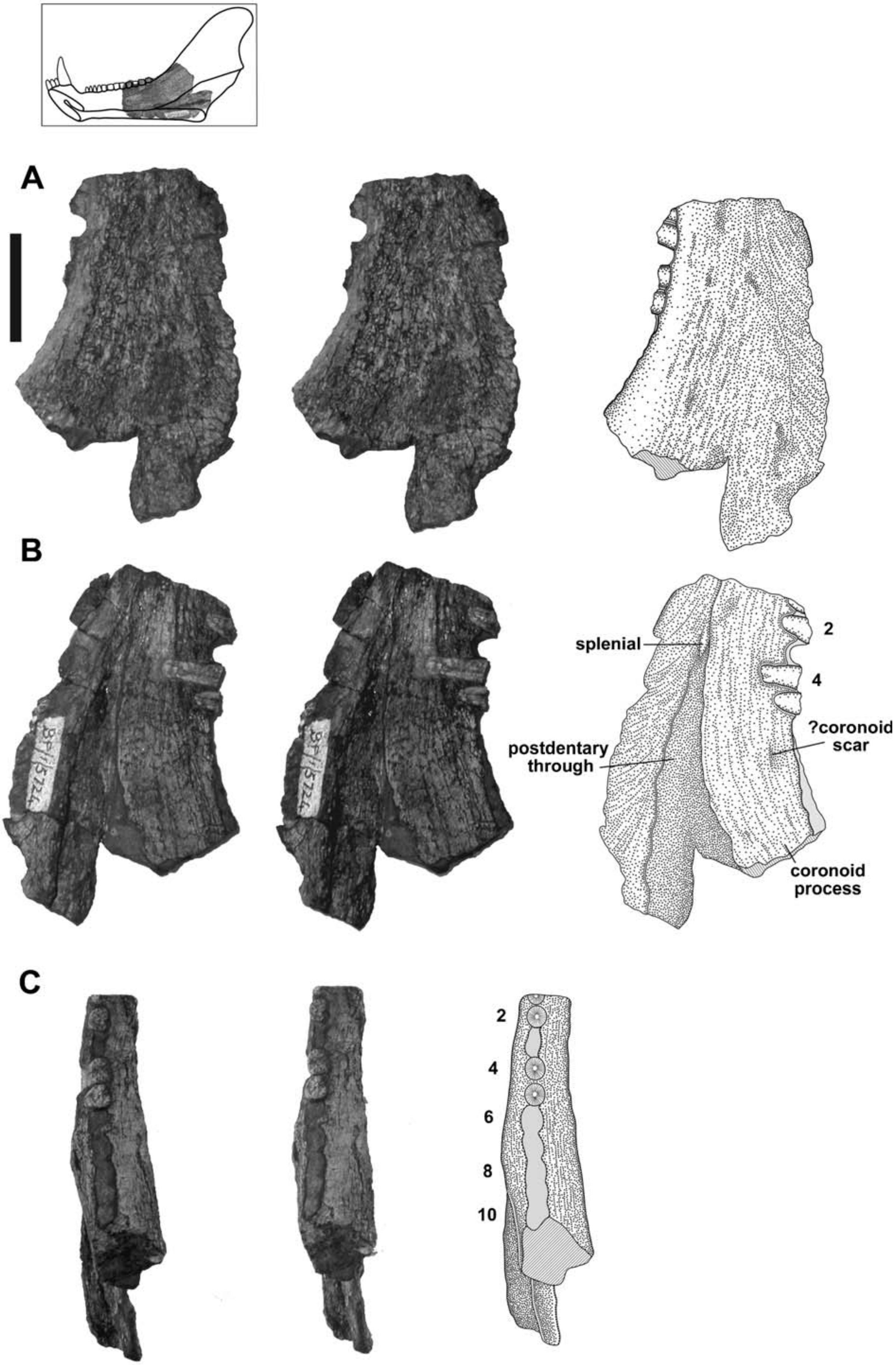

Figure 2. Stereophotographs and interpretive drawings of BP/1/5724 in (**A**) labial, (**B**) lingual, and (**C**) occlusal views. Numbers refer to tooth positions, as discussed in the text. Inset, BP/1/5724 superimposed on the mandible of *Diademodon,* viewed lingually (after Brink 1963). Scale bar = 3 cm.

Figure 3. **A**, Stereophotograph of a partial skull and lower jaw of *Diademodon* in lateral view (BP/1/1169). Arrow indicates the location of the last lower postcanine. Note the different orientation of the fibres in the lower jaw. Scale bar 3 cm. **B**, Labial and lingual view of the partial left lower jaw of *Diademodon* (part of specimen SAM-PK-K177). Note the extension of roots in the lingual view. Scale bar = 2 cm.

variable: (1) the dental series may finish just anterior to the coronoid process (e.g. SAM-PK-4002); (2) the last postcanine may be concealed in lateral view by the rising margin of the process (e.g. SAM-PK-K5877); (3) the last postcanines may be implanted well along the ascending margin of the coronoid process (e.g. BP/1/1169, SAM-PK-K177, MB R1004) (Fig. 3). To our knowledge, the third arrangement is recorded only in *Diademodon* and in a small lower jaw (NM QR3251) of the trirachodontid *Langbergia modisei* from subzone A of the *Cynognathus* AZ (Abdala *et al.* 2006). Based on the combination of postcanine bases that are circular in outline, and tooth alveoli that are located on the ascending margin of the coronoid process, we consider the most plausible identity for BP/1/5724 to be diademodontid.

The Post-Anisian gomphodont cynodont record

Gomphodont cynodonts [*sensu* Abdala & Ribeiro (2003) and Abdala *et al.* (2006), i.e. including Diademodontidae, Trirachodontidae and Traversodontidae, but not Tritylodontidae] appear in the late Olenekian and by the Anisian had already diversified into the three main groups: Trirachodontidae, Diademodontidae and Traversodontidae. The Trirachodontidae and Diademodontidae are thought to have become extinct by the end of the Anisian, although Lucas *et al.* (1999) assigned three isolated teeth from the Redonda Formation of New Mexico, originally attributed to the archosauromorph taxon Trilophosauridae (see Lucas *et al.* 1999, 332), to Trirachodontidae, which, if correct, would extend the temporal range of that group into the Rhaetian. However, Abdala *et al.* (2005, 2006) regarded this record as tenuous because the teeth differ from trirachodontid gomphodont postcanines (i.e. two of them lack cingular cusps on one of the bucco-lingually expanded margins). In addition, the strongest evidence presented by Lucas *et al.* (1999) to demonstrate the cynodont affinity of these teeth is the presence of columnar enamel. The enamel microstructure is not clear in the illustration provided by Lucas *et al.* (1999, fig. 4), probably because the tooth was not sectioned and polished. Therefore, the interpretation of the tubules as columnar units (or synapsid columnar units) that they provide does not seem guaranteed. In addition, columnar enamel is also widely distributed among reptiles, in some cases with columnar units having a similar diameter to that of synapsids (Sander 1999). More recently, the teeth from the Redonda Formation were considered to represent an indeterminate cynodont by Heckert (2004). At this stage, we are not able to confirm a cynodont identity for these teeth.

Traversodontids, by contrast, have a rich post-Anisian record, the youngest being in the latest Norian to Rhaetian faunas of Saint-Nicolas-de-Port, France, and Habay-la-Vieille, Belgium (Godefroit & Battail 1997, but see Hopson & Sues 2006). In Gondwana, the youngest traversodontid record is that of *Scalenodontoides* from the Norian Lower Elliot Formation. Abundant traversodontids in the rich Ladinian and Carnian faunas of South America (Rogers *et al.* 1993, 2001; Abdala & Ribeiro 2003) support the notion that traversodontids were the only gomphodont cynodonts to survive beyond the Anisian. However, the specimen described herein suggests the survival of Diademodontidae beyond the Anisian, as a residual component of Ladinian to Norian faunas, at least in southern Gondwana. Diademodontidae then would be a Lazarus taxon (Erwin 1996), apparently disappearing from the fossil record by the end of the Anisian (Crompton 1955; Brink 1963; Hammer 1995; Smith & Swart 2002; Abdala *et al.* 2005) then reappearing in the Norian of South Africa, a stratigraphic interval of some 21 million years.

Fauna of the Lower Elliot Formation

The tetrapod fauna of the Lower Elliot Formation (reviewed in Anderson *et al.* 1998; Galton & Van Heerden 1998, and Knoll 2004) is characterized by an abundance of dinosaur body fossils, particularly sauropodomorphs (Yates, pers. obs.). This includes five sauropodomorphs (Galton & Van Heerden 1998; Yates 2003; Yates & Kitching 2003), an unnamed ornithischian (Butler 2005), and one dinosaur *incertae sedis* (*Aliwalia rex*). This dominance is also expressed in the footprint record (Ellenberger 1970; Olson & Galton 1984), with three of the four types of ichnofamilies interpreted as produced by Archosauriformes-like animals and two of them, *Brachychirotherium* and *Grallator,* being the more abundant types in the formation (Olson & Galton 1984). *Grallator* tracks are thought to pertain to a theropod (Olson & Galton 1984).

The Lower Elliot fauna also includes teeth with crenulated margins, maxillary and lower jaw fragments, and large postcranial bones associated with osteoderms attributed to rauisuchids (Hopson 1984; Galton & Van Heerden 1998), while cranial and mandibular remains of large chigutisaurid temnospondyls also occur (Warren & Damiani 1999). In stark contrast to the therapsid-dominated Beaufort Group fauna, the only therapsids represented by body fossils in the Lower Elliot fauna are the traversodontid *Scalenodontoides macrodontes,* currently known from at least seven specimens (Crompton & Ellenberger 1957; Hopson 1984; Gow & Hancox 1993; Knoll 2004; Battail 2005; Abdala, pers. obs.), the tritheledontid *Elliotherium kersteni* represented by its holotype skull (Sidor & Hancox 2006), and the diademodontid BP/1/5724. In addition, the ichnofossil *Pentasauropus* is attributed to dicynodonts (Olson & Galton 1984). Nevertheless, cynodonts now comprise the second most diverse tetrapod group in the Lower Elliot fauna. Three groups of cynodonts, Tritheledontidae, Tritylodontidae and Mammaliaformes, are also represented in the Lower Jurassic Upper Elliot Formation, but only tritheledontids are common to both the Lower and Upper Elliot faunas.

BP/1/5724 was found by L.F. Allott during a collecting trip with R.D. in February 2000. For access to specimens, we thank S. Kaal and R. Smith (SAM), J. Welman (formerly NM), W-D. Heinrich (MB), A. Milner and S. Chapman (BMNH), and J. Clack and R. Symonds (UMZC). R. Butler and A. Heckert provided information on the ornithischian from the Lower Elliot Formation and on the teeth from the Redonda Formation respectively. We thank B. Battail and J. Hopson for their reviews. This research was made possible by funding from the University of the Witwatersrand and the National Research Foundation of South Africa. The Royal Society of London and PAST (Palaeontological Scientific Trust, Johannesburg) provided grants that allowed F.A. to visit paleontological collections in the United Kingdom.

INSTITUTIONAL ABBREVIATIONS

BMNH	Natural History Museum, London
BP	Bernard Price Institute for Palaeontological Research, Johannesburg
MB	Humboldt Museum für Naturkunde, Berlin
NM	National Museum, Bloemfontein
SAM	South African Museum, Cape Town
UMZC	University Museum of Zoology, Cambridge.

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Ammonites from offshore deposits near Bogenfels, Namibia

Herbert Christian Klinger[1*] **& Ian K. McMillan**[2]

[1]*Natural History Division, Iziko South African Museum, Iziko Museums of Cape Town, P.O. Box 61, Cape Town, 8000 South Africa*

[2]*School of Earth, Ocean and Planetary Sciences, Cardiff University, Cardiff CF10 3YE, U.K.*

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Pyritized ammonite nuclei and fragments were recovered by vibracore sampling from offshore deposits near Bogenfels, Namibia. Although these could only be identified at genus level, the association of *Baculites* and *Scaphites* suggest a Coniacian age for these deposits which conforms with the age of the associated foraminifera.

Keywords: ammonite nuclei, Coniacian.

INTRODUCTION

During the course of routine vibracore sampling during diamond exploration off the coast of Namibia, several pyritized ammonite nuclei and fragments were recovered from washed microfossil sieve residues. The vibracore was recovered not far off the Bogenfels coast at 27°30′56.8229″S, 15°18′03.0174″E. The vibracore intersected 0.44 m of section, beneath which was a core cutter sample from 0.44 to 0.66 m. The stratigraphic sequence in descending order is:

1. A thin Holocene veneer at 0.0.
2. A thin unit of fine, clean greenish sand of latest Pleistocene (Eemian-Weichselian) age from 0.0 to 0.32 m.
3. A uniform, stiff, dark grey, fine-grained clay from 0.32 to 0.66 m.

Foraminifera are abundant in the two clay samples studied: Sample Dn 3061 at 0.41–0.44 m and sample Dn 3060 at 0.44–0.64 m. Foraminifera include the benthonic species *Gavelinella plummerae* (Tappan), *Spiroplectinella* cf. *laevis cretosa* (Cushman) and *Nodosaria* cf. *zippei* Reuss, and the planktonic species *Discarinella primitiva* (Dalbiez). This is a typical Late Coniacian assemblage: there is no sign of *Gaudryna 'algulhasensis'*, which would indicate an Early Coniacian age. The pyritized ammonites come from sample Dn 3060. Unusually well-preserved *Gavinella plummerae* from the same sample have been illustrated by MacMillan (2003, fig. 13). The Cretaceous clay samples were washed in warm water through a stainless steel sieve with 63 μm mesh. The ammonite fragments are mostly about the same size as the foraminifera tests, and most were caught in the 250 μm dry sieve fraction.

DESCRIPTION OF AMMONITE MATERIAL

Ammonites from the sieve residues are represented by pyritized internal moulds of ammonitellas, i.e. embryonic shells and straight and curved septate fragments. The straight fragments (Fig. 1A,D) undoubtedly belong to the family Baculitidae (see Klinger & Kennedy 2001 for a review), and, based on the associated Coniacian foraminifera, probably to the genus *Baculites* Lamarck, 1822. During the course of preparing the specimens for coating for SEM examination, a curved specimen representing the uncoiled part of a scaphitid was unfortunately damaged beyond repair. The ammonitellas (Fig. 1B,C,E), one of which (Fig. 1E) shows the primary varix clearly, as well as the globular protoconch (Fig. 1B,C) have a quadrilobate primary suture and represent the early stages of either *Baculites* or a scaphitid genus, probably *Baculites s.s.* According to Landman (1982: 1238; see also Landman 1987: 142, fig. 19), *Scaphites* and *Baculites* ammonitellas differ in the size of the ammonitella angle, i.e. the angle measured from the proseptum to the ammonitella edge (primary varix). In *Baculites* this angle averages 331°, whereas in *Scaphites* it averages 290°. The ammonitella angle of the specimen in Fig. 1E of *c.* 310° suggests that it could belong to the genus *Baculites.* The association of *Baculites* and *Scaphites* suggests, but does not prove unambiguously, a Coniacian age for these deposits, similar to the second division of the Coniacian recorded by Kennedy & Klinger (1975: 278) from KwaZulu-Natal.

SIGNIFICANCE AND DISCUSSION

Even though the ammonite fragments and ammonitellas alone without foraminiferal support do not permit precise dating of these offshore deposits, their presence holds promise for future offshore biostratigraphic work based on ammonite remains in sieve residues (see also Wiedmann 1977). The ammonite remains are of further significance in being the only records of Cretaceous molluscan faunas from the entire Namibian coast apart from a single offshore specimen of *Sphenoceramus* aff. *S. schmidti* (Fig. 2B) and the isolated onshore inlier of the Wanderfeld IV Beds at near Bogenfels (see Haughton 1925; Klinger 1977; Klinger & Kennedy 1989), which has to date only yielded a single ammonite, *Placenticeras merenskyi* Haughton, 1925, and numerous specimens of the ostreid bivalve *Rhynchostreon suborbiculatum* (Fig. 2A) . To this sparse and unique Cretaceous fauna at Wanderfeld IV, Bogenfels may be added a fragment of a ribbed heteromorph ammonite, probably referable to the genus *Glyptoxoceras* (Fig. 2C) found by I.K.M., again in a washed microfossil sample residue. According to the abundant planktonic and benthonic foraminifera and ostracoda, the

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[*]Author for correspondence. E-mail: hklinger@iziko.org.za

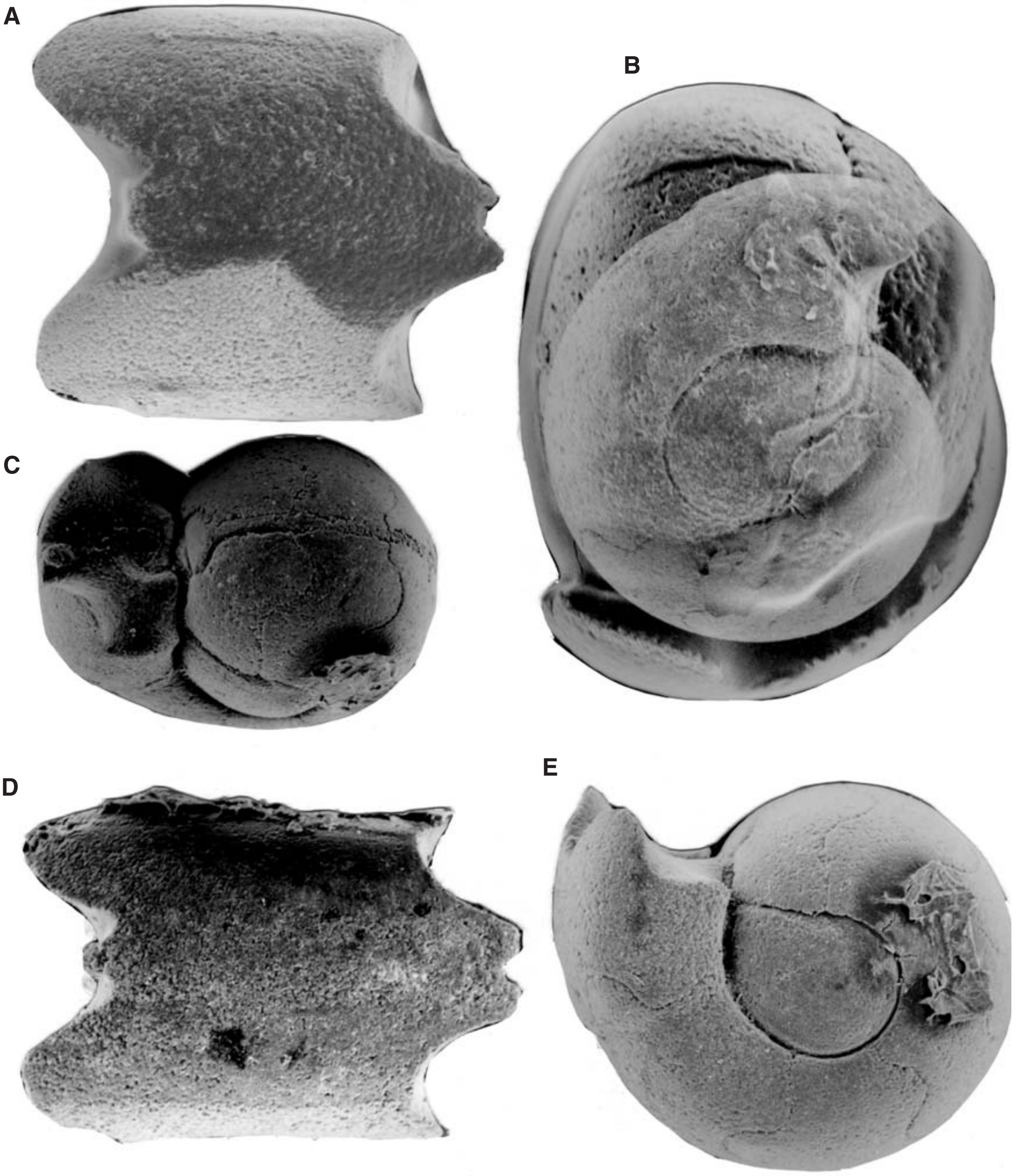

Figure 1. **A**,**D**, *Baculites* sp.: **A**, SAM-PCN22090; **D**, SAM-PCN22091. **B, C, E,** *Baculites* ? sp. ammonitellas: **B**, SAM-PCN22092; **C**, SAM-PCN22093; **E**., SAM-PCN22094; ammonitella showing globular protoconch and primary varix; All from offshore deposits at 27°30′56.8229″S, 15°18′03.0174″E on the Namibian coast. All ×100.

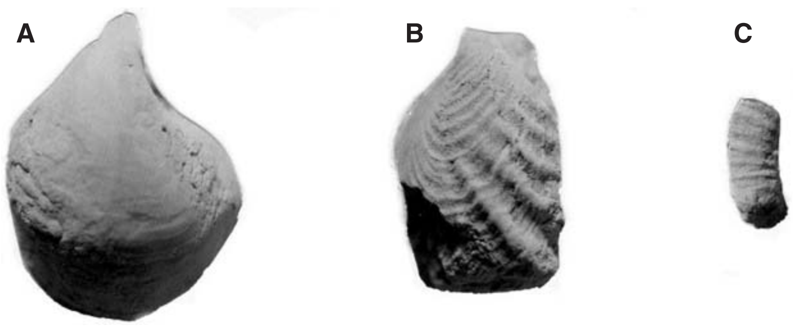

Figure 2. **A**, *Rhynchostreon suborbiculatum*, SAM-PCN22095; **C**, *Glyptoxoceras* ? sp., SAM-PCN22097; both from onshore deposits at Wanderfeld IV, Bogenfels, Namibia. **B**, *Sphenoceramus* aff. *S. schmidti*, SAM-PCN22096 (ex. PCS5504) from dredge sample off Namibian coast at 28°23′S,15°25′E. All ×1.

Wanderfeld IV inlier may be dated as Early Santonian (McMillan 2003: 543).

This material was collected while I.K.M. was employed by De Beers Marine (South Africa). Permission to publish by De Beers is acknowledged. We thank Derek Ohland (Natural History Division, Iziko Museums of Cape Town) for assistance with the SEM images and Kerwin van Wiellinhg with photography.

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New mammutid proboscidean teeth from the Middle Miocene of tropical and southern Africa

Martin Pickford

Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS, Case postale 38, 57 rue Cuvier, 75005, Paris, France
E-mail: pickford@mnhn.fr

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The genus *Zygolophodon* is widespread but rare in Middle Miocene deposits of Eurasia, and until recently it was not reliably reported from sub-Saharan Africa. Most previous records of the genus in the latter continent are based on specimens of another proboscidean *Eozygodon morotoensis.* In 1985 a tooth from Tunisia was attributed to *Zygolophodon* and in 2002 four teeth from Egypt were attributed to the same genus, while in 2005 a fragment of lower third molar was found at Daberas Mine, Orange River, Namibia, and two upper molars were found in the Ngorora Formation, Tugen Hills, Kenya. The purpose of this note is to describe and interpret the Ngorora molars. Two newly discovered specimens of *Eozygodon morotoensis* from Uganda complete the paper.

Keywords: *Zygolophodon, Eozygodon*, Proboscidea, Mammutidae, Kenya, Namibia, Middle Miocene, biogeography.

INTRODUCTION

The rare but geographically widely distributed Middle Miocene proboscidean *Zygolophodon* (Fig. 1) has had a chequered taxonomic history, partly on account of the paucity of its remains but mainly because its cheek dentition superficially resembles those of bunodont gomphotheres (Tobien 1975; Tassy 1985). There are, however, several characters which distinguish the teeth of these two groups, although in advanced wear stages it can be difficult to attribute teeth correctly.

Zygolophodon was previously reported from tropical African deposits (Madden 1980) based on a fragment of an upper premolar from Moruorot, Kenya, dated to *c.* 16.2 Ma. However, Pickford & Tassy (1980) and Tassy & Pickford (1983) reclassified the specimen as *Eozygodon morotoensis,* which has flattened lower tusks, thinner enamel in the cheek teeth, and more antero-posteriorly compressed cusps than in *Zygolophodon,* among other characters. However, with the discovery and naming of *Zygolophodon aegyptensis,* the affinities of the Moruorot

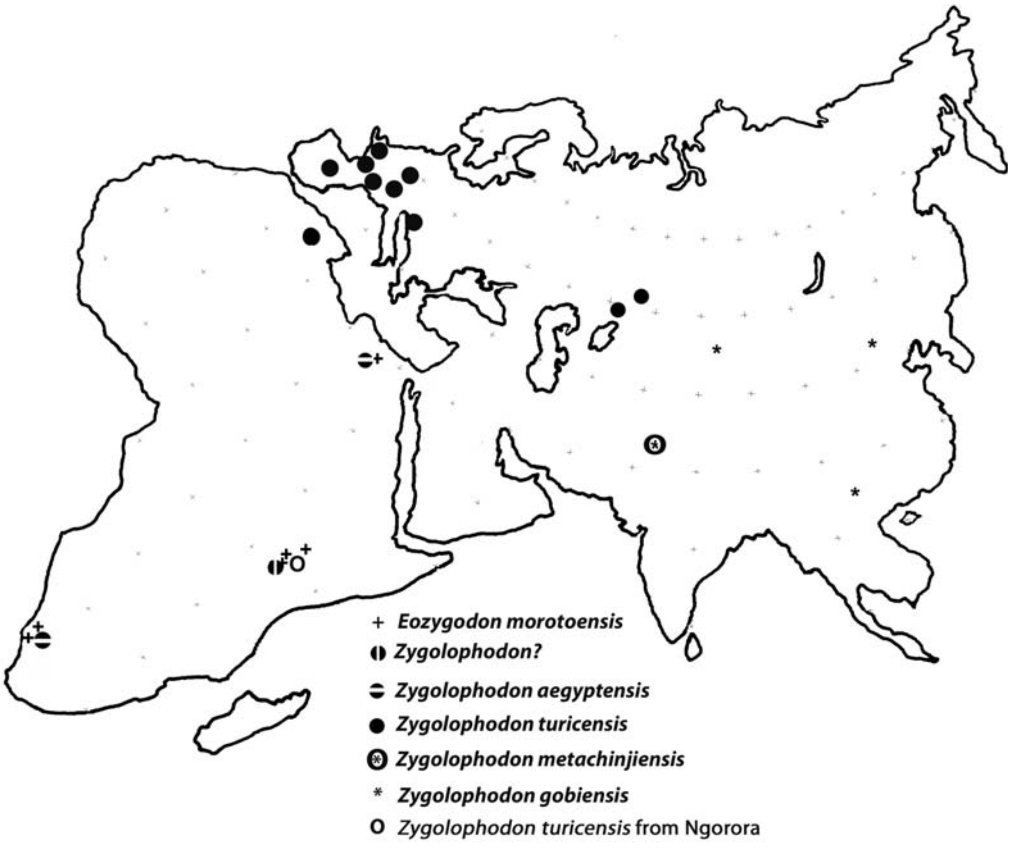

Figure 1. Old World distribution of *Zygolophodon* species and *Eozygodon.* The Kenyan material is closest in size to *Z. gobiensis* from Tung Gur, China, but is morphologically similar to *Z. turicensis* from Europe. The Rusinga (Kenya) records require confirmation.

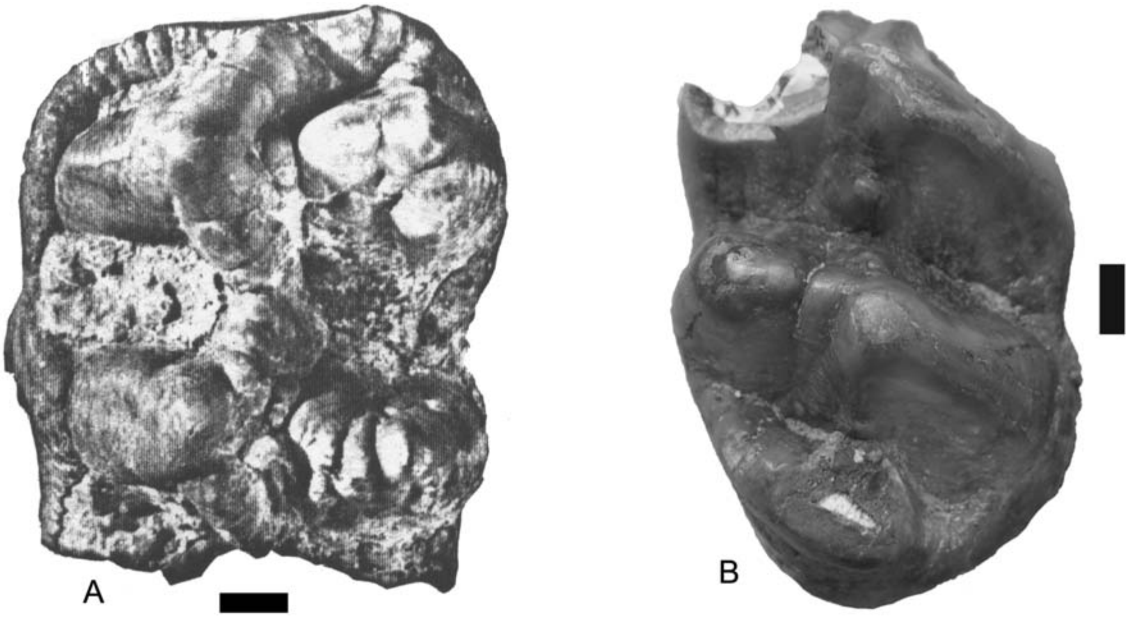

Figure 2. *Zygolophodon* from Tunisia and Namibia. **A**, *Zygolophodon turicensis* from Jebel Cherichera, Tunisia (photograph reproduced from Tassy, 1985); **B**, *Zygolophodon* cf. *aegyptensis* from Daberas, Namibia. Scale bars = 10 mm.

specimen requires reassessment. Two specimens from the Maghreb have been tentatively attributed to *Zygolophodon,* a deciduous tooth from the Late Miocene of Menacer, Algeria (Thomas & Petter 1986), which is possibly a specimen of *Zygolophodon borsoni,* and an incomplete upper molar from the Middle Miocene of Jebel Cherichera, Tunisia, found more than a century ago (Errington de la Croix 1887) and attributed to *Zygolophodon turicensis* by Tassy (1985, pp. 509–510, fig. 213). The specimen possesses a well-developed lingual cingulum (Fig. 2A). Sanders & Miller (2002) described the species *Zygolophodon aegyptensis* on the basis of four teeth from Wadi Moghara, Egypt and Pickford (2003) mentioned the possible presence of *Eozygodon morotoensis* at the same site on the basis of a mandible with lower third molar roots that indicate a crown size considerably shorter than any of the teeth of *Zygolophodon aegyptensis.*

Several teeth from Rusinga Island, Kenya, originally identified as *Trilophodon angustidens kisumuensis* by MacInnes (1942) were attributed to *Zygolophodon* by Van Couvering & Van Couvering (1976) and tentatively to *Archaeobelodon* by Tassy (1986). The two upper second molars in the sample possess antero-posteriorly compressed lophs, zygodont crests and a median sulcus, all features that occur in mammutids, but they appear to lack the lingual cingulum that is usually present in these proboscideans. The third molars from Rusinga show some resemblances to those of *Z. aegyptensis* from Wadi Moghara, Egypt, described by Sanders & Miller (2002). The status of these specimens requires re-examination.

The Daberas, Namibia, specimen is the rear half of a lower third molar (Pickford, in press) with compressed and oblique lophids typical of mammutids. It is quite small, (breadth of penultimate lophid is 59 mm) being the same order of magnitude as the holotype of *Z. aegyptensis* (breadth of first lophid 55.8 mm (Sanders & Miller 2002)) but differs from it by having somewhat straighter posterior lophids which are not as anteriorly convex as those of the Egyptian specimen. It differs from the two well-preserved specimens of *Eozygodon morotoensis* from East Africa (Pickford & Tassy 1980; Tassy & Pickford 1983) by its more oblique lophids, the stronger development of the anterior and posterior ridges (acr and pcr) and the strongly sloping buccal margin of the pretrite cuspids. Its enamel is also about 33% thicker (4 mm compared to 3 mm for *Eozygodon morotoensis*) (Fig. 2B).

The fossils which are the main focus of this paper are from Grildain, near Bartabwa, in Member A of the Ngorora Formation, Tugen Hills, Kenya, a late Middle Miocene deposit (*c.* 13 Ma) (Fig. 1). The fossils were found by Mr Kiptalam Cheboi during the Kenya Palaeontology Expedition. The aim of this note is to describe and interpret these teeth and to discuss their biochronological and biogeographic implications. Newly recovered specimens of *Eozygodon morotoensis* are included in the analysis.

SYSTEMATIC DESCRIPTIONS

Order Proboscidea Illiger, 1811
Family Mammutidae Hay, 1922
Genus *Zygolophodon* Vacek, 1877

Species *Zygolophodon turicensis* (Schinz, 1824), Figs 1–3

Material. Bar 158’05, left and right M2/s.

Locality. Grildain, near Bartabwa, Tugen Hills, Kenya.

Age. Member A, Ngorora Formation, *c.* 13 Ma.

Description. Bar 158’05 comprises left and right second upper molars in medium wear (Fig. 3, Tables 1 & 2). The crowns are trilophodont, with antero-posteriorly compressed lophs, the pretrite half being separated from the posttrite half by a clear median sulcus. The pretrite cusps are trifoliate, with prominent anterior (acr) and posterior (pcr) ridges (anterior and posterior accessory conules) leading towards the median sulcus (Tobien 1996) but not crossing it. The posttrite cusps are almost rectangular in occlusal outline with rounded corners, and the buccal

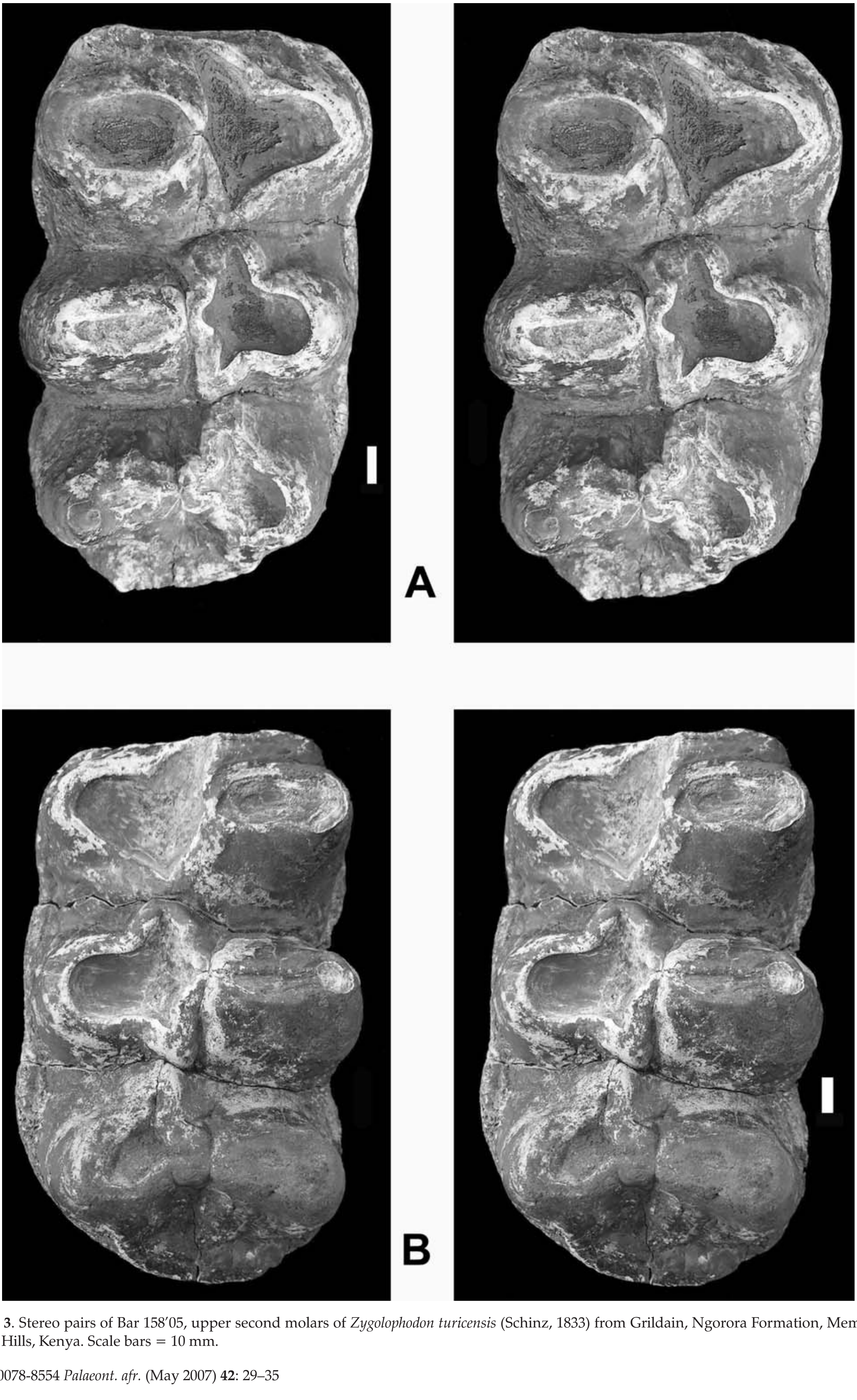

Figure 3. Stereo pairs of Bar 158'05, upper second molars of *Zygolophodon turicensis* (Schinz, 1833) from Grildain, Ngorora Formation, Member A, Tugen Hills, Kenya. Scale bars = 10 mm.

Table 1. Measurements (in mm) of Bar 158′05, upper second molars attributed to *Zygolophodon turicensis.*

Tooth	Length	Breadth 1st loph	Breadth 2nd loph	Breadth 3rd loph
Right M2/	134.5	79.6	81.3	77.3
Left M2/	133.3	80.5	82.8	80.0

wall is almost vertical. The posttrite cusps possess zygodont crests (zc) which have been somewhat reduced in stature by wear, but which are nevertheless perfectly clear, particularly in the left upper molar. The interloph valleys are broad, especially in the posttrite half. The lingual cingulum is continuous from mesial to distal but is not as prominent opposite the lophs as between them. The anterior cingulum stretches the full breadth of the tooth, but the posterior one is not as broad, extending across only about two-thirds of the breadth. Finally, the enamel is appreciably thicker in these specimens than it is in *Eozygodon morotoensis* (Pickford & Tassy 1980) (Fig. 4).

Discussion. The morphology of the Ngorora upper molars is compatible more with the genus *Zygolophodon* than with *Eozygodon.* Molar dimensions and thickness of the enamel differentiate the two genera, as does the degree of compression of the lophs. The Ngorora teeth are large for *Zygolophodon,* plotting out at the top end of the range of variation close to material from Tung Gur, China, the type locality of *Zygolophodon gobiensis* Osborn & Granger (1932) and somewhat larger than most of the European teeth attributed to *Zygolophodon turicensis.* The specimen from Jebel Cherichera, Tunisia (1886-15 MNHN) attributed to *Zygolophodon turicensis* is appreciably smaller (breadth first loph 66.9 mm, second loph 68.6 mm) (Tassy, 1985) (Fig. 2A) than the Tugen specimens (breadth first loph of the two specimens, 81.3 and 82.3 mm) (Fig. 3). In view of the vast distance between the Tugen Hills and the Gobi Desert, and the fact that the Kenyan sample is restricted, the Ngorora teeth are attributed to *Zygolophodon turicensis.*

Genus *Eozygodon* Tassy & Pickford, 1983

Species *Eozygodon morotoensis* (Pickford & Tassy, 1980), Figs 1 & 4

Material. Mor II 18′01, left M2/, Mor II 19′05, right M2/.

Locality. Moroto II, northeast Uganda.

Age. Base of the Middle Miocene (although some authors (Gebo *et al.* 1997) have estimated a basal Early Miocene age in excess of 20 Ma).

Description. The left upper second molar Mor II 18′01 is an almost complete though damaged specimen in medium wear. The tooth has broken into sections which have drifted apart in the sediment, but have retained their positions relative to one another. There are three lophs and a beaded distal shelf-like cingulum. The thin enamel (3 mm on the pretrite cusp of the second loph), perfectly formed lophs with a central sulcus and a continuous beaded lingual cingulum are all features that are typical of *Eozygodon morotoensis*, the type locality of which is Moroto I (Pickford & Tassy 1980; Tassy & Pickford 1983). Taking into account the displacement of the various pieces, the crown measures *c.* 89 mm long by *c.* 60 wide at the second loph (Table 2).

Mor II 19′05 is an unworn but damaged right M2/ (Fig. 4, Table 2). The lophs are extremely antero-posteriorly compressed with sharp transversely oriented apices. The

Table 2. Metric comparison of upper second molars, Bar 158′05, *Zygolophodon turicensis* from Grildain, Ngorora Formation, Member A (*c.* 13 Ma), Tugen Hills, Kenya (original data) with M2/s of European *Zygolophodon* species (data from Göhlich, 1998), *Eozygodon morotoensis* (data from Pickford & Tassy 1980, and original data), possible *Zygolophodon* from Rusinga (data from MacInnes 1942) and material from Wadi Moghara (data from Sanders & Miller 2002).

Specimen	Locality	Taxon	Length	Breadth
Din 687	Esselborn	*Z. turicensis*	103	73
Din 868	Esselborn	*Z. turicensis*	115	72
Din 724	Esselborn	*Z. turicensis*	114	79
A/V 0039	Elgg	*Z. turicensis*	92	63
1996 I 28a	Montréjeau	*Z. turicensis*	82	59
LVPVH	Rajégats	*Z. turicensis*	126	80
Si 13	Simorre	*Z. turicensis*	113	68
SML 356	Malartic	*Z. turicensis*	107	69
SML 501d	Malartic	*Z. turicensis*	111	79
SML 501c	Malartic	*Z. turicensis*	110	79
Mor I′61 rt	Moroto I	*E. morotoensis*	89.3	62.4
Mor I′61 lt	Moroto I	*E. morotoensis*	89.2	62
ME 7545	Meswa Bridge	*E. morotoensis*	83	63.8
Mor II 18′01	Moroto II	*E. morotoensis*	89	60
Mor II 19′05	Moroto II	*E. morotoensis*	81.5	66.5
AM 02 1994	Auchas	*E. morotoensis*	86.8	62.4
AM 02 1994	Auchas	*E. morotoensis*	84.6	62.3
Bar 158′05 rt	Ngorora A	*Z. turicensis*	134.5	81.3
Bar 158′05 lt	Ngorora A	*Z. turicensis*	133.3	82.8
2202–4	Tung Gur	*Z. gobiensis*	130	88
2202–5	Tung Gur	*Z. gobiensis*	128	88
DPC 5932	Moghara	*Z. aegyptensis*	112.5	68
M 15323	Rusinga	*Zygolophodon?*	105	64
M 15324	Rusinga	*Zygolophodon?*	104	60

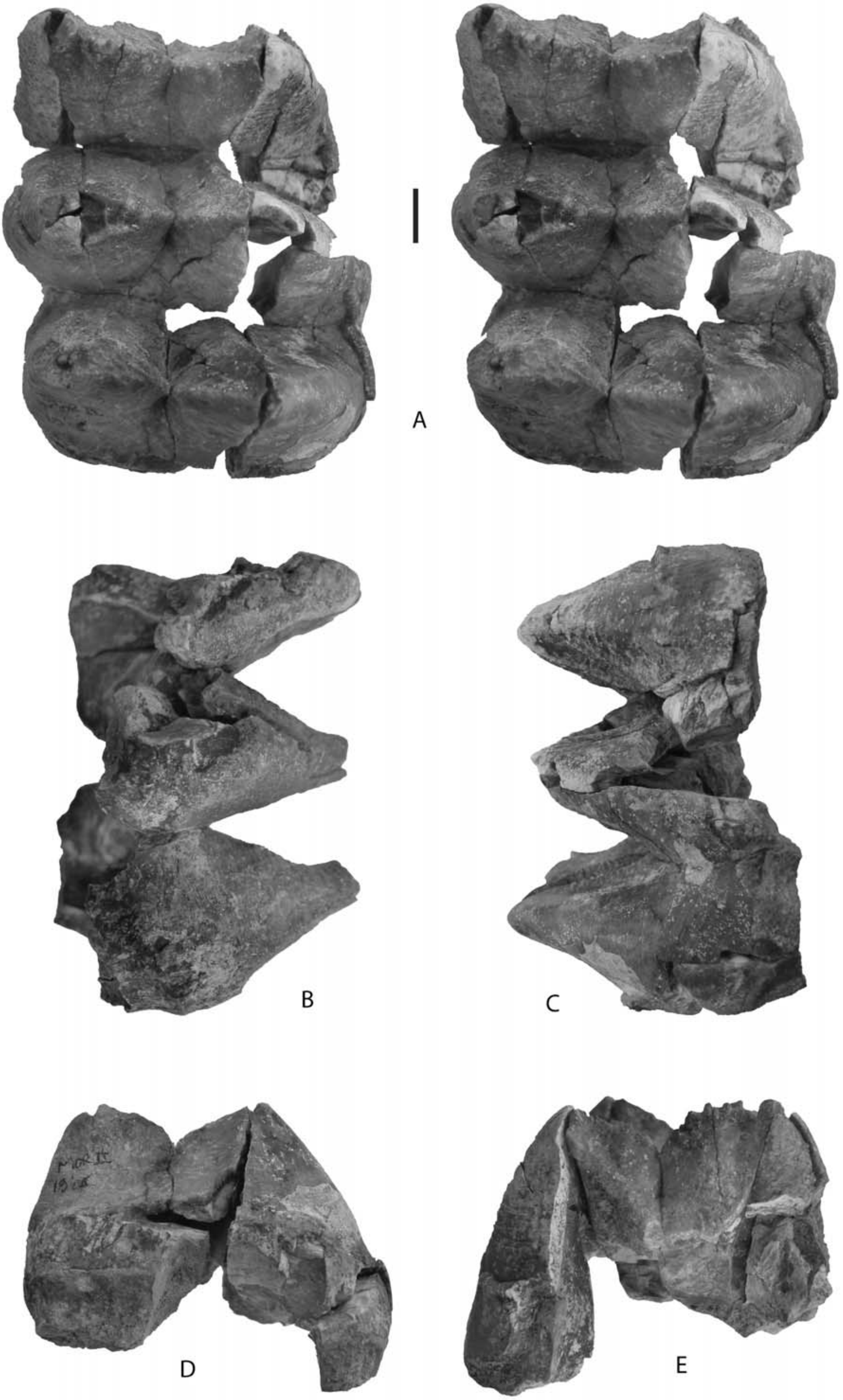

Figure 4. Mor II 19’05, right M2/, *Eozygodon morotoensis,* from Moroto II, northeast Uganda. Scale bar = 10 mm.

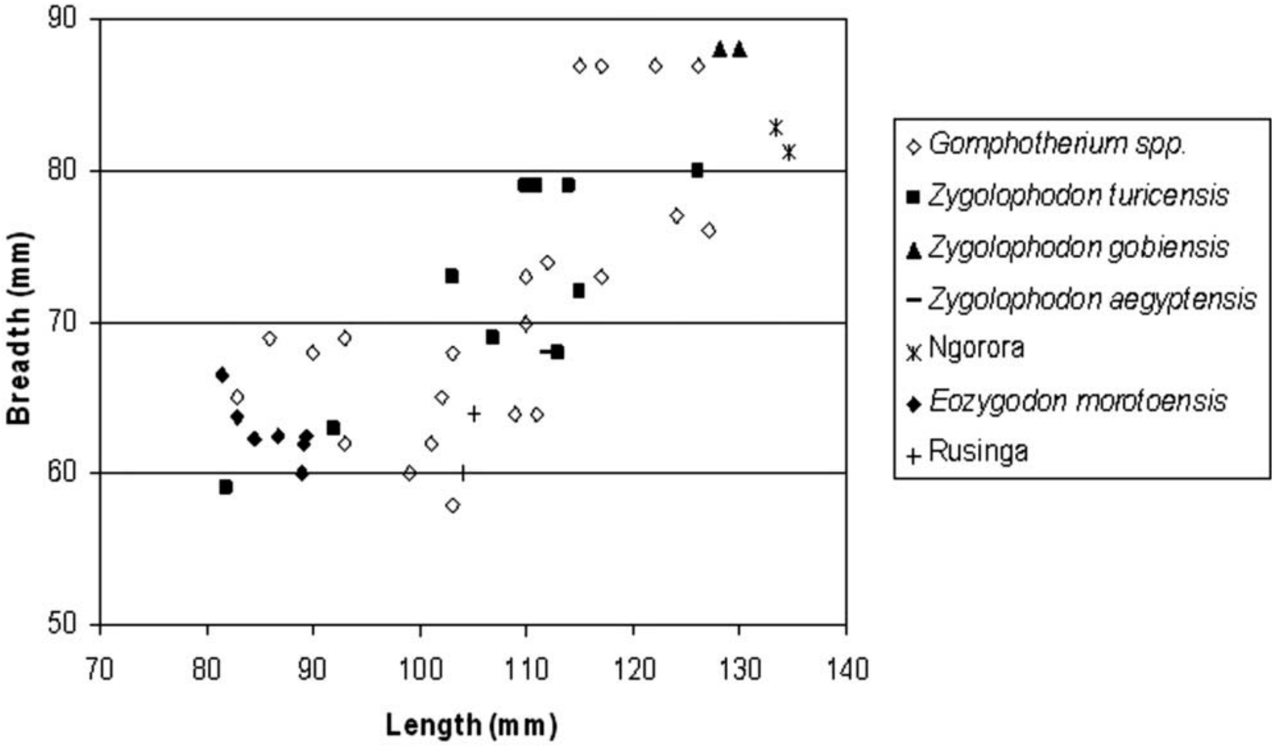

Figure 5. Bivariate plot (in mm) of M2/s of gomphotheres (open symbols) and mammutids (closed symbols). The almost complete overlap in dimensions reveals that mammutid teeth are not particularly wide when compared to those of gomphotheres, as previously claimed (Tobien 1975). It is the third molars which are shorter than expected, not wider than expected.

profile of the cutting edges of the lophs descends from the apex of the cusps toward the median sulcus (Fig. 4D,E). The central sulcus is deep, and the anterior (acr) and posterior (pcr) ridges of the pretrite cusps are weakly expressed, so that the transverse valleys are not blocked (Fig. 4B,C). The zygodont crests are weakly developed, and the buccal walls of the posttrite cusps are more vertical than the pretrite ones. There is a prominent lingual cingulum on the third loph, but it has broken off in the other two cusps. In this unworn specimen it is possible to see that the half lophs are subdivided at the apex into about 12 or 13 beads, presumably small cones, but the sulci between the beads quickly fade cervically, so that even with slight wear, all signs of the beads disappear and the lophs take on a rectangular outline with rounded corners.

Discussion. These two upper molars from Moroto II are extremely similar to the type material from Moroto I. They represent a new locality record for the species *Eozygodon morotoensis.*

GENERAL DISCUSSION

There has been a great amount of uncertainty about the systematic status and material content of the genus *Zygolophodon,* summarized but not completely resolved by Osborn (1936). Historically, many fossils have been erroneously attributed to *Zygolophodon* and some genuine mammutid specimens have been misidentifed as gomphotheres. Tobien (1975, 1996) clarified the situation by showing that there were only a few species which were quite variable in details of morphology and size, but which showed constancy in certain morphological characters in the molars such as the presence of zygodont crests, a median sulcus, almost vertical posttrite cusp walls, and presence of lingual cingulum, among other features.

Some authors have tended to create new taxa on the basis of minor variants within these few species. In Europe, Tobien (1975, 1996) recognized two species, *Zygolophodon turicensis* and *Mammut borsoni.* In mid-latitude Asia he recognized *Zygolophodon gobiensis* (Dubrovo 1970; Osborn & Granger 1932) and *Mammut borsoni* (Borissiak 1936), and in India *Zygolophodon metachinjiensis* (Tassy 1983) (Fig. 1). In North America there are several taxa of mammutids, some of which Tobien (1975 1996) considered to be very close to *Zygolophodon* (e.g. *Miomastodon merriami*), but others distinct *Pliomastodon matthewi* and *Mammut americanum.* In Africa, the only mammutid known to Tobien was *Eozygodon morotoensis* (Pickford & Tassy 1980; Tassy & Pickford 1983).

Tobien (1975, 1996) concluded that the molars of mammutids tended to be wider than those of gomphotheres, but this is only apparent in the third molars. Upper second molars of gomphotheres and mammutids overlap almost completely in dimensions (Fig. 5), which reveals that in fact mammutid molars are not markedly broader than those of gomphotheres, but that their third molars are shorter, the talon/id complex being less pronounced than those of gomphotheres.

A bivariate plot of the upper second molars of mammutids reveals that the Ngorora specimens fall at the upper end of the range of metric variation of the species belonging to *Zygolophodon,* in particular they are close in dimensions to teeth of *Z. gobiensis* from Tung Gur, Mongolia. The latter site is late Middle Miocene, often being considered equivalent in age to MN 7/8 of the European biozonation. This is close to the age of the

Ngorora specimens, *c.* 13 Ma. Basal Middle Miocene specimens are generally smaller, and the smallest of all are the teeth of *Eozygodon morotoensis* which range in age from 22–16.5 Ma. It is likely that as in many proboscidean lineages, the mammutids increased in size through the Middle Miocene, but the quantity of specimens is rather too low for them to be used as a biochronological tool. Tobien postulated a long chronological range for the species *Z. turicensis,* from MN4 to MN 12–13 (Göhlich, 1999).

Prior to the discovery of the Tugen mammutid teeth, the only confidently identified African material attributed to *Zygolophodon,* was from Tunisia (Tassy 1985) and Egypt (Sanders & Miller 2002). The Kenyan and Namibian specimens thus represent major range extensions of the palaeodistribution of the genus *Zygolophodon.*

CONCLUSIONS

Newly recovered teeth from basal Middle Miocene deposits at Moroto II, Uganda, fall comfortably within the range of metric and morphological variation of *Eozygodon morotoensis* (Pickford, & Tassy 1980).

A partial lower third molar from Daberas Mine, Orange River Valley, Namibia, has thicker enamel than *Eozygodon morotoensis* and it has better developed anterior and posterior pretrrite ridges, indicating that it belongs to *Zygolophodon,* possibly the species *Z. aegyptensis* recently described from Wadi Moghara, Egypt (Sanders & Miller 2002). This find suggests a basal Middle Miocene age for the deposits at Daberas from which the tooth came, possibly quite early in the period on account of the diminutive dimensions of the specimen.

Two mammutid upper molars from Grildain, Ngorora Formation (*c.* 13 Ma), Tugen Hills, Kenya, are close in size to specimens of *Zygolophodon gobiensis* from Tung Gur, Mongolia (Osborn & Granger 1932) but are more similar in morphology to specimens of *Zygolophodon turicensis* from Europe. They are interpreted to represent a large individual of the latter species.

The discovery of these teeth in tropical and southern Africa indicates that mammutids were not only extremely widespread in Eurasia and the New World, but were equally widespread in Africa. The known geochronological range of mammutids in Africa spans the period 22.5 to 13 Ma.

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Morphological trends in the molars of fossil rodents from the Fayum Depression, Egypt

Patrick J. Lewis[1*] **& Elwyn L. Simons**[2]

[1]*Department of Biological Sciences, Sam Houston State University, Huntsville, Texas, 77341 U.S.A.*

[2]*Duke University Primate Center, Division of Fossil Primates, Durham, North Carolina, 27705 U.S.A.*

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While many of the mammalian taxa from the Fayum of Egypt, such as the primates and hyraxes, have been well-studied, little is known about the rodents. Species described to date have all been referred to the endemic family Phiomyidae. Many rodent species from this family have been named and their importance to biogeography addressed, but what this fauna can reveal about the palaeoenvironment of the Fayum has yet to be determined. The study of palaeoenvironmental trends begins with a general examination of species diversity and morphology of the specific rodent lineages. A statistical analysis of available molar measurements of Fayum rodents estimates general size and shape trends and changes in rodent diversity through the stratigraphic sequence of the Fayum. This analysis finds stability in species diversity and an increase in the average body size of taxa using molar length as an estimate of body size. The body size pattern of the rodents is similar to the pattern found among the Fayum primates. Analysis of molar length and width has been performed to test whether these variables could discriminate accurately between taxa. If molars that are too worn to be identified by cusp pattern can be identified confidently based on length and width, more specimens could be included in future analyses and a more accurate depiction of the small mammal fauna attained. Length is significantly different between most of the species, and several species can be identified by length and width alone. Length and width relationships were consistent for species within the same genus.

Keywords: evolutionary trends, Fayum, palaeoenvironment, molar morphology.

INTRODUCTION

The Fayum Depression of Egypt has long been known for its wealth of primate fossils and its importance in the study of biogeography during the late Eocene and early Oligocene. Among the qualities that separate the Fayum from other localities of this period are the great diversity of species, excellent fossil preservation, and large number of fossils that many of its quarries produce. One of the most common mammalian groups recovered in the deposits of the Fayum are the rodents. These mammals gain importance for they can be used as palaeoenvironmental indicators. The rodents of the Fayum, however, have yet to be studied for what they may reveal about environmental changes throughout the Fayum stratigraphic sequence. Such an analysis first requires an assessment of general changes in species diversity and variation to determine if appreciable differences exist between rodent faunas from successive stratigraphic layers. This preliminary study of the Fayum rodents, therefore, seeks to determine if variation in the rodent fauna is sufficient to warrant a further investigation.

The excellent preservation of fossils found in the Fayum has produced a highly varied rodent fauna having substantial sample sizes for many species. The rodent fauna is composed of seven genera and 13 species (Table 1) ranging from the latest Eocene to early Oligocene in age (Holroyd 1994). These taxa are diagnosed principally based on molar cusp patterns, but many species also have distinctive overall molar morphologies. If these morphological features differ sufficiently, those fossil specimens currently too worn to be identified confidently by cusp patterns may be identified by measuring their overall size and shape. The use of overall molar morphology may allow us to estimate the species identification of more fossil specimens and ultimately provide a better understanding of the relative abundance of the various species. As any environmental data that can be gathered from the rodent fauna will depend not only on the presence or absence of various taxa but on their relative abundance, the identification of as many molars (i.e. different individuals) as possible is desirable.

The following research tests the degree of variation present in the molars of Fayum rodents through time and across taxonomic classification, and assesses the degree that size and shape of molars are appropriate for classifying species. Trends in size and shape are analysed for consistency within species and genera, and through lineages, using length and width of the lower first (M_1) and second (M_2) molars to test for differences between various taxa. Lastly, the relative diversity of taxa and morphological trends through the stratigraphic sequence are discussed.

MATERIALS AND METHODS

The Fayum Depression lies in Egypt on the eastern edge of the Sahara Desert. The site has been collected for fossils since the latter part of the 19th century, and has produced a large variety of late Eocene and Oligocene fossils of land mammals (Simons & Rasmussen 1995, and references cited there). These fossils are found in the Birket Qarun, Qasr el Sagha, and Jebel Qatrani formations. The Widen el Faras Basalt caps the Jebel Qatrani formation, and has been dated to *c.* 25–27 million years, although some debate occurs over these dates (Kappelman *et al.* 1992; Prothero & Berggren 1992; Seiffert *et al.* 2005; Seiffert 2006). Specimens studied here have been recovered at various stratigraphic levels within the Jebel Qatrani Formation. The geologically younger quarries (M, I, G, V,

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[*] Author for correspondence. E-mail: pjlewis@shsu.edu

Table 1. Mean length and width data with standard deviations for each rodent species

Species	M1					M2					
	n	L	S.D.	W	S.D.	*n*	L	S.D.	W	S.D.	Location
Phiomys andrewsi	11	1.44	0.09	1.22	0.06	8	1.22	0.06	1.41	0.09	B, E
Phiomys stellae	2	1.40	–	1.20	–	2	1.30	0.14	1.25	0.07	I
Phiomys troctatus	11	1.63	0.10	1.51	0.07	8	1.69	0.08	1.51	0.08	I, M
Acritophiomys adaios	27	1.83	0.90	1.53	0.10	26	1.91	0.11	1.69	0.12	A, B, E
Acritophiomys bowni	4	2.05	0.06	1.73	0.06	5	2.10	0.12	1.96	0.09	L-41
Acritophiomys woodi	22	1.66	0.08	1.47	0.07	19	1.77	0.09	1.66	0.06	L-41
Metaphiomys beadnelli	27	2.61	0.13	2.09	0.08	27	2.87	0.15	2.55	0.09	V, I, M, P
*Metaphiomys schaubi**	7	2.44	0.09	2.17	0.08	4	2.48	0.10	2.40	0.17	G, V, L-12
Gharbalamys simonsi	11	3.36	0.11	3.19	0.19	15	3.55	0.25	3.39	0.29	I, M
Gaudeamus aegypticus	16	1.71	0.11	1.63	0.12	18	1.81	0.21	1.81	0.18	E
Gaudeamus hylaeus	8	2.00	0.09	1.94	0.11	11	2.06	0.16	2.07	0.09	L-41
Elwynomys lavocati	14	1.06	0.05	0.99	0.06	14	1.04	0.05	1.01	0.06	L-41, E

Data from Holroyd (1994), * = not recognized in Holroyd (1994). *Phiocricetomys minutus* and *Phiomys paraphiomyoides* (found at quarries G,V, I, and M) are not listed due to lack of sufficient material for this analysis.

and P) are thought to date to approximately 30–31 mya (Seiffert 2006). The older quarries (L-41, A, B, and E) are dated to the early Oligocene, approximately 33–34 mya (Seiffert 2006). In general, the palaeoenvironment during the time of sediment deposition was a heavily forested tropical landscape with meandering streams (Bown & Kraus 1988).

All the Fayum rodents in this study belong in the superfamily Thryonomyoidea and the infraorder Phiomorpha. The Thryonomyoidea have hysticognathous mandibles and hystricomorphous attachments for the masseteric muscle (Nowak 1991). The Phiomorphs differ from the caviomorphs mainly in biogeographic ranges and the two are likely sister taxa (Lavocat 1973). Whereas some disagreement exists over the taxonomy of the Fayum rodents (see Wood 1968; Holryod 1994), the diagnoses of Holryod (1994) are followed here.

Several ancestor/descendent relationships are probable within the Fayum rodents (Wood 1968; Holroyd 1994). *Phiomys andrewsi* is suggested as the probable ancestor for later taxa including *Gaudeamus* spp., *Metaphiomys* spp., and *Phiomys lavocati* (Wood 1968). *Phiomys andrewsi* itself ranges from the late Eocene through the early Oligocene. *Metaphiomys schaubi,* a proposed descendant of *P. andrewsi,* also is suggested to be the ancestor of *M. beadnelli* (Wood 1968). Holroyd (1994), however, considers the two *Metaphiomys* species to be synonymous.

Of the 13 known species, two are not represented in this analysis due to the absence of either the M$_1$ or M$_2$ in any available specimen (*Phiomys paraphiomyoides* and *Phiocricetomys minutus*). *Metaphiomys beadnelli* (*sensu* Holryod) specimens are subdivided into *M. beadnelli* and *M. schaubi* following Wood (1968). All measurements in this analysis are from Holroyd (1994), and consist of the length and width of the M$_1$ and M$_2$. While measurements are available for other molars, these molars were selected as they demonstrated the largest sample sizes.

Descriptive statistics, regression, discriminant analysis, and several ratios are used to examine how molar length and shape (defined as the relationship between the length and width variables) vary between taxa. All measurements are transformed to natural logarithms before analysis to linearize allometric relationships and to make variation relative to tooth size rather than absolute. Multiple analysis of variance (MANOVA) tests for significant length differences between the molars of different species. A correlation matrix indicates that molar length and width are highly correlated (all measurements >0.95), making analysis of covariance (ANCOVA) inappropriate. Analysis of variance (ANOVA), therefore, is used to test for differences between molar length-to-width ratios between species and pairwise *post hoc* Bonferroni/Dunn tests are performed on length-to-width ratios to determine what species are responsible for any significant results from the ANOVAs. An α of 0.05 is used for all statistical procedures except for the multiple pairwise tests, where the α is adjusted in accordance with the Bonferroni correction (Sokal & Rohlf 1995). Lastly, discriminant analysis (DA) is used to explore the suitability of the M$_1$ and M$_2$ measurements to distinguish between the different species when both molars are present. Statistical tests are run on Minitab 5.2 software.

RESULTS

No overlap occurs in length and little overlap in width in the M$_1$ or M$_2$ of *Gharbalamys simonsi* and *Elwynomys lavocati* with any of the other species analysed (Table 1; Fig. 1A,B). Length against width plots for both molars reveal distinct clusters for several species, although substantial overlap occurs for many (Fig. 1A,B). Length and width plots for *Metaphiomys beadnelli* and *Phiomys andrewsi* also represent distinct groups for both molars. Simple regression lines for the M$_1$ length and width grouped by species are positively sloped, with the exception of *M. beadnelli* where molar width actually decreases with length (Fig. 2). Regression lines for the M$_2$ are all positive, although the line for *M. beadnelli* is very shallow, and molar width increases only slightly with increased length (Fig. 3). All species exhibit M$_1$ molars that are either equally long relative to width or longer than they are wide. Length ratios (Table 2) show that the molars of all species have longer M$_1$ than M$_2$ molars except *Elwynomys lavocati* and *Phiomys stellae,* both of which have slightly longer M$_2$ molars. MANOVA for M$_1$ and M$_2$ lengths and widths

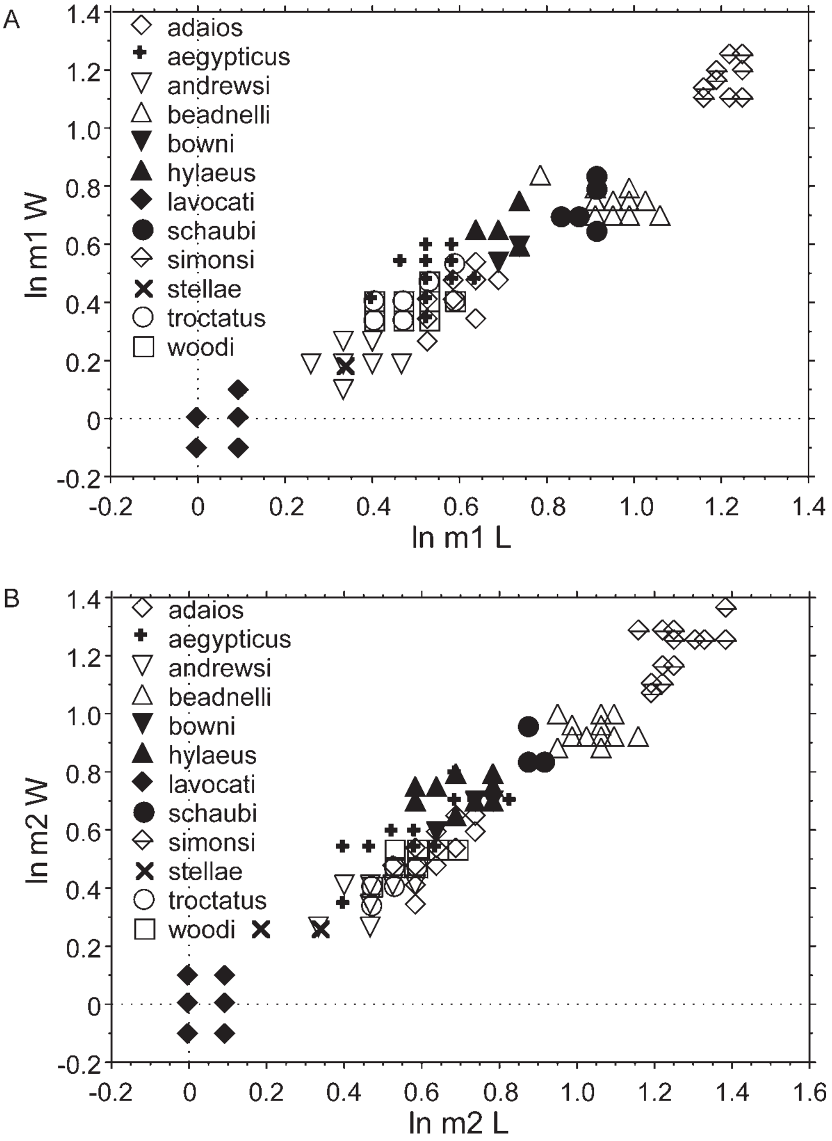

Figure 1. Plots of natural log length and width for (**A**) M_1 and (**B**) M_2 (data from Holroyd 1994).

returns significant results (d.f. = 94, $P < 0.001$).

Length-to-width ratios of M_1 molars fall roughly into two groups, with several species ranging from 1.05–1.08 and the remainder ranging from 1.16–1.25 (Table 2). These groups, however, vary within the genera morphologically such that species of the same genera exhibited differently shaped molars. Length-to-width ratios for the M_2 molars are less variable than M_1 ratios, with ratio values ranging from 0.99 to 1.13. ANOVA results for M_1 length-to-width ratios are significant ($P < 0.001$), with *post hoc* Bonferroni/Dunn tests finding 21 of 66 pairwise tests significant (Table 3). An ANOVA for the M_2 length-to-width ratios is also significant ($P < 0.001$), but Bonferroni/Dunn tests find only 10 of 66 pairwise tests significant (Table 3).

Discriminant analysis correctly identifies species with an overall 86% accuracy rate using length and width of the M_1 and M_2. *Acritophiomys bowni, Elwynomys lavocati, Gharbalamys simonsi, Metaphiomys schaubi, Phiomys stellae,* and *P. andrewsi* are each discriminated without error (100%). *Metaphiomys beadnelli* (94%), *Gaudeamus hylaeus* (85%), *A. woodi* (82%), and *P. troctatus* (75%) also are identified effectively, whereas *G. aegypticus* (63%) and *A. adaios*

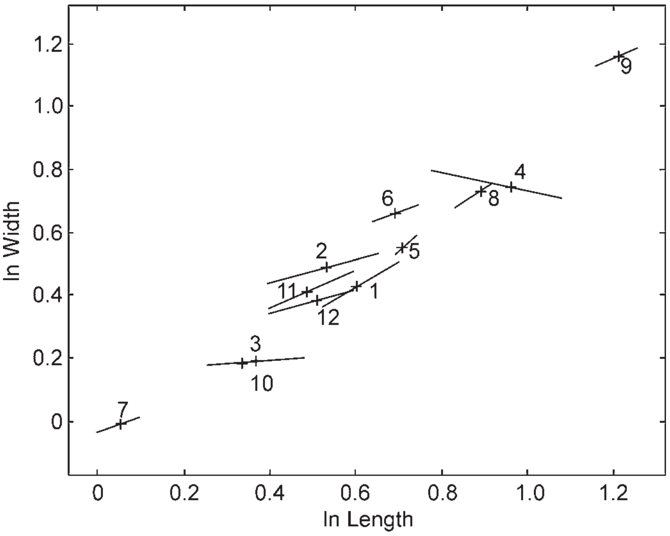

Figure 2. Regression lines and centroids for the M_1 molars of the 12 Fayum rodent species analysed (data from Holroyd 1994). 1 = *Acritophiomys adaios*, 2 = *Gaudeamus aegypticus*, 3 = *Phiomys andrewsi*, 4 = *Metaphiomys beadnelli*, 5 = *A. bowni*, 6 = *Gaudeamus hylaeus*, 7 = *Elwynomys lavocati*, 8 = *M. schaubi*, 9 = *Gharbalamys simonsi*, 10 = *P. stellae*, 11 = *P. troctatus*, 12 = *A. woodi*.

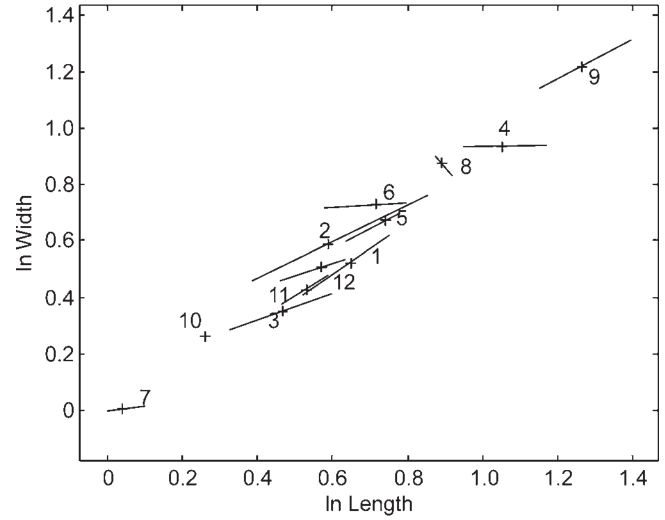

Figure 3. Regression lines and centroids for the M_2 molars of the 12 Fayum rodent species analysed (data from Holroyd 1994). 1 = *Acritophiomys adaios*, 2 = *Gaudeamus aegypticus*, 3 = *Phiomys andrewsi*, 4 = *Metaphiomys beadnelli*, 5 = *A. bowni*, 6 = *Gaudeamus hylaeus*, 7 = *Elwynomys lavocati*, 8 = *M. schaubi*, 9 = *Gharbalamys simonsi*, 10 = *P. stellae*, 11 = *P. troctatus*, 12 = *A. woodi*.

Table 2. Mean length and width ratios for each rodent species.

Species	M_1L/M_2L	M_1L/M_1W	M_2L/M_2W
Phiomys andrewsi	0.90	1.20	1.12
Phiomys stellae	1.08	1.17	1.00
Phiomys troctatus	0.94	1.08	1.11
Acritophiomys adaios	0.96	1.19	1.13
Acritophiomys bowni	0.94	1.17	1.07
Acritophiomys woodi	0.94	1.13	1.06
Metaphiomys beadnelli	0.93	1.25	1.13
*Metaphiomys schaubi**	0.99	1.18	1.02
Gharbalamys simonsi	0.94	1.06	1.05
Gaudeamus aegypticus	0.99	1.05	1.00
Gaudeamus hylaeus	0.98	1.05	0.99
Elwynomys lavocati	1.02	1.07	1.04

Raw data from Holroyd (1994), * = not recognized in Holroyd (1994).

(60%) are discriminated least accurately. While those specimens of *G. aegypticus* that are not identified correctly are assigned to a variety of taxa, those of *A. adaios* incorrectly identified are all assigned to other species of the same genus (*Acritophiomys*).

DISCUSSION

Species identification

Statistical results indicate significant differences in molar size (as defined by length) and shape (as defined by the relationship of length to width) for many of the species studied. Several species, particularly *Elwynomys lacovati* and *Gharbalamys simonsi,* clearly are discernible from the other rodent species on size alone, having no overlap in M_1 or M_2 length (Fig. 1). In general, molars associated with the largest and smallest taxa are discriminated most reliably, whereas those of more intermediate sized taxa overlap and are recognized less easily. Results of the MANOVA and DA, however, suggest that many of the Fayum rodents can be diagnosed reliably based on simple length and width measurements, particularly when both M_1 and M_2 are present. That many of the pairwise tests of length-to-width ratios for both molars were significant likewise suggests that molar shape is sufficient to diagnose several of the species tested. This consistency of particular sizes and shapes of molars within many of the taxa shows that molars showing high rates of occlusal wear may be identified at the species level based on general molar morphology. The ability to identify more specimens using size and shape will allow a more detailed description of the rodent fauna and ultimately a better understanding of the palaeoenvironment. Our preliminary results using only length and width variables suggest that the use of more variables to more finely define molar shape may allow a more confident assessment of species and better separation of those taxa that were not identifiable reliably in this analysis.

Variability

Size and shape variability within the rodent taxa of the Fayum is low. Length and width standard deviations are all less than one, with all species but *Gaudeamus hylaeus* with less than 0.3 (Table 1). Such limited variation is surprising in fossil species, as values under two standard deviations are suggested to be consistent with variation found in modern subspecies (Lande 1986). The low standard deviations, however, could be an artifact of

Table 3. Results of Fisher's *post hoc* pairwise tests for M_1 and M_2 length-to-width ratios.

	P. andrewsi	*P. stellae*	*P. troctatus*	*A. adaios*	*A. bowni*	*A. woodi*	*M. beadnelli*	*M. schaubi**	*G. simonsi*	*G. aegypticus*	*G. hylaeus*	*E. lavocati*
P. andrewsi		n	n	n	n	n	n	n	n	s	s	n
P. stellae	n		n	n	n	n	n	n	n	n	n	n
P. troctatus	s	n		n	n	n	n	n	n	s	s	n
A. adaios	n	n	s		n	n	n	n	s	s	s	s
A. bowni	n	n	n	n		n	n	n	n	n	n	n
A. woodi	n	n	n	s	n		n	n	n	n	n	n
M. beadnelli	n	n	s	n	n	s		n	n	s	s	n
*M. schaubi**	n	n	n	n	n	n	n		n	n	n	n
G. simonsi	s	n	n	s	n	n	s	n		n	n	n
G. aegypticus	s	n	n	s	n	s	s	s	n		n	n
G. hylaeus	s	n	n	s	n	s	s	s	n	n		n
E. lavocati	s	n	n	s	n	n	s	n	n	n	n	

Significant results are indicated by 's', and insignificant results by 'n'. Shaded rows are for tests on the ratios of the M_2, and unshaded rows are for tests on the ratios of the M_1. *See Table 2 for explanation.

discriminating molar measurements to the nearest 0.1 mm on such small specimens. That some true species may currently be categorized incorrectly into multiple species is also a possibility, although other morphological analyses suggest that this is unlikely (Holroyd 1994). Nevertheless, even if the actual variation were twice that indicated, the taxa studied here would be surprisingly homogeneous in terms of interspecific molar morphology. Low variability in these fossil rodent species may indicate that the samples represent short temporal durations.

Using molar length as proxy for size suggests that the rodent fauna was increasing in overall body size through time. The earlier species (those lowest in the stratigraphic sequence), represented by specimens from quarries L-41, A, B, and E, have an average combined length of the M_1 and M_2 of 3.35 mm. Those species from the more recent dating quarries of I, M, G, V, and P average 5.22 mm (36% larger). This difference, however, may be the result of differential preservation, as quarry L-41 often has superior preservation to any of the stratigraphically higher quarries. While small taxa are found in the younger quarries, only a few specimens represent the smallest species (such as *Phiocricetomys minutus* and specimens placed in the genus *Phiomys*). Given the relative rarity of small fossils in these more recent quarries, a preservation bias favoring larger taxa is likely. Increased size through time, however, is a common trait in many mammalian lineages (MacFadden 1986; Cope 1896) and also is found in the primate fauna from the Fayum.

Examining size change within particular lineages also supports a trend for increased size. *Phiomys andrewsi* is suggested as the ancestor of *M. schaubi*, with *M. schaubi* ancestral to *M. beadnellii* (Wood 1968). The *P. andrewsi*/*M. schaubi*/*M. beadnelli* lineage shows increasing size for both the M_1 and the M_2 through time (Table 1; Fig. 4). While the lack of absolute dates precludes a quantitative estimate of evolutionary rates, a qualitative examination, nevertheless, is possible. The rate of change appears rapid in the earlier stages of the lineage (Fig. 4). An apparently rapid rate of size increase occurs between *P. andrewsi* from localities B and E and its presumed descendent *M. beadnelli* (*sensu* Holroyd) from the quarries G and V (37% increase in combined M_1 and M_2 length). While the amount of sediment deposition between quarries G and V is similar to the amount of sediment deposition between quarries M and I, there is a much more modest increase in size between the *M. beadnelli* specimens from those quarries (11% increase in size). Quarries I and M are very nearly the same age, based on their close stratigraphic locations and similar faunas (Bown & Kraus 1988), and very little difference in size exists in the *M. beadnelli* specimens from them. A substantial thickness of sediment exists between quarries G and V and quarry I, however, and there could also have been a period of nondeposition suggesting that the slowing rate of change in the *P. andrewsi*/*M. schaubi*/*M. beadnelli* lineage is real. This overall pattern indicates that either a much greater amount of time separates quarries B and E from quarries G and V than separates quarries G and V from quarries M and I, or that the rate of size increase slows through time.

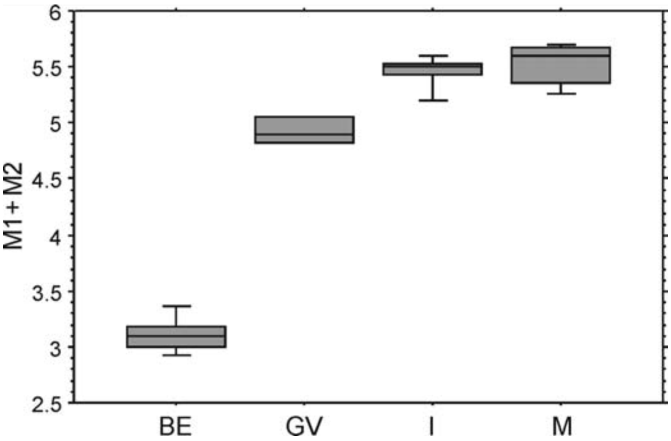

Figure 4. Cumulative lengths of M_1 and M_2 of *Phiomys andrewsi* from localities B and E, and *Metaphiomys beadnelli* (*sensu* Holroyd) from the sequentially dated quarries G, V, I, and M (data from Holroyd 1994).

The three species of *Acritophiomys* also are found at multiple quarries, with *A. woodi* and *A. bowni* found at quarry L-41 and *A. adaios* from the more recent quarries of A, B, and E. If *A. bowni* is viewed as the ancestor to *A. adaios,* a decrease in size is indicated. If *A. woodi* is viewed as the ancestor to *A. adaios,* an increase in size is indicated (Table 1). As the true relationships between these taxa are unclear, no trend in body size can be suggested. However, specimens of *A. adaios* from the lower quarries of A and B can be compared to *A. adaios* specimens from the stratigraphically higher quarry E. Unfortunately, 22 of the 27 *A. adaios* M_1 specimens are from quarry E, limiting the utility in examining changes in the lineage. A combined sample of quarry A and B specimens compared to specimens from quarry E finds no notable differences between the two groups in molar length, although the small sample size from quarries A and B likely affects this outcome.

Species diversity

Relative stability appears to exist in species diversity at the Fayum through time. The earlier quarries of L-41, A, B, and E contain four genera and seven different species. The more recent quarries of M, I, G, V, and P contain four genera and six species. While a preservation bias may exist that favors the older quarries, small and delicate species (such as the primate *Afrotarsius chatrathii* and the rodent *Phiocricetomys minutus*) have been recovered from these latter stratigraphically higher quarries. Sampling at these more recent quarries, however, has been carried out for roughly twice as long as on the older quarries. Also, it is likely that new species of rodents have been discovered at quarry L-41 since the last study of the rodent fauna in the early 1990s. But, given available data, the apparent stability in species diversity may indicate little change in the environment inhabited by these taxa. Normally, the introduction of new predators, removal or addition of new competitors, or dramatic changes in resources may be expected to have caused an increase or decrease in species diversity. As many of the earlier rodent taxa are arboreal (Holroyd 1994), they likely inhabited similar niches as did the primates from these quarries. Since the primates from more recent quarries are, on the whole, larger than those from older quarries, it might be anticipated that niche space would have been opened for rodents to occupy. It does not appear that new rodent species migrated in from Asia to fill postulated emptied niches, nor does it appear that a radiation of endemic rodents took place.

The apparent diversity of the rodent fauna may be influenced by taxonomic approaches, as many of the younger species were described long before and by different researchers than the new taxa from the stratigraphically lower quarries, particularly taxa from the single most productive of these quarries, L-41. Little disagreement exists, however, between the various researchers regarding taxonomy. An exception is Wood's (1968) belief that *Metaphiomys schaubi* from quarries G and V is a species separate from *M. beadnelli,* while Holroyd (1994) places both of them in *M. beadnelli.* Molar size and shape data, presented in this study, indicate substantial morphological differences between *M. schaubi* and *M. beadnelli* and support distinct species in accordance with Wood (1968). While the nature of the differences separating the taxa is primarily size (generally a poor character for separating taxa), the relationship between molar length and width variables also is different (Figs 2 & 3).

SUMMARY

This analysis revealed significant size and shape differences between molars of many of the Fayum rodent species. Statistical analyses indicated that the differences in overall M_1 and M_2 morphology allow accurate recognition of many of the different species, particularly when both molars are present. These differences in molar morphology should allow many mandibles with worn molars to be accurately identified, thereby allowing a more complete picture of the small mammal fauna. Overall increases in molar length through time for the rodent fauna suggests a trend toward increased body size, although little change in the overall diversity of species occurred. While little variation within taxa existed and homogeneity within genera was found, size and shape differences within the *Metaphiomys* genus supports the presence of two species.

This preliminary study was focused on molar dimensions, species diversity, and molar morphological trends of the rodent fauna of the Fayum examined throughout the stratigraphic sequence. These rodents were found to be a dynamic group, exhibiting distinct temporal trends in size and diversity. The results suggest that a more detailed study of the Fayum rodents, defining molar morphology and expanding the analysis to include incisors, may provide useful data in the future. More specimens should be diagnosable and thereby provide as accurate an estimate of relative species abundance as possible. As the relative abundance of rodent taxa associated with particular strata is better defined, biostratigraphic correlations will be possible. A comparison of the Fayum rodents with modern, closely related rodents may also help better understand the Fayum flora. Comparisons of the diet of modern rodents of similar size, having similar molar morphology, and exhibiting similar dental microwear patterns as the Fayum rodents, could provide proxy data for inferring plant types present in the Fayum. Such an analysis holds the potential to reveal changes in the environment and could tell us more about the evolutionary forces acting in the late Eocene and early Oligocene of north Africa. Such a study is relevant not only to the rodents but also to the many other taxa, including anthropoid primates, that are preserved in the deposits of the Fayum.

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Dental mesowear and the palaeodiets of bovids from Makapansgat Limeworks Cave, South Africa

Blaine W. Schubert

Center of Excellence in Paleontology and Department of Physics, Astronomy, and Geology, Box 70636, East Tennessee State University, Johnson City, TN 37614, U.S.A. E-mail: schubert@etsu.edu

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The palaeodiet of seven bovids from Makapansgat Limeworks Cave are analysed using dental mesowear. Results suggest that *Tragelaphus pricei* had a highly attritional diet and was thus a browser. *Tragelaphus* sp. aff. *T. angasii* and *Aepyceros* sp. were also browsers, having diets similar in texture to the extant mule deer (*Odocoileus hemionus*). *Gazella vanhoepeni* had an intermediate attrition-abrasion wear signal and groups most closely with extant mixed feeders. *Redunca darti* and *Makapania broomi* are at the abrasion end of the wear continuum and cluster with living grazers, such as the hippotragines and reduncines. *Parmularius braini* had a highly abrasive diet similar to extreme grazers like the American bison (*Bison bison*) and topi (*Damaliscus lunatus*). The bovid mesowear data were compared to previous palaeodietary studies using taxonomic uniformitarianism, ecomorphology (hypsodonty), and stable carbon isotopes on the same Makapansgat taxa. This comparison showed that the mesowear results are most closely in-line with the isotope data, both of which are non-genetic signals that reflect diet during an extended portion of an animal's life.

Keywords: Makapansgat, Plio-Pleistocene, bovids, mesowear, palaeodiets.

INTRODUCTION

Makapansgat Limeworks Cave is a well known Plio-Pleistocene site located northeast of Johannesburg, approximately 15–20 km east-northeast of the town of Mokopane in Limpopo Province, South Africa (24°12′S, 29°12′E). The vertebrate assemblage is extensive and includes a wide variety of taxa, ranging from sabre-toothed cats to chalicotheres and hominins (*Australopithecus africanus*) (Maguire *et al.* 1980; Reed 1996). Bovids are the most abundant large mammal from the site and have been studied by a number of researchers (e.g. Wells & Cooke 1956; Vrba 1987; Reed 1996; Sponheimer *et al.* 1999).

Palaeoenvironmental reconstructions of Makapansgat are numerous and vary widely (Rayner *et al.* 1993; Reed 1996; Sponheimer *et al.* 1999; McKee 1999). The driving force behind these palaeoecological reconstructions has been to better understand the ecology of *A. africanus.* Such environmental reconstructions have focused on Member 3, the main fossil-bearing unit of the deposit. Member 3 dates to about 2.5–3.2 Ma based on biostratigraphic (Harris & White 1979; Vrba 1982; Delson 1984) and palaeomagnetic evidence (Partridge *et al.* 2000; Herries 2003).

Bovids are often used as palaeoenvironmental indicators because they are common in Plio-Pleistocene sites and they can be divided into dietary groupings that are closely linked to habitat types. Browsers are those taxa that eat primarily dicots and typically occur in more densely vegetated habitats, grazers eat mostly monocot grasses and are generally associated with open habitats, and mixed feeders are a large group that vary their diets between graze and browse (Fortelius & Solounias 2000).

In this paper the palaeodiets of seven bovids from the Member 3 fauna are reconstructed using the attrition-abrasion wear gradient, also known as dental mesowear. These results are compared to previously published studies on the diets of these bovids using taxonomic uniformitarianism, ecomorphology (hypsodonty), and isotopic studies (Sponheimer *et al.* 1999), in an attempt to further evince the dietary classifications of these taxa. Schubert *et al.* (in press) compare the results of these data with dental microwear on the same Makapansgat bovids, further elucidate the strengths and weaknesses of the proxy measures, and discuss the palaeoenvironmental implications for Makapansgat.

METHODOLOGICAL BACKGROUND

Mesowear, described by Fortelius & Solounias (2000), is a relatively new technique for reconstructing the diet of ungulates. This method is based on the degree of facet development (cusp height and shape) on the buccal cutting edges of cheek teeth. Wear on teeth can be divided into two categories: attrition (tooth-on-tooth contact) and abrasion (food-on-tooth contact). The difference between a diet that is high in abrasives and one that is not correlates well with traditional dietary categories (Fortelius & Solounias 2000). For example, grazers eat mostly grasses that are composed of silica phytoliths which cause abrasion (McNaughton *et al.* 1985). This results in high percentages of rounded or blunt cusps. Browsers focus on foods that cause less abrasion, resulting in sharper cusps. Some relatively high cusps are found in all dietary categories, but a high percentage of low cusps is a diagnostic feature of extreme grazers (Fortelius & Solounias 2000).

Mesowear has been utilized extensively in ungulate palaeodietary studies (e.g. Franz-Odendaal 2002; Kaiser & Fortelius 2003; Franz-Odendaal & Kaiser 2003; Kaiser & Croiter 2004; Semprebon *et al.* 2004). The original mesowear method was based on the analysis of the upper second molar (M2) only (Fortelius & Solounias 2000). This method has now been extended to include other upper

Table 1. Mesowear and hypsodonty data for Makapansgat bovid taxa. Hypsodonty indices and categories are from Sponheimer *et al.* (1999) and are based on the technique of Janis (1988). Hyp-ind = hypsodonty index, Hyp = hypsodonty index categories, b = brachydont, m = mesodont, h = hypsodont. % high = percentage of high cusps, % l ow = percentage of low cusps, % sharp = percentage of sharp cusps, % round = percentage of round cusps, % blunt = percentage of blunt cusps.

Taxon	*n*	% high	% low	% sharp	% round	% blunt	Hyp-ind	Hyp
Tragelaphus pricei	13	1.000	0.000	0.846	0.154	0.000	2.50	b
Tragelaphus sp. aff. *T. angasii*	8	1.000	0.000	0.625	0.375	0.000	2.11	b
Aepyceros sp.	8	1.000	0.000	0.625	0.375	0.000	3.59	h
Gazella vanhoepeni	27	1.000	0.000	0.480	0.520	0.000	3.16	m
Makapania broomi	23	0.739	0.261	0.000	0.957	0.043	3.42	m
Redunca darti	23	0.727	0.273	0.000	0.864	0.182	2.93	m
Parmularius braini	5	0.000	1.000	0.000	0.600	0.400	5.11	h

tooth positions in equids (Kaiser & Solounias 2003).

Kaiser & Fortelius (2003) explored differential mesowear in upper and lower equid molars and found a shift in the mesowear towards the grazing end of the spectrum in lowers. To adjust for this, they introduced a calibration factor that allowed comparable mesowear results between upper and lower teeth (Kaiser & Fortelius 2003). Unfortunately, extension of the original method to other teeth in non-equid groups has met with little success (Fortelius & Solounias 2000; Franz-Odendaal & Kaiser 2003). Franz-Odendaal & Kaiser (2003) tested other teeth in ruminants and found that while upper M3s gave the same mesowear signature as upper M2s, lower cheek teeth score significantly different than uppers.

Fortelius & Solounias (2000) compare mesowear to morphology and microwear. They note that morphology (e.g. hypsodonty) is genetic, reflecting deep time and long-term adaptation. Dental microwear is at the other extreme, recording only the last few meals of an animal (Teaford & Oyen 1989). Like microwear, mesowear is a non-genetic signal that reflects the cumulative diet of an animal during its life. The difference is it records diet over an extended period of the animal's lifetime, and thus falls between microwear, which provides a dietary snapshot, and ecomorphology, which reflects adaptation and phylogeny over deep time (Fortelius & Solounias 2000).

MATERIALS AND METHODS

One hundred and seven maxillary bovid teeth from Makapansgat Member 3 were included in the analysis (Appendix I). All utilized specimens are housed at the University of Witwatersrand, Johannesburg, South Africa.

Methods follow Fortelius & Solounias (2000) and Fortelius (pers. comm., 2004). In sum, two variables are scored in mesowear analysis: cusp relief (high or low) and cusp shape (sharp, round, or blunt). The sharper of the two cusps, either the paracone or mesocone is used. Cusps are considered 1) sharp if they come to a distinct point at the apex where mesial and distal facets meet (Fig. 1A–C), round if the cusp is rounded between the mesial and distal facets (Fig. 1D–F), and 3) blunt when this area is flattened and lacks distinct facets. Cusp relief is based on the height of cusps relative to the valley between them. A relief index was calculated for specimens where this was not clear. For this index, the vertical distance between a line connecting the cusp tips and the shallowest point between them is measured and divided by the length of the tooth. Those with a value at or above 0.1 are considered to be high while those below are considered to be low (Fortelius & Solounias 2000). Note, in the original description of the method, Fortelius & Solounias (2000) make an erroneous statement when describing occlusal relief as the 'vertical distance between a line connecting two adjacent cusp tips and two adjacent valley bottoms'(Fortelius, pers. comm., 2004). It should also be noted that some of the figures in this paper are incorrect (e.g. Fortelius & Solounias 2000, fig. 20A,B,G). Thus, while general methodological directions in the text are reliable, some of the figures are not.

Individual Makapansgat bovid teeth were scored for both variables with a ×10 hand lens. Following Franz-Odendaal & Kaiser (2003), both upper M2s and M3s were used. Only teeth with the entire occlusal surface in-wear were included. Excessively worn teeth were not used in the analysis (Fortelius & Solounias 2000).

The mesowear of nineteen extant ruminant artiodactyls (bovids, giraffids and cervids) were used for comparison in this study. The mesowear results for this baseline are from Fortelius & Solounias (2000, table 1). These taxa were chosen because they were considered to be 'typical' feeders within conservative dietary categories (Fortelius & Solounias 2000, table 1).

Percentages of each category were tabulated and hierarchical cluster analyses were used to group taxa into dietary categories based on mesowear variables, $\delta^{13}C$ values and hypsodonty. These cluster analyses were run using complete linkage (furthest neighbors) and Euclidean distance in SYSTAT 7.0. Complete linkage was used to enhance the distinctness of clusters (following Fortelius & Solounias 2000).

MESOWEAR RESULTS

The mesowear results are summarized in Table 1 and Figs 2 and 3. These data show clear differences in the types of wear on the bovid teeth, separating them into two broad groups. *Tragelaphus pricei*, *T.* sp. aff. *T. angasii*, *Aepyceros* sp. and *Gazella vanhoepeni* have high percentages of sharp cusps and 100% high cusps, while *Makapania broomi, Redunca darti* and *Parmularius braini* lack sharp cusps and have at least some low cusps.

Hierarchical cluster analysis of mesowear data from the 19 extant ruminant artiodactyls (from Fortelius & Solounias 2000) separated the taxa into distinct dietary categories, with attrition dominated browsers like the

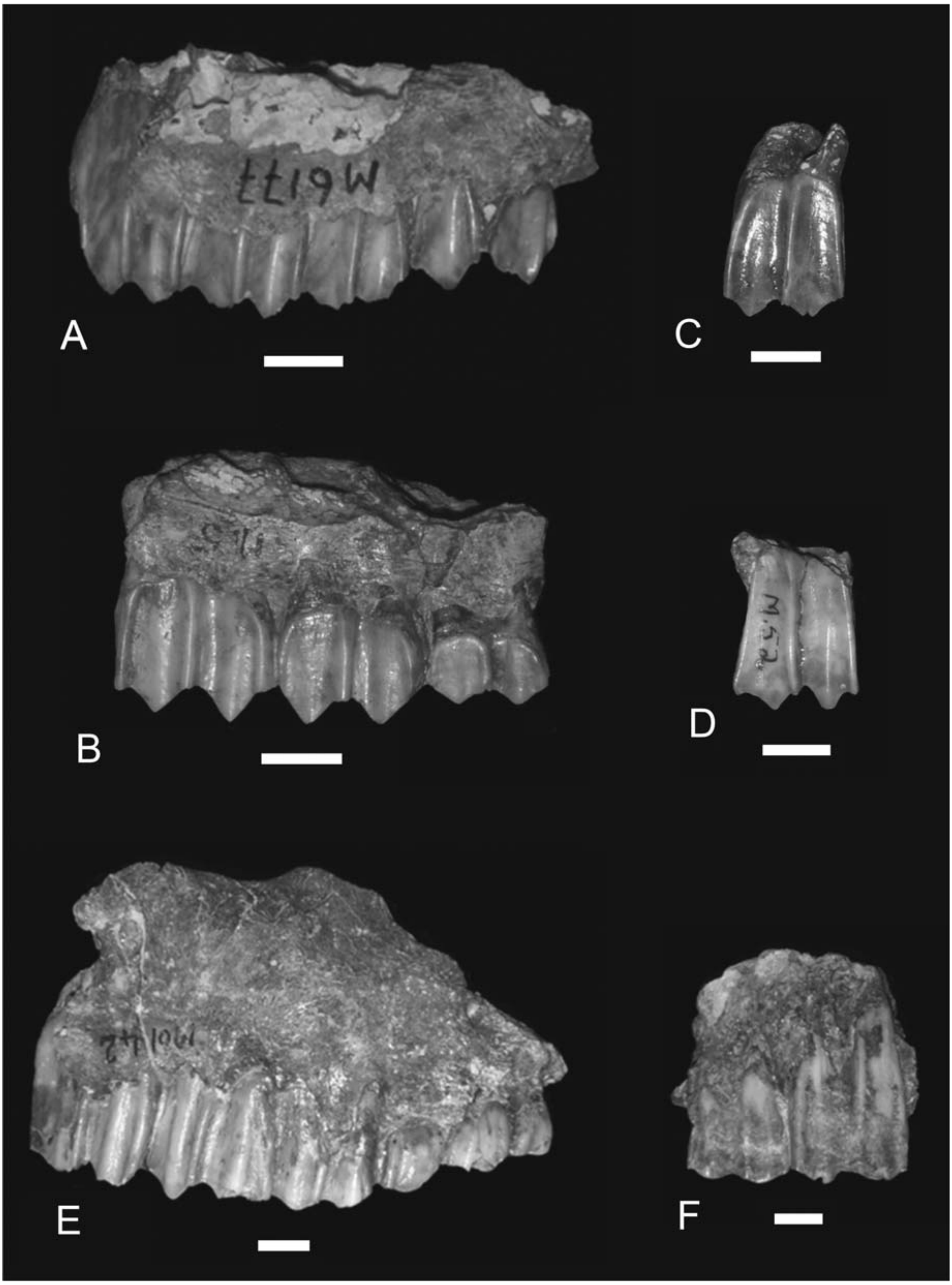

Figure 1. Examples of Makapansgat specimens used in the mesowear analysis. **A**, *Tragelaphus pricei* right P3–M3 (M6177); **B**, *Tragelaphus* sp. aff. *T. angasii* right M1–M3 (M5); **C**, *Aepyceros* sp. left M2 (M7502); **D**, *Gazella vanhoepeni* right M2 (M52); **E**, *Makapania broomi* right P2–M3 (M6142); **F**, *Parmularius braini* left M1–M2 (M6171).

moose (*Alces alces*) at one end of the spectrum, and extreme grazers such as the American bison (*Bison bison*) at the other (Fig. 4). This cluster analysis separates the taxa into four primary groups.

The first group is attrition dominated and contains one Makapansgat bovid, *Tragelaphus pricei*. This species groups most closely with two extreme browsers, the giraffid *Okapia johnstoni* and the cervid *Odocoileus virginiana.*

The second group divides into three subgroups, ranging from browsers to mixed feeders. Two Makapansgat taxa, *Tragelaphus* sp. aff. *T. angasii* and *Aepyceros* sp. cluster with the browsing mule deer (*Odocoileus hemionus*). The other two subgroups are composed of extant mixed feeders. The

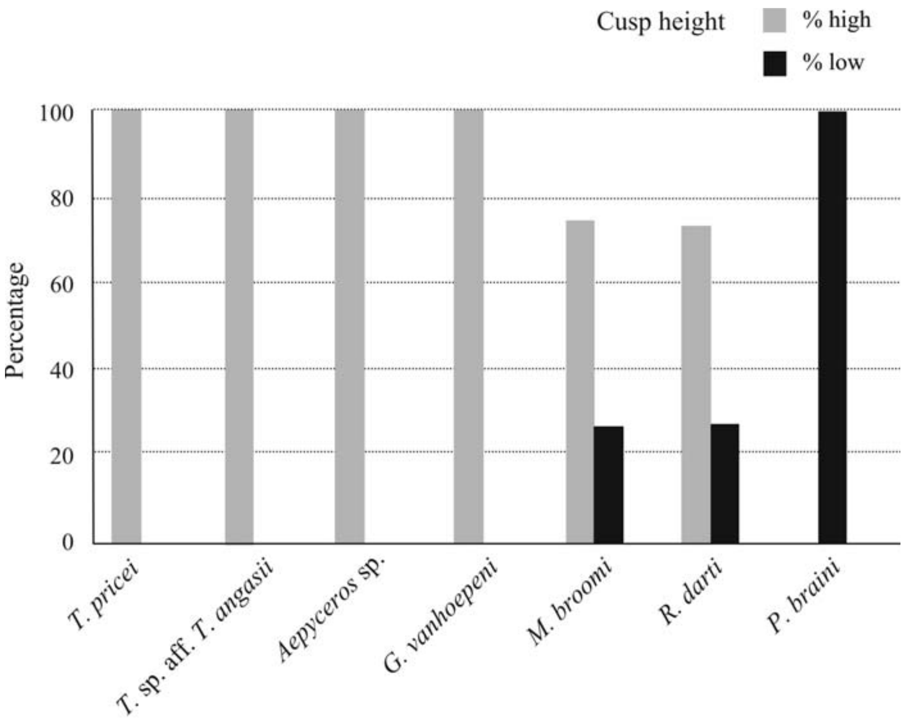

Figure 2. Histogram of mesowear variables % high cusps and % low cusps for the Makapansgat bovids.

Makapansgat gazelle, *Gazella vanhoepeni* has higher and rounder cusps than its congeners *G. thomsoni* and *G. granti,* both of which are mixed feeders. This species (*G. vanhoepeni*) groups most closely with the attrition/abrasion levels of *Taurotragus oryx* and *Tragelaphus scriptus.* While *T. oryx* is considered to be a mixed feeder, there is disagreement over whether or not *T. scriptus* is a browser (Gagnon & Chew 2000) or a seasonal-regional mixed feeder (Fortelius & Solounias 2000; Solounias & Semprebon 2002; Merceron *et al.* 2004). Here the latter interpretation is followed because the species is known for eating tender young grasses when available (Estes 1991) and microwear evidence clearly suggests browsing and grazing populations (Merceron *et al.* 2004).

The third group is composed of three extant grazers, one hypotragine (*Hippotragus niger*) and two reduncines (*Redunca redunca* and *Kobus ellipsiprymnus*). Two Makapansgat taxa are in this cluster, *Makapania broomi* and *Redunca darti. Redunca darti* has lower cusps than the compared extant members of its tribe. In terms of abrasion, the

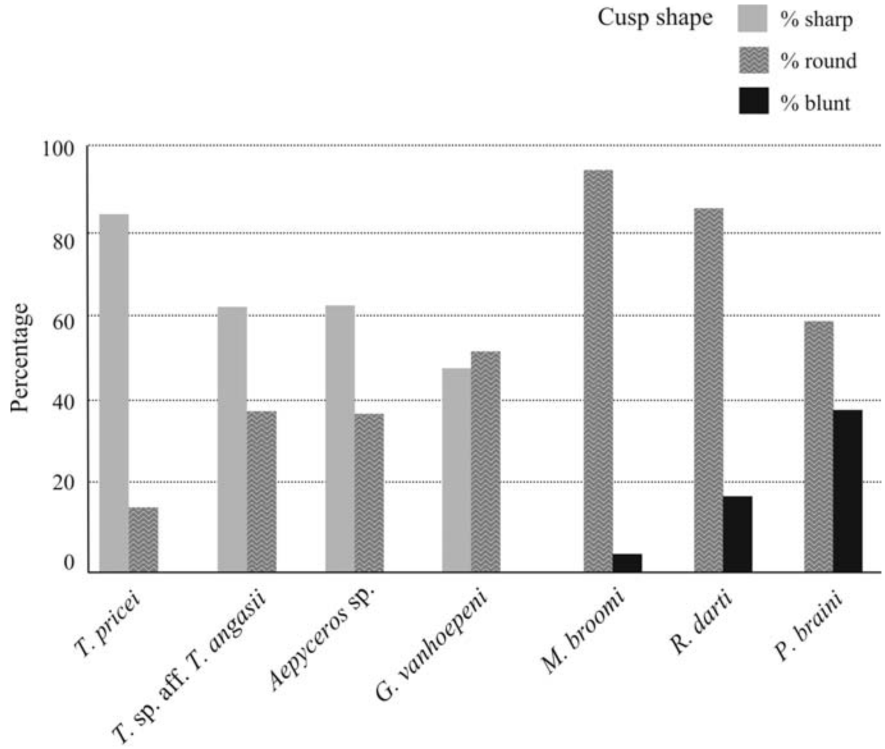

Figure 3. Histogram of mesowear variables % sharp cusps, % round cusps and % blunt cusps for the Makapansgat bovids.

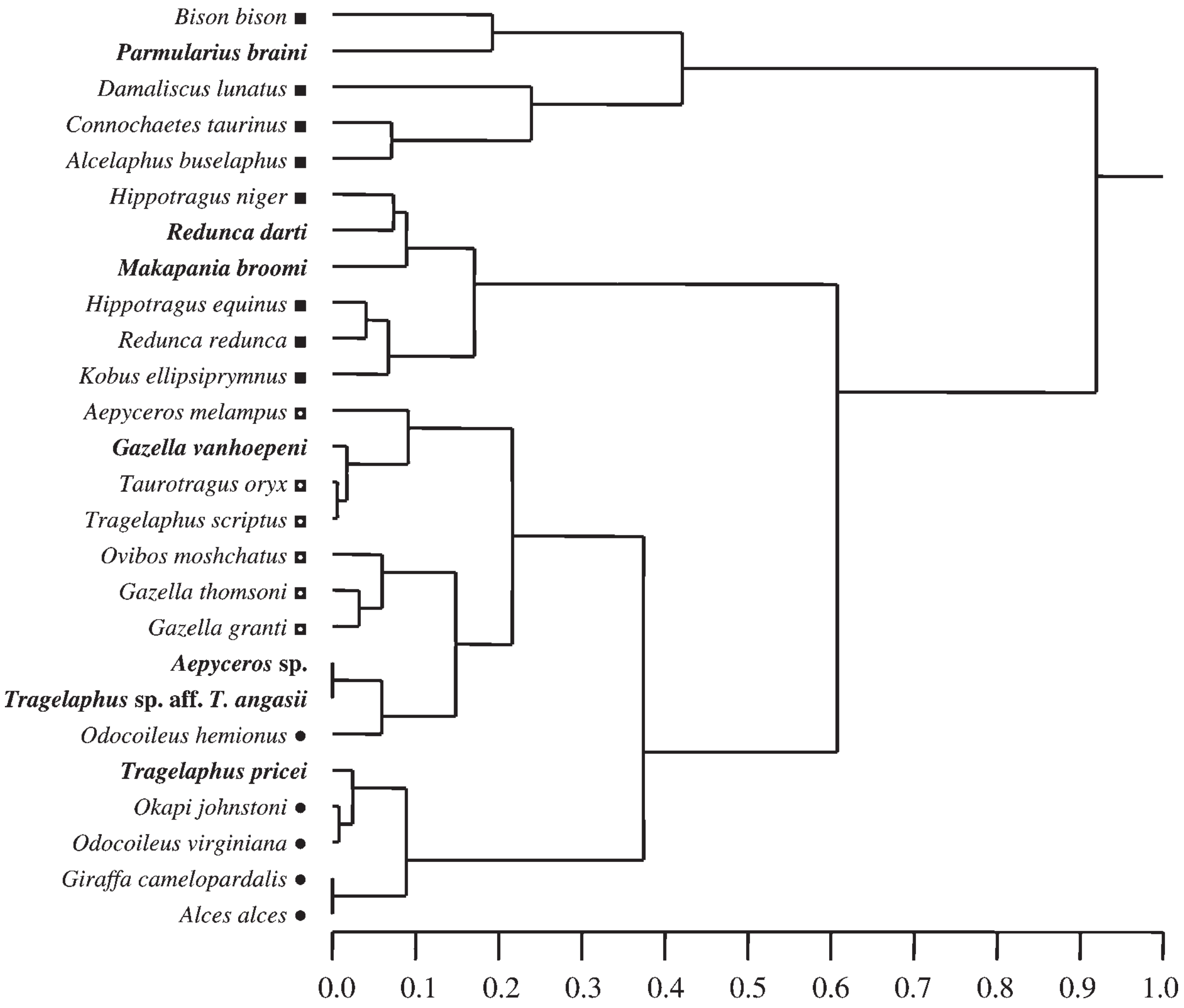

Figure 4. Hierarchical cluster diagram of % high, % sharp and % blunt cusps. Clusters are based on the mesowear data for nineteen 'typical' extant ruminant artiodactyls (from Fortelius & Solounias 2000) and the seven Makapansgat taxa. The extant grazers are represented by solid squares, mixed feeders by circles in squares, and browsers by solid circles. The Makapansgat bovids are in bold. The scale is Euclidean distance (root-mean-squared difference).

Makapansgat *R. darti* seems to be more closely aligned with hippotragines than to the extant reduncines.

The final primary grouping contains those taxa with highly abrasive diets and includes one Makapansgat species, the alcelaphine *Parmularius braini.* This taxon has abrasion features most similar to *Bison bison* and extant members of the alcelaphine tribe (*Connochaetes taurinus, Damaliscus lunatus, Alcelaphus buselaphus*), all of which are relatively pure grazers (Kingdon 1997).

DISCUSSION OF MESOWEAR RESULTS

Mesowear results suggest that the Makapansgat bovids ranged from browsers to extreme grazers. *Tragelaphus pricei* had the most attritional diet and probably did more browsing than the other taxa. *Tragelaphus* sp. aff. *T. angasii* and *Aepyceros* sp. group most closely with each other and an extant browser and are considered to have had a similar diet. Extant tragelaphines range in diet from mixed feeders to browsers (Kingdon 1997; Fortelius & Solounias 2000), while the only living member of the genus *Aepyceros* (*A. melampus*) is a mixed feeder. Thus, the Makapansgat *Aepyceros* sp. had a more attritional diet than its extant relative. *Gazella vanhoepeni* had intermediate attrition-abrasion levels, and based on mesowear alone, is considered to be a mixed feeder like extant members of the genus.

Makapania broomi and *R. darti* nested within a group of grazing taxa in the multivariable cluster analysis (Fig. 4). *Makapania broomi* is an ovibovine and its closest living relatives are mixed feeders. Fortelius & Solounias (2000) note that the reduncines, unlike other grazers, have a low percentage of blunt cusps and a high percentage of rounded cusps and they attribute this to fresh grass grazing. However, hippotragines also have similar mesowear variables and are not fresh grass grazers. Further, *R. darti* groups more closely to the hippotragines in terms of abrasion than to the extant reduncines. Based on mesowear, *R. darti* is certainly considered to have been a grazer, but not necessarily a specialized fresh grass grazer. The mesowear of *Parmularius braini* indicates it was an extreme grazer like living members of its tribe, the alcelaphines.

COMPARISONS

Hypsodonty

The crown height of teeth has been used extensively as a dietary signal and is best understood in terms of a measurement called the hypsodonty index (Janis 1988).

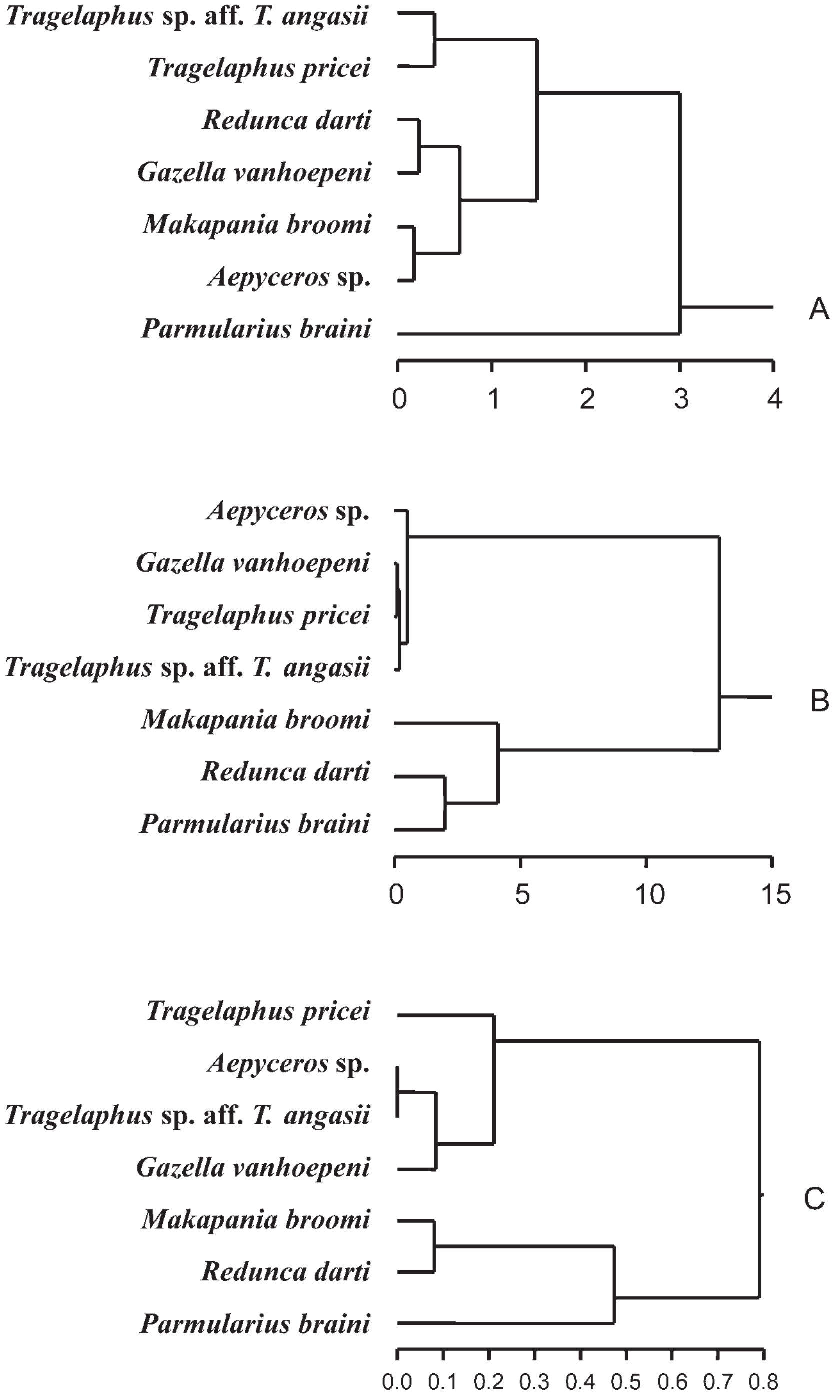

Figure 5. Hierarchical cluster diagrams based on (**A**) hypsodonty indexes [data from Fortelius & Solounias (2000) and Sponheimer *et al.* (1999)], (**B**) δ^{13}C values from Sponheimer *et al.* (1999) and (**C**) mesowear variables % high, % sharp and % blunt cusps for the Makapansgat bovids. The scales are Euclidean distance (root-mean-squared difference).

This index is calculated by dividing the width of an unworn third lower molar by its length. For ruminant artiodactyls, high-crowned or hypsodont teeth are generally those of grazers and usually have indices of 3.5 or higher, mesodont teeth typically belong to mixed feeders and have indices between 2.6 and 3.4, and brachydont teeth are generally those of browsers, with an index of 2.5 or lower (Janis 1988).

This method is often considered to be one of the best morphological predictors of diet in ungulates (Janis 1988; Fortelius & Solounias 2000), and it is the only ecomorphological character that is readily available for all taxa used in this comparative analysis. Fortelius & Solounias (2000) made comparisons between hypsodonty and mesowear variables and found that hypsodonty was the best single variable for correctly calculating the diet of all 64 of their extant taxa (65% correct). When only including the conservative typical taxa, 81% of these were correctly classified (Fortelius & Solounias 2000, table 3).

Makapansgat hypsodonty indices from Sponheimer *et al.* (1999) are shown in Table 1. A hierarchical cluster analysis of these data divides the bovids into four groups, with distinct separation between the hypsodont *Parmularius braini* and brachydont *Tragelaphus* species (Fig. 5). *Redunca darti* and *Gazella vanhoepeni,* which fall in the mesodont category, group together in the middle while

Makapania broomi (considered to be mesodont) and *Aepyceros* sp. (hypsodont) cluster towards the hypsodont end of the spectrum.

Stable carbon isotopes

This method is based on the fact that C_4 plants (grasses and sedges) accumulate more of the heavier ^{13}C isotope during fixation of CO_2 than do C_3 plants (e.g. trees, shrubs and bushes). Consequently, C_4 consumers have a higher level of $\delta^{13}C$ in their teeth and bones than do C_3 feeders. Mixed feeders that incorporate various amounts of C_3 and C_4 vegetation vary greatly in their $\delta^{13}C$ values but typically fall between the browser and grazer ranges (Lee-Thorp *et al.* 1989; Sponheimer *et al.* 1999). While isotope analysis is certainly a powerful tool for determining whether or not an animal was a C_4 grazer, C_3 consumer, or something in between, it provides limited dietary discrimination. It does not, for example, distinguish whether or not an animal with a C_3 diet was a C_3 browser or C_3 grazer.

The $\delta^{13}C$ values for the Makapansgat bovids (from Sponheimer *et al.* 1999) divide into two major groups (Fig. 5B). The C_3 consumers (*Aepyceros* sp., *Gazella vanhoepeni* and the *Tragelaphus* species) cluster together tightly, while the second major group is divided into C_4 consumers (*Redunca darti* and *Parmularius braini*) and a mixed C_4/C_3 consumer (*Makapania broomi*) that falls towards the C_4 end of the spectrum. Based on these values, *Aepyceros* sp., *Gazella vanhoepeni* and the *Tragelaphus* species are considered to be browsers, *Redunca darti* and *Parmularius braini* are grazers, and *Makapania broomi* is labelled as a mixed feeder preferring grass (Sponheimer *et al.* 1999).

Comparative summary

Hypsodonty is an ecomorphological character that reflects long-term adaptation, and does not necessarily indicate the diet of a given animal or population. The discrepancies between the morphological data (Fig. 5A) and the non-genetic data (stable carbon isotopes and mesowear) suggest that hypsodonty (at least in this case) is a poor indicator of actual diet. In contrast, the non-genetic results produce hierarchical clusters that are very similar and divide the taxa into two primary groups (Fig. 5B ,C). A close association between these non-genetic methods was expected since both measure diet over an extended period of an animal's life.

Using these two non-genetic methods in tandem results in more accurate reconstructions of dietary behavior. As noted above, an animal with a C_3 diet could either be a C_3 browser or a C_3 grazer. However, *Tragelaphus pricei, T.* sp. aff. *T. angasii* and *Aepyceros* sp. from Makapansgat had C_3 diets that were highly attritional (based on mesowear) and therefore they were browsers and not C_3 grazers. Similarly, *Parmularius braini* and *Redunca darti* had primarily C_4 diets and this is reflected in the amount of abrasion on their teeth. These species were most likely grazers. *Makapania broomi* was placed in a grass-dominated mixed feeder category based on stable carbon isotopes (Sponheimer *et al.* 1999) but mesowear (Fig. 4) groups the taxon most closely with grazers. This discrepancy is minor though because the isotope data (Sponheimer *et al.* 1999) comes very close to placing this species in a grazing category. The only large outlier is *Gazella vanhoepeni,* which is nested with extant mixed feeders in the multivariable mesowear cluster analysis (Fig. 4), however, its carbon isotope signal indicates it was primarily a C_3 consumer. One possible explanation for this is that *G. vanhoepeni* included C_3 grass in its diet. This inclusion would have increased abrasion while at the same time raising $\delta^{13}C$ values in the bones and teeth. A combined mesowear/isotope investigation of extant taxa that eat C_3 grasses may help answer this question and provide a means for distinguishing C_3 grass consumption in the fossil record.

CONCLUSION

Mesowear analysis was conducted on seven bovids from Makapansgat Limeworks Cave, Limpopo Province, South Africa. A hierarchical cluster analysis that included the mesowear data of the Makapansgat bovids and a baseline of extant artiodactyls divided the taxa into browsing, mixed feeding and grazing categories.

Comparison of the mesowear results with other dietary proxy measures indicates a poor relationship between the dietary predictions of this method and that of taxonomic uniformitarianism and hypsodonty. This is not surprising since these genetic signals of diet reflect long term adaptations while mesowear, a non-genetic signal, is a measure of diet during an extended period of an animal's life. The stable carbon isotope results, another non-genetic signal, divided the Makapansgat taxa into nearly identical dietary categories. Combination of these measures results in more accurate dietary assessments because these two non-genetic signals provide information about different aspects of diet. In this case the following can be concluded about the Makapansgat bovids: *Parmularius braini* was an extreme grazer with a highly abrasive C_4 diet, *Redunca darti* had an abrasive C_4 diet and was a grazer, *Makapania broomi* was a grazer or mixed feeder with an abrasive diet, *Tragelaphus pricei, T.* sp. aff. *T. angasii* and *Aepyceros* sp. had attritional C_3 diets and were browsers, and *Gazella vanhoepeni* had an enigmatic C_3 diet that was somewhat abrasive.

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APPENDIX 1

Dental specimens used in this study. L = left, R = right, M2 = second upper molar, M3 = third upper molar.

Makapania broomi: M7776 LM2, M8873 LM2, M8609 RM2, M7674 LM3, M8520 RM2, M971 RM3, M7681 RM3, M7764 LM2, M7655 RM3, M8490 LM2, M7668 RM3, M7765 RM2, M8425 RM2, M7680 LM3, M7117 LM3, M6142 RM2, M7654 RM2, M2940 RM2, M8347 RM2, M7675 LM2, M8827 LM3, M974 LM3, M30 RM2.

Redunca darti: M8838 RM2, M6060 RM2, M881 RM2, M6097 RM2, M6079 LM2, M808 RM3, M812 RM2, M6043 LM2, M6059 LM2, M822 RM3, M852 RM3, M7242 RM2, M7250 RM2, M7246 RM2, M6974 RM2, M7169 RM2, M7260 RM2, M7591 RM2, M8483 LM2, M8601 LM2, M7153 LM2, M8177 RM3, M1329 LM2.

Tragelaphus pricei: M6177 RM2, M609 RM2, M7489 LM2, M1694 LM2, M662 RM2, M1678 LM2, M1373 LM3, M7488 LM3, M7797 LM3, M7736 LM3, M7461 LM3, M7388 RM3, M1611 RM3.

Tragelaphus sp. aff. *T. angasi*: M6187 LM3, M195 RM3, M7780 LM3, M7597 RM3, M7716 LM3, M7141 LM3, M5 RM2, M6175 RM2.

Parmularius braini: M8351 RM2, M774 RM3, M6171 LM2, M1061 LM2, M2943 RM2.

Gazella vanhoepeni: M600 LM2, M612 RM2, M613 RM2, M611 RM2, M602 LM2, M615 RM2, M2955 RM2, M7261 RM2, M7615 RM2, M7598 RM2, M8549 RM2, M7369 RM2, M7370 RM2, M7614 RM2, M55 RM2, M7140 RM2, M7577 RM2, M657 RM2, M7144 RM2, M52 RM2, M7605 RM2, M7604 RM2, M51 LM2, M7477 LM2, M1622 LM2, M7506 LM2, M7735 LM2.

Aepyceros sp.: M7088 LM2, M7502 LM2, M7733 LM2, M8652 RM2, M7758 RM2, M763 RM3, M44 LM3, M1643 LM3.

Hipparion pomeli sp. nov from the late Pliocene of Ahl al Oughlam, Morocco, and a revision of the relationships of Pliocene and Pleistocene African hipparions

Vera Eisenmann[1*] **& Denis Geraads**[2]

[1]UMR 5143 du CNRS, Paléobiodiversité et Paléoenvironnements, Département Histoire de la Terre, CP 38,
8 rue Buffon, 75005 Paris. E-mail: vera@mnhn.fr
[2]UPR 2147 du CNRS, 44 rue de l'Amiral Mouchez, 75014 PARIS, France. E-mail: dgeraads@ivry.cnrs.fr

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This paper addresses three points: 1) the description of a new species (*H. pomeli* sp. nov.) of Late Pliocene hipparion from Morocco; 2) preliminary notes on hipparion skulls from Langebaanweg E Quarry (*H. hendeyi* sp. nov.) and Chad Kossoum Bougoudi; 3) a new interpretation of African hipparion relationships. The Appendix presents practical techniques allowing the estimation of adult dimensions in juvenile skulls and correlations between two mandibular and skull dimensions. *H. pomeli* was a medium-sized species related to, but smaller than, *H. hasumense* from East Africa. The distance vomer–basion was small and there was no reduction of the third incisors. The lower cheek teeth were caballine, moderately hypsodont, with moderate ectostylids. The limb proportions were cursorial. *H. pomeli* differed from the true *'Eurygnathohippus'* (*H. afarense* and *H. cornelianum*) by the basi-cranial proportions and the lack of reduction of the third incisors. *H. hendeyi* had an extremely short vomer–basion distance, a short distance between the orbit and the POF, primitive teeth, and slender limb bones. It cannot be derived from *H. africanum* or from *H. turkanense.* The greatest resemblances are with (the much smaller) *H. moldavicum* of Taraklia and *H. giganteum* of Grebeniki. The tentative reconstruction of *H. feibeli*'s skull indicates a possible relationship with *H. hendeyi.* The very large skull from Kossoum Bougoudi, Chad, resembles, but is much larger than, the Chinese *H. dermatorhinum*; its dimensions are compatible with the European *H. crassum* and the Mongolian *H. tchicoicum.* It is proposed that more than two migrations gave rise to the various African species of hipparions.

Keywords: Equidae, Mammalia, Hipparion, phylogeny, Africa, Morocco.

INTRODUCTION

Pliocene and Pleistocene hipparions are relatively well documented in East Africa, but till now they were very poorly known in the Maghreb. The late Pliocene hipparion of Ahl al Oughlam is the first represented by skull, teeth and limb bones.

Ahl al Oughlam is a karst and fissure filling near Casablanca that has yielded a very rich fauna of micro- and macromammals (Raynal *et al.* 1990, 2001; Geraads 1993, 1995, 1996, 1997, 2002, 2004a,b, 2006; Alemseged & Geraads 1998; Geraads & Amani 1998; Geraads *et al.* 1998; Geraads & Metz-Muller 1999) together with some fishes, reptiles (Bailon 2000) and many birds (Mourer-Chauviré & Geraads, in press). The sediments are not stratified, and the faunal sample is homogeneous, showing that the filling of the fissures was virtually instantaneous. Biochronological comparisons with East Africa suggest an age of *c.* 2.5 Ma, thus roughly contemporaneous with Omo Shungura Member D, or the gap in the Koobi Fora succession.

SYSTEMATIC PALAEONTOLOGY

Family Equidae Gray, 1821
Genus *Hipparion* De Christol, 1832

***Hipparion pomeli* sp. nov.**, Figs 1, 8, 23

Holotype. AaO-3647, skull, virtually complete but transversely crushed.

Type locality. Ahl al Oughlam, Casablanca, Morocco. About 2.5 Ma.

Diagnosis. A Hipparion of medium size; basion to vomer distance short; muzzle moderately long and wide; faint POF 50 mm in front of the orbit. Incisor arcade rounded. Cheek teeth large, moderately hypsodont; lower cheek teeth caballoid, with moderate ectostylid but sometimes an accessory one.

Etymology. In acknowledgement of Auguste Pomel's prominent contributions to the palaeomammalogy of North Africa.

Description

Skull. AaO-3647 (Fig. 1A) is the skull of an adult male (canines 12 mm long; all teeth erupted but not very worn). It is entire but distorted by lateral crushing. Most of the interesting featured can nevertheless be noted. The size is medium, the basion to vomer distance is short, the muzzle moderately long and wide. There is a faint POF 50 mm in front of the orbit. Comparisons are made with other hipparion skulls by ratio diagrams, taking the average *H. dietrichi* skull from Samos as reference; the corresponding data are given in Table 1. Some of the dimensions used in the ratio diagrams represent the supposed adult state, estimated from juvenile skulls (KNM ER 3539, Olduvai BK II-283). Some muzzle dimensions were also estimated from mandibles (AL 177-21, KNM ER 1626, Omo C, COR 679). Data and explanations are given in the Appendix.

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*Author for correspondence.

Figures 2 and 3 are ratio diagrams comparing the Moroccan skull to other hipparions. In Africa, AaO-3647, although smaller, resembles AL-340-8 from the Denen Dora member of the Hadar Formation (Eisenmann 1976, plate 1). Bernor & Armour-Chelu (1997) referred the latter to *H. hasumense* (described on lower cheek teeth from locality 204, Tulu Bor member, East Turkana, Eisenmann 1983) and noted similarities with WW-1528-92 of Wembere Manonga. WW 1528-92, appears to have a longer muzzle but is otherwise quite similar. Other specimens that present some resemblances were found in the Denen Dora and Kada Hadar members of Hadar, and possibly in Member C of Shungura Formation. BKII-2845/6 of Olduvai, unfortunately distorted, seems also rather similar.

The next ratio diagrams (Figs 4 & 5) illustrate the pattern of a second group of late African hipparions. The main difference is in the shape and position of the posterior border of the vomer relatively to the basion and the posterior border of palate (measurements nos. 4 and 3). The vomer–basion distance is much longer. As far as we know, such 'hypercaballine' proportions are unique. Moreover, in the adult type skull (AL 363-18) of *H. afarense* from Hadar KH and in the juvenile skull KNM ER-3539, the vomer has an acute V-shaped posterior border and an acute median ridge (Eisenmann 1976, plates 2 & 3). In probable correlation with the long vomer–basion distance, the Postorbital line (no. 24) looks longer relative to the Anteorbital line (no. 23). In addition, the muzzle width (no. 15) is very large when compared to the cheek teeth and muzzle lengths (nos. 9 & 1), reminding of *H. dietrichi* of Samos.

Scatter diagrams (Figs 6 & 7) illustrate the differences between the two groups. The corresponding data (including those that were not plotted) are given in Table 2.

Thus, in a very schematic way, at least two groups of skulls may be distinguished:

1. *H. hasumense* group: *H. hasumense* (Hadar AL 340-8 and Wembere Manonga WW 1528/92) and *H. pomeli* (AaO-3647 and Olduvai BK II-2845/6). The muzzle is long and narrow; the basion to vomer distance is short; the cheek teeth are relatively large. We refer to *H. hasumense* the Hadar skulls and skull fragments AL 116-115, AL 155-6, AL 164-3, AL 241-18, possibly AL 142-18, and the mandibles AL 177-21 [the latter was first referred to *H. afarense* by Eisenmann, but we presently agree with Bernor & Armour-Chelu (1999a) that it belongs to the *H. hasumense* group]; Omo 18-1968-363 and Omo 18-1969-90. Thus the group is documented, besides Ahl al Oughlam, in the Hadar Formation, SH2, DD, and KH 1–2 members; Wembere-Manonga Valley, Kilolei member; Shungura Formation member C; Olduvai BK II.
2. *H. afarense* group: *H. afarense* (Hadar AL 363-18, and probably AL 164-3) and *H. cornelianum* (East Turkana KNM ER-3539). The vomer has an acute V-shaped posterior border and an acute median ridge; the basion to vomer distance is long; the muzzle is short and wide; the cheek teeth are relatively small. These two species differ mostly by the degree of reduction of the third incisors. We refer to *H. cornelianum* the skull fragments Olduvai BK II-264, BK II-283, BK II-067/5465, and the mandibles or fragments of mandibles Hadar AL 59-9, East Turkana KNM ER-1626; Omo 118-1972-5; Olduvai no no. (Leakey 1965, plate 20), Olduvai 067/5344, Olduvai 1955-293; Cornelia Cor 679. This group is documented in the Hadar Formation, KH 2-3 member; East Turkana Formation, Burgi member; Shungura Formation, member F; Olduvai Bed II; Cornelia.

None of these skulls has a real POF, but some of them exhibit a more or less marked depression a few centimetres in front of the orbit. It may be clearly seen on the Olduvai skull illustrated by Hooijer (1975, plate 7-1) and on AL 241-18 of Hadar. In both groups the lower cheek teeth are caballine and with ectostylids.

Mandible. AaO-197 is a left mandible without the symphyseal part (Fig. 8B2). The cheek tooth series is 159 mm long and the length of the ascending ramus behind the cheek series is 129 mm. The heights are: *c.* 60 mm in front of p2 and 70 mm below p4.

Incisors. The upper, not very worn, incisors of the skull AaO-3647 are large (Fig. 1A2). From I1 to I3 the mesio-distal diameters are *c.* 18, 22 and 19 mm. The incisival arcade is rounded and not very wide, because the I3 are placed behind the I2. Their position does not seem to result from postmortem deformation but from premaxillaries that are too small to accommodate large incisors. The maximal incisor arcade width (across the I2s) is 65 mm. A prominent ridge is visible on the labial surface of the left I3. On the occlusal surface, it comes in contact with the distal border of I2.

Another complete set of not very worn upper incisors is AaO-2104. From I1 to I3 the maximal heights are 68, 64, and *c.* 55 mm; the mesio-distal diameters are 21, 21, and *c.* 22 mm; the labio-lingual diameters are 10, 11, and 9.5 mm. There again, the I3s were placed behind the I2s as shown by a clear indentation along the distal buccal border of the I2s. At mid-crown, the diameters are 15 × 13 on I1, 16.5 × 14 on I2, and 15 × 11 on I3.

Even in *Equus,* the distinction between upper and lower incisors may be difficult, and it is even more so in hipparions. Most of the isolated incisors, often fragmentary, from AaO cannot be sorted with certainty. But it is clear that during their wear they did not remain wide (mesio-distally) and shallow (labio-lingually) for as long a time as those of *H. afarense s.l* and *H. cornelianum.* On the other hand, when they are only slightly worn, their width is much larger than in AL 155-6 (also slightly worn) from the Denen Dora member, and more like AL 177-21 (even less worn and also from Denen Dora). In the Shungura Formation, the more similar incisors are from unit C8 (Eisenmann 1985, plate 1-1).

Permanent upper cheek teeth. Eight individuals are represented by complete series or associated teeth (Fig. 1A3,B, C; Table 3). There are moreover 20 isolated cheek teeth (Table 4). The sample looks homogeneous. The teeth are moderately or very plicated, with plis caballins ranging in number from one to four. Protocones are lenticular or lingually concave (Eisenmann *et al.* 1988, fig. 5C4,C6). In

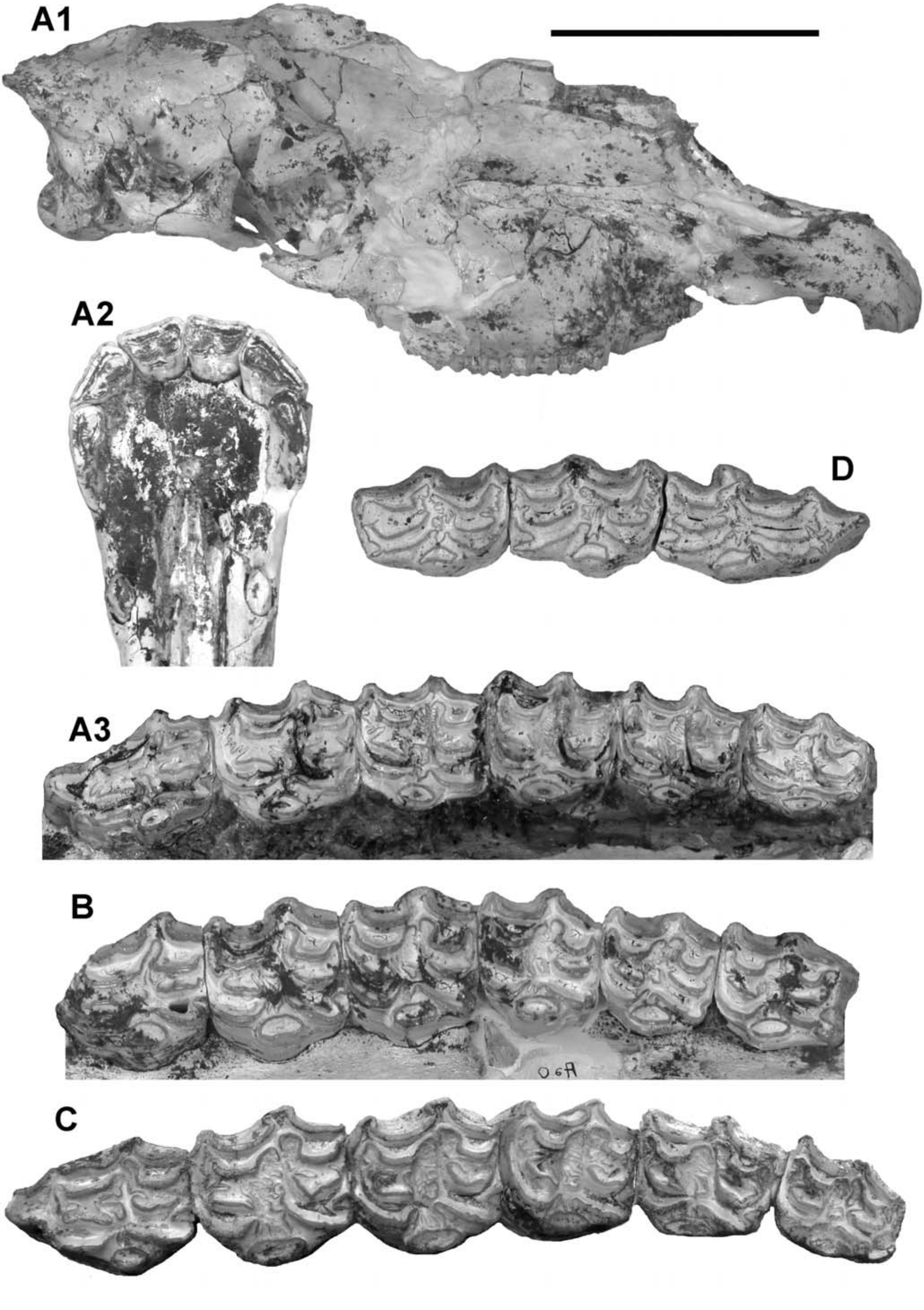

Figure 1. *Hipparion pomeli* sp. nov. from Ahl al Oughlam. **A**, holotype skull AaO-3647; **A1**, dorso-lateral view; **A2**, occlusal view of upper incisors; **A3**, cheek teeth; **B**, upper cheek teeth AaO-2048 (reversed from the right side); **C**, upper cheek teeth AaO-198 (M2 and M3 reversed from the right side); **D**, upper milk premolars AaO-4073. Scale bar = 15 cm for Fig. A1, 7.5 cm for Fig. A2, 5 cm and all others.

Table 1. Measurements in mm of hipparion skulls. *n*: number of specimens; approximate data in brackets.

		Oued el Hammam *n* = 1–9 *H. africanum*	LGB E L22187	Chad KB KB 9-AL 97-13	Hadar DD 2 AL340-8	Hadar KH 1–2 AL 164-3	Hadar KH 2–3 AL 363-18	AaO AAO 3647	Olduvai BK II 2845/6	Samos *n* = 2–14 *H. dietrichi*	Grebeniki *n* = 1–4 *H. giganteum*	Taraklia *n* = 1–8 *H. moldavicum*	Villaroya *n* = 2 *H. crusafonti*	Kvabebi K 48 *H.* cf. *crusafonti*	Sor PIN 3544 *H. garedz major*	Qiul, pers. comm. *H. houfenense* THP 10508	Qiu *et al.* 1988 *H. houfenense* THP 10733	*H. huangheense* FAM 11820
Muzzle length	1	125.5	125		140	>130		126	144	97.2	117	110.3	130	100	128	119	125	135
Palatal length	2	111	123	[140]	[135]	[155]	[126]	124	116	111.1	113.8	96	117	113	118	113	109	118
Vomerine length	3		113	135		[128]	[100]	112		94	109.5	104		103	[108]	[88]	[97]	
Postvomerine length	4		92			123,0	145	108		103.5	94	69				[122]	[108.7]	
Postpalatal length	5		198			[251]		220	[192]	183	216	178					200	250
Basilar length	6		452			>536		470		386	452.5	380				[431]	432	500
Premolar length	7	80.4		[85]	91	96	91	85		76.3	83.6	70.5	90	88	85–90	84	81	91
Molar length	8	67.8		82	75	76	73	77		64.8	67.5	59.8	73	71	69	67	38.5	80
Cheek teeth length	9	147.8	[152.1]	[173]	166	172	164	160	146.5	139.7	152	129.2	161	155	154	150	148	167
Choanal length	10		61	[74]			84	[52]		60.5	60.3	56.5	53		57			71
Minimal choanal width	11		[40]							31.8	36	30						31
Maximal choanal width	12	45.8	47	[43]			[47]			40	41	36		45	36			40
Palatal width	13	71.5	65	[90]			[80]			64.1	67.8	60.4		75	67			66
Minimal muzzle width	14	49	45		[31]	44		[35]		38.8	39.5	32.6	[40]	37	>33		[30]	42
Muzzle width at I3	15	59	57		57	60	80	60	70	63	58.9	42	[56]	52	[45]		[51]	66
Length of temporal fossa	16	71	78							71.3	85.5	69.8					82	82
Basion to foram. ethm.	17		135							162.3	157.5	122.5						
Frontal width	18	170	198				228	[190]		163.4	177	157		196		128		185
Bizygomatic width	19	180	192				221			163.6	180					136	[139]	188
Supraoccipital width	20		70		70		83	55				45					48	
Basioccipital width	21		92.5							95.3	99	88.5					92	110
Occipital height	22		71					65			75	61					71	
Anterior ocular line	23	352	363		400			390	360	300.8	343.8	300	365	320		334	320	380
Posterior ocular line	24		192		[190]		230	177		160	198.5	157				181	175	[205]
Facial height	25		118		102		110			82.3	87.2	91.3			102	98	90	112
Cranial height	26		106		[98]		[98]			80.9	92	75.8				109	96	
Height of auditive meatus	27		[10]								15.1							
Ant–post. orbital diameter	28	76	60				70	60		54	59.5	47.8	[62]	[51]		58	54	62
Vent–dors. orbital diameter	29		49			58	[54]	52		49.7	51.3	47.9	[45]			45	48	55
Length of naso-incisival notch	30	140.5	145		168			151	144	117.3	134.6	123.7	[150]		159	[154]	143	160
Cheek length	31	157	180	[130]	174		158	151	164	149	165	146.8	158			[156.8]	141	170
Orbit to preorbital fossa (POF)	32	46.5	40	43				50		44.9	48	26.9			34			
Length of POF	33	65,5	[55]	84						68.9	70	74.2			51			
POF to foramen infraorbitale	34	102 ?	–	90						50.4	56	76.7			62			
Height of POF	35	32	31	34						32.5	37.7	51.8			42			
POF to facial crest	36	52	[98]	47				66		39.7	39.7	25.3			27			
For. infraorb. to alveol. border	37	31	62	79						52.9	47	43.3			44		60	60
POF to alveolar border	38	58.5	–	113				[87]			54.5	67.3			63			
P2 - Orbit			182	207	196		192	175	168	143.2	169.5	148.3		166		[176.4]	[150]	185
Diastema					116			90										
Width of occipital condyles					74	81	85	>68										
Width of foramen magnum					33	38	39	[34]										

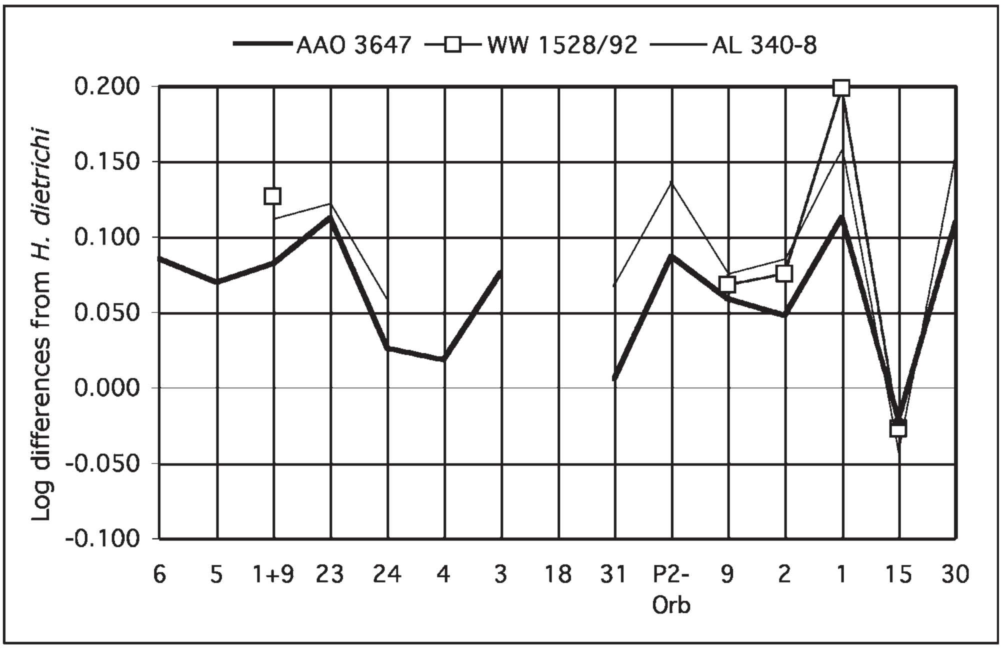

Figure 2. Ratio diagram comparing the holotype skull of *Hipparion pomeli* (AaO-3647) to *Hipparion hasumense s.l.* of Wembere Manonga Kilolei WW 1528/92 (data Bernor & Armour-Chelu 1997), and *H. hasumense* of Hadar DD AL 340-8. Data in Tables 1 & 2.

P3 and P4, the occlusal surface tends to be flat, while molars tend to have transversal ridges.

In Tunisia, the upper cheek teeth of Aïn Brimba are larger while those of Ichkeul are about the same size (Fig. 9; Tables 5 & 6). In East Africa, the more similar sizes may be found in the skull of *H. afarense* of the Kada Hadar and Sidi Hakoma members of Hadar, in Usno, and in member B of Shungura Formation. The Denen Dora teeth are often larger, while most of the Omo teeth are smaller.

A scatter diagram compares the hypsodonty of upper unworn or little worn M3s, plotting the height at the mesostyle versus length at mid-crown (Fig. 10). Schematically, three groups may be distinguished: less hypsodont in Chad (Kollé and Toros Menalla), Ichkeul; middle hypsodont ranging in time from Omo A (4–3.5 Ma) to Omo E (2.4–2.3 Ma); very hypsodont from Omo C (3–2.5 Ma) to Olduvai. Note that one of the two M3s of Omo C plots with middle hypsodont and the other with very hypsodont, indicating the possible presence of two species. The little worn M3 of AaO appears moderately hypsodont. The Hypsodonty Index (HI = mesostyle height × 100/length at mid-crown) is 221–235 in the less hypsodont group, 241–276 in the middle hypsodont, and 297–315 in the very hypsodont one.

Three groups appear again for unworn or little worn other upper cheek teeth (Fig. 11). A very hypsodont group (HI = 318–340) comprises teeth from Olduvai, KBS, Omo F, Omo G, but also, surprisingly, one tooth from Omo B.

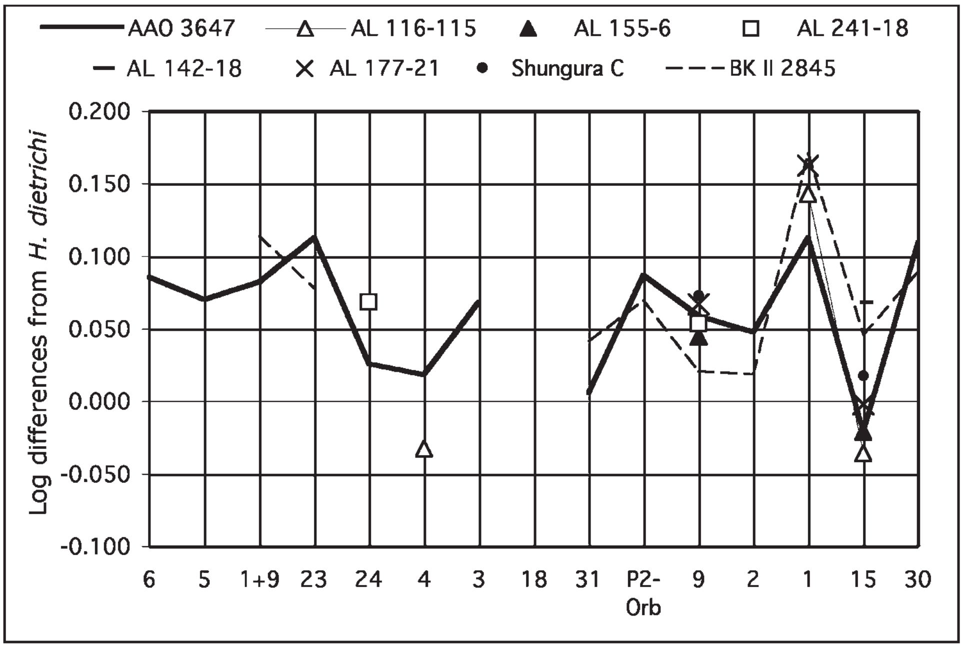

Figure 3. Ratio diagram comparing the Moroccan skull (AaO 3647) to *Hipparion hasumense s.l.* of Hadar SH (AL 142-18), DD (AL 116-115, AL 155-6, AL 241-18, AL 177-21), Shungura C (18-1968-363 and 18-1969-90), and Olduvai BK II 2845/6. Data in Table 2.

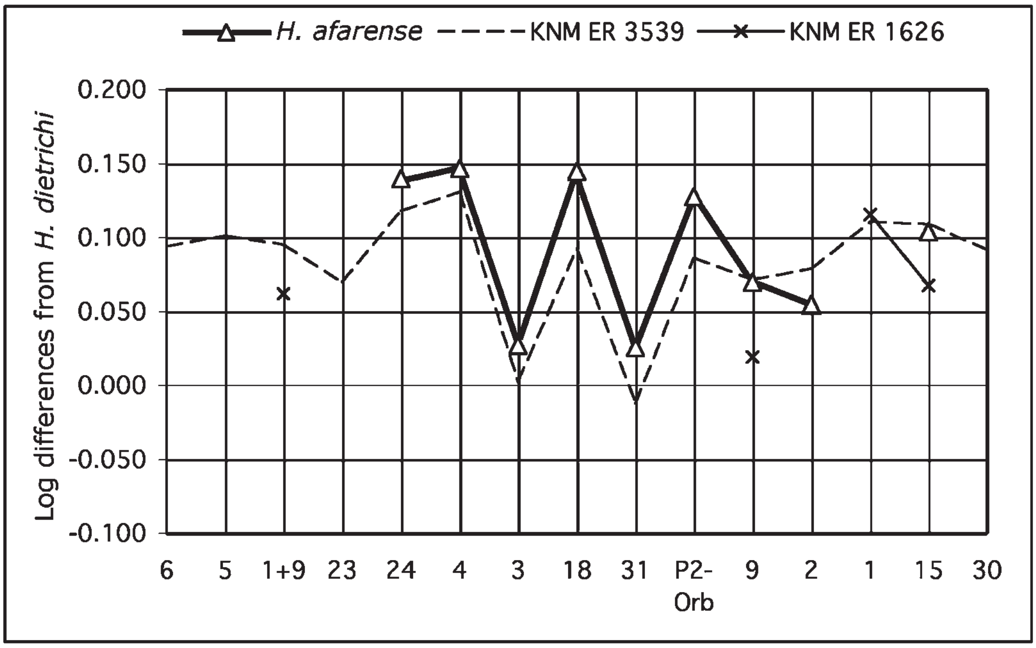

Figure 4. Ratio diagram illustrating the pattern of *Hipparion afarense* type skull and *H. afarense s.l.* from East Turkana Burgi (KNM ER 3539) and *Notochoerus scotti* Zone (KNM ER 1626). Data in Table 1, Appendix Table 2, and Appendix Text.

The middle hypsodont group (HI = 264–298) comprises specimens from Hadar DD and unknown levels, Omo C, Omo F, and Kossom Bougoudi, Chad. Aïn Brimba and Ichkeul plot with the less hypsodont group (HI = 243–257). Again, there is possible evidence for two species at the same time: at Hadar DD2, Omo F, and at Chad Kossom Bougoudi. There are no data for AaO.

Deciduous upper cheek teeth. They are moderately plicated but with large or bifid plis caballins (Fig. 1D). Data are provided in Table 7.

Permanent lower cheek teeth. Four individuals are represented by complete series (Fig. 8A,B; Table 8). There are also 12, mostly isolated, specimens (Table 9). The teeth are caballoid, with protostylids (plis or isolated) and ectostylids. Most ectostylids are not very large, although they are larger at the base of the crown. In two molars there are additional ectostylids, very small but reaching the occlusal surface at least *c.* 3 cm from the roots. The caballoid pattern of the lower cheek teeth indicates without any doubt that the AaO hipparion is an 'advanced' hipparion. What additional indications may be gathered from the presence of ectostylids ?

The development of ectostylids and their possible use for biostratigraphy has been discussed in detail for samples from Hadar, Omo, and East Turkana (Eisenmann 1977). Although there are no extensive analyses of the function of ectostylids, it seems likely that they do have some function, possibly in increasing grinding ability. It is

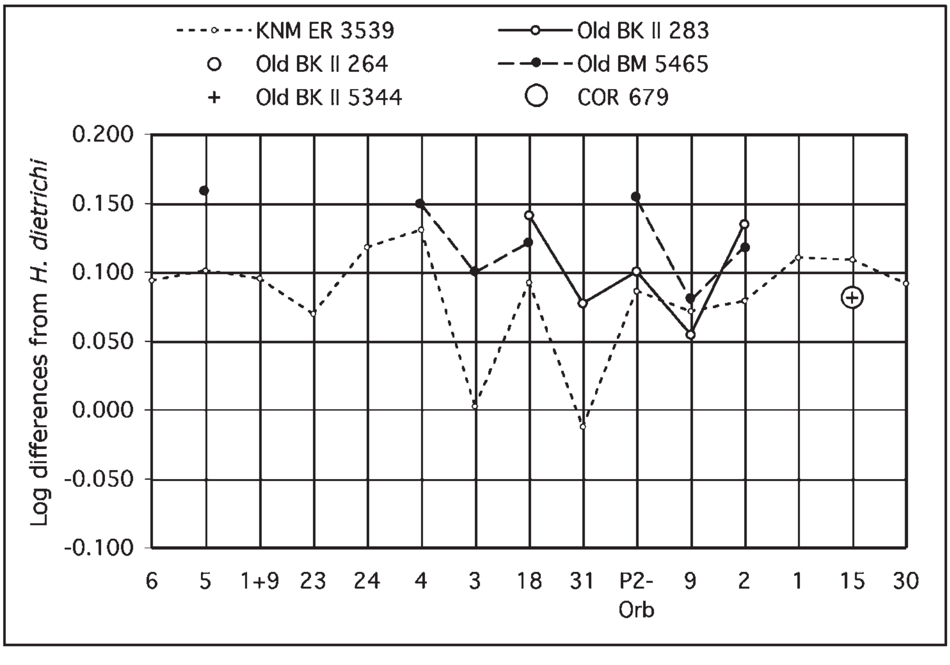

Figure 5. Ratio diagram illustrating the pattern of other *Hipparion afarense s.l.* skulls from Olduvai Bed II (BK II 264, 283, 5344) and unknown (BM 5465), and Cornelia. Data in Table 2, Appendix Table 2, and Appendix Text.

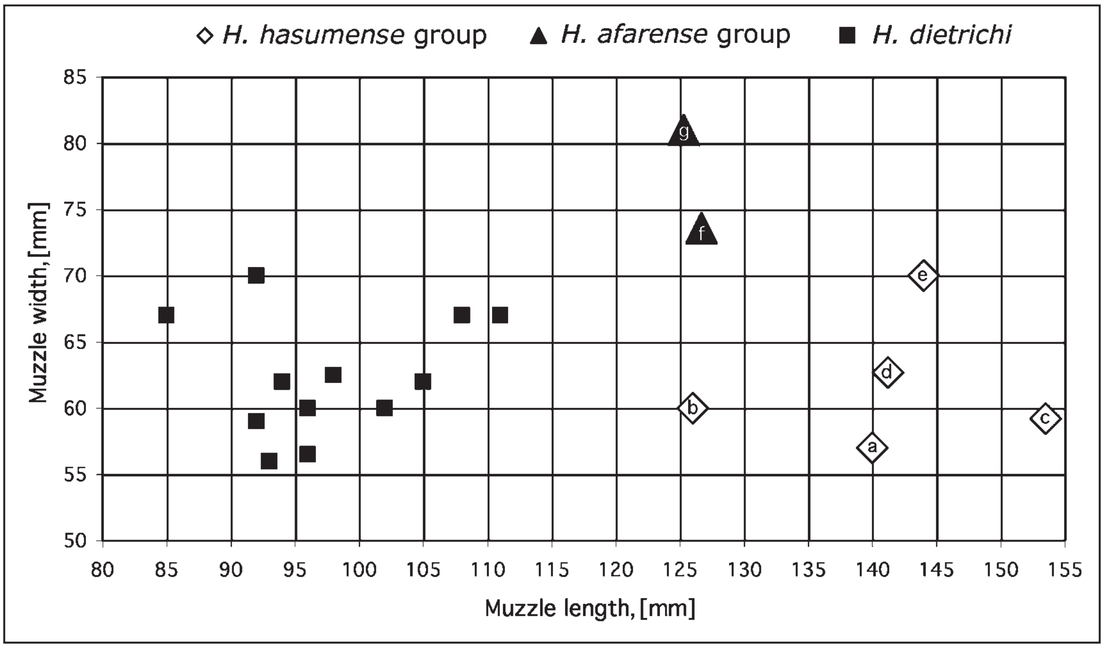

Figure 6. Scatter diagram of muzzle lengths and widths in *Hipparion dietrichi* of Samos (Table 2), *H. hasumense s.l.* a: AL 340-8, Hadar DD; b: AaO 3647, Ahl al Oughlam; c: WW 1528/92, Wembere Manonga, Kilolei; d: AL 177-21, Hadar DD; e: Olduvai BK II 2845/6; and *H. cornelianum* f: KNM ER 1626, East Turkana *Notochoerus scotti* zone; g: KNM ER 3539, East Turkana Burgi.

clear, however, that whatever their function, as long as ectostylids are not yet in wear, the plis caballinid appear as some kind of 'vicariants' of ectostylids, providing occlusal enamel at the very position occupied later by ectostylids. A good illustration is provided by the molar Omo C 40-68-3015 (Eisenmann 1985, plate 2-17-18) and by several teeth from Aïn Brimba (Arambourg 1970, plate XVII-11,11a):

— On the occlusal surface of a little-worn m2, the pli caballinid is very well developed; the apex of a first ectostylid appears 12 mm below the occlusal surface; the apex of a second ectostylid is visible 10 mm below the first; at that level, the first ectostylid is about 5 mm long; a few millimetres below, the second ectostylid is nearly as long as the first; if they were to fuse, the total ectostylid length would be about 8–9 mm.

— On the slightly more worn m1 of the same series, the first ectostylid is already beginning to wear, taking the place of the nearly absent pli caballinid; the apex of the second ectostylid is visible 32 mm below the occlusal surface.

— On the unerupted p4, an ectostylid appears *c.* 10 mm below the occlusal surface; between the occlusal surface and the ectostylid there is a well-developed pli caballinid.

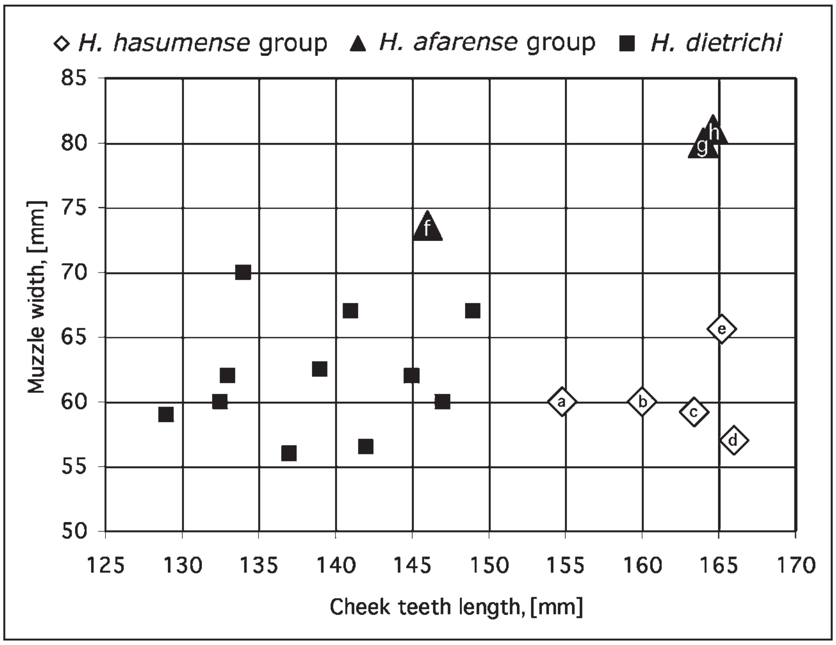

Figure 7. Scatter diagram of P2-M3 lengths and muzzle widths in *Hipparion dietrichi* of Samos (Table 2), *H. hasumense s.l.* a: AL 155-6, Hadar DD; b: AaO 3647, Ahl al Oughlam; c: WW 1528/92, Wembere Manonga, Kilolei; d: AL 340-8, Hadar DD; e: 18-198-363 & 18-1969-90, Omo C; and *H. afarense s.l.* f: KNM ER 1626, East Turkana *Notochoerus scotti* zone; g: AL 363-18, Hadar KH; h: KNM ER 3539, East Turkana Burgi.

Table 2. Measurements in mm of hipparion skulls. Numbers refer to the measurements defined in Table 1. Approximate data in brackets. Asterisks indicate skull estimations from mandibular data (see Appendix). Data for Manonga WW 1528/92 are according to Bernor & Armour-Chelu (1997).

	1	4	3	9	15	23	24
H. hasumense s.l.							
Hadar AL 116-115	[135]	[96]			58		
Hadar AL 155-6				154.8	60		
Hadar AL 177-21	141.2*				62.7*		
Hadar AL 241-18				[158]			[195]
Shungura C 18.1968.363				165.2	65.6*		
Manonga WW 1528/92	153.5			163.4	59.2		
Olduvai BK II 2846	144			163.5	[70]	[360]	
H. afarense s.l.							
AL 142-18					74		
Shungura F 118-1972-5				142			
KNM ER 1626	126.7*			146	73.6*		
Olduvai BK II 264					76		
Olduvai BK II 067-5344					75.8*		
Cornelia COR 707					74*		
H. dietrichi							
Münster SI 7	93			137	56	290	
FAM Q1 no number	111				67		
FAM Q1 20559 A	91			148		295	
FAM Q1 20596	85	97	92	149	67	300	155
FAM Q1 20598	92		106		70	310	
FAM Q1 20608	102			147	60	305	
FAM Q1 20692				134	70		
FAM Q1 20997	94		94	145	62	310	
FAM Q1 94907				140			
FAM Q4 22860	108	110	91	141	67	325	
FAM Q6 22990	96			142	56.5	305	165
Darmstadt 1914	98			139	62.5		
Chicago 12868	96		87	132.5	60	294	
Bern 45	92			129	59	280	
Bern 109	105			133	62	295	
H. crassum s.l.							
Pp 208 mandible	154.5*			177	61.2*		
Chamar 3381-53.	146.8*			176	63.4*		

Measurements of Aïn Brimba lower cheek teeth are given in Table 10.

At Ichkeul, the apex of the ectostylid on an unworn premolar is about 9 mm from the occlusal surface. The tooth was sectioned at 2 cm from the occlusal surface. At this level, the length is 28 mm, the width is 14.7 mm, the double knot is 14.7 mm long, the postfossette 12.2, the ectostylid 3 mm. The rest of the tooth is broken.

The growth of teeth proceeding from apex to roots, the distance between the apex of the tooth and the apex of the ectostylid(s) should be more meaningful in terms of evolution than the height of the ectostylid from the base of the crown. In the Omo C5-8 little worn m2 (Eisenmann 1985, plate 2-18) the first ectostylid appears more 'evolved' – i.e. closer to the occlusal surface, than in the m2 of Aïn Brimba while in an unworn p4 of the Kilolei Member of Wembere-Manonga Valley (Bernor & Armour-Chelu 1997), the distance is the same as in the p4 of Aïn Brimba. Naturally in different species the development of ectostylids may be different: from the Ibole Member of Wembere-Manonga Valley (Bernor & Armour-Chelu 1997), the ectostylid of one m2 (large species) is at more than 37.6 mm from the occlusal surface, while in another m2 (small species), the distance is only 13 mm. But in the m2 of the large species of Kilolei member, the ectostylid has grown to less than 13.9 mm from the occlusal surface.

In Omo member F, the first ectostylid at least is already formed at the apex of the crown (Eisenmann 1985, plate 2-5). Three or even four ectostylids appear on sectioned teeth from Omo G (Eisenmann 1985, plate 2-9). Their fusion results in a peculiar, inflated and trifid ectostylid, at times almost fused with the pli caballinid (Eisenmann 1985, plate 2-12-15). This seems to be the ultimate degree of ectostylid evolution. A trifid pattern is already present in some teeth of the Denen Dora member of Hadar (AL 183-41). It may also be seen at Koobi Fora (KNM ER 2766 SU-, Burgi and KBS).

At AaO, there are no unworn lower p3–m2 so we do not know if ectostylids had already developed at the apex of the crown. There is no evidence of the peculiar trifid pattern of Omo G; the ectostylids are not very large but a second ectostylid may occur (AaO-4072). In East Africa, the pattern would be consistent with an age older than 3 Ma.

Deciduous lower cheek teeth. Most teeth are in the very first stages of wear (Fig. 8C; Table 11). Protostylids are always present and may sometimes be isolated. Ectostylids are not very large. They appear about 10 mm below the top of the tooth. Secondary ectostylids appear about 5 mm lower. It may be noted that the double knots of dp2 grow

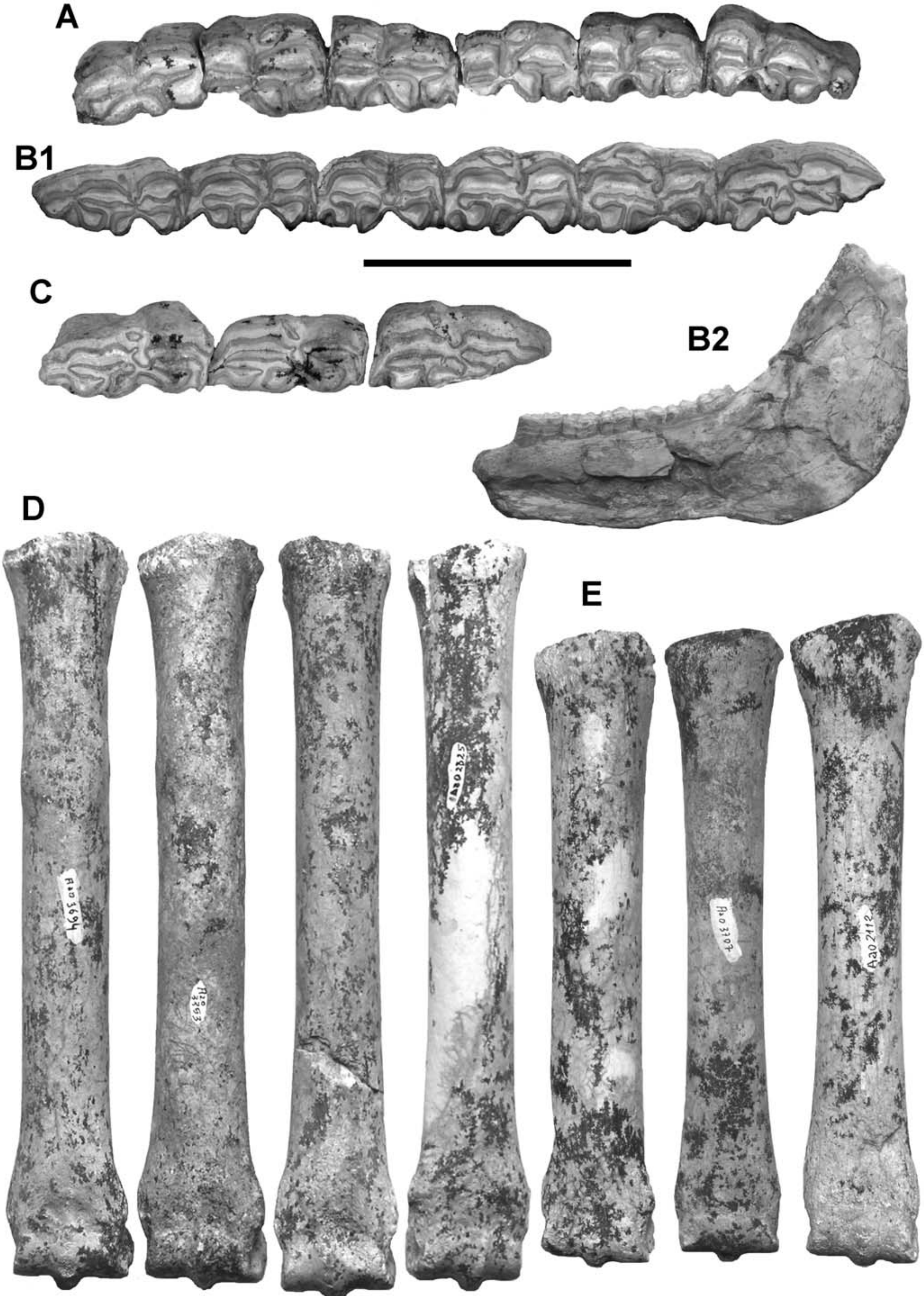

Figure 8. *Hipparion pomeli* sp. nov. from Ahl al Oughlam. **A**, lower cheek teeth AaO-2993. B: mandible AaO-197; **B1**, cheek teeth, **B2**, lateral view. **C**, lower milk premolars AaO-4070. **D**, four metatarsals, from left to right: AaO-3694, AaO-3353; AaO-3700, AaO-2825. **E**, three metacarpals, AaO-4267, AaO-3307, AaO-2112. Scale bar = 20 cm for Fig. 2; 10 cm for Figs D–E; 5 cm for all others.

Table 3. Permanent upper cheek series or associated teeth from Ahl al Oughlam. Measurements in mm, approximate values in brackets.

AaO 198		P2	P3	P4	M1	M2	M3
Wear stage		2	2	2	2	2	2
Length	Occlusal	35.5	29	27	26	25	24
Width	Occlusal	24	28	28	25	24	19.5
Protocone L	Occlusal	8	11	10.5	9.5	9	9
Protocone W	Occlusal	5	4.9	4.7	4.3	4.3	4
Plis fossette		5	12	13	12	13	8
Plis caballin		1	3	3	3	2	3
AaO 1452		**P2**	**P3**	**P4**	**M1**		
Wear stage		2	2	2	2		
Height		37	[30]	[38]			
Length	Occlusal	35	29.5	27	[24]		
Width	Occlusal	25	27	25	25		
Protocone L	Occlusal	7.3	10.7	8.8	8.5		
Protocone W	Occlusal	4	4	4.1	3.9		
Plis fossette		9	15		[16]		
Plis caballin		1	3	1	2		
AaO 2048		**P2**	**P3**	**P4**	**M1**	**M2**	**M3**
Wear stage		2–3	2–3	2–3	2–3	2–3	2–3
Height					42	40	30
Length	Occlusal	[31]	25	24	21.5	21	23
Width	Occlusal	24	25.5	26	24.1	22	20
Protocone L	Occlusal	8	9	8.5	8.5	8	8
Protocone W	Occlusal	5	5	4.9	4.7	4	3.9
Plis fossette		7	9	>8	12	13	12
Plis caballin			2	2	1	1	1
AaO 3495		**P2**	**P3**	**P4**	**M1**	**M2**	
Wear stage		2	2	2	2	2	
Height		40	52	57	52	57	
Length	Occlusal	36	28	28	25	26	
Width	Occlusal	26	28	27.2	25	23	
Protocone L	Occlusal	9.2	10	9	8	8.5	
Protocone W	Occlusal	4.2	4.3	4.2	4	4	
Length	at 2 cm	35	27	26	24	24	
Width	at 2 cm	24.7	27	26.7	26	24	
Length	at 1 cm	34	25	24.2	22.1	23	
Width	at 1 cm	24	26.2	27	26	24	
Plis fossette		12	17	16	18	14	
Plis caballin		1	1	2	2	2	
AaO 3647		**P2**	**P3**	**P4**	**M1**	**M2**	**M3**
Wear stage		2	2	2	2	2	2
Length	Occlusal	33.5	27.5	25	24	23.5	24
Width	Occlusal	24	26	25	25	24.5	20
Protocone L	Occlusal	7	8.5	7	9	9	7
Protocone W	Occlusal	4	4.9	4	4	4.1	3
Plis fossette		9	16	24	16	16	11
Plis caballin		2	1	1	1	1	1
		AaO 1429a P2	**AaO 1429b P3**		**AaO 1431 M1**	**AaO 1432 M2**	**AaO 1433 M3**
Wear stage		2–3	2–3		2	2	1–2
Height		42	46		53	59	61
Length	Occlusal		29		25	26	22
Width	Occlusal	24.5	27		24	24	18
Protocone L	Occlusal	8	8		9	8.3	9
Protocone W	Occlusal	4.4	4.2		4	4.5	3.6
Length	at 2 cm		28		24	24	24
Width	at 2 cm	24.7	25		24	24	21.5
Length	at 1 cm		26		23	23	25
Width	at 1 cm	23	25		25.2	23	21

Continued on p. 61

Table 3 (*continued*)

		AaO 1429a P2	AaO 1429b P3		AaO 1431 M1	AaO 1432 M2	AaO 1433 M3
Plis fossette		12	22		22	24	
Plis caballin		1	4		2	1	
		AaO 3937a P4	AaO 3937b M1	AaO 3937c M2		AaO 3167 M1	AaO 3167 M2
Wear stage		3	3	3		4	4
Height		[30]	[30]	33		17	
Length	Occlusal	24	23	22.2		23	23.2
Width	Occlusal	25.1	25.2	23.2		27.2 sic	23
Length	at 1 cm	24	23	22.5			
Width	at 1 cm	26	25	24			
Protocone L	Occlusal	8	8.2	8		9.8	10
Protocone W	Occlusal	5	4.5	4		6	6
Plis fossette		[16]	19			10	10
Plis caballin		1	1	0			

in the same way as the ectostylids, i.e. by fusion with a secondary enamel pillar a few millimetres below the top of the crown.

Size index, variability of limb bones, and sexual dimorphism. Obviously, the size of a specimen can be qualified by comparisons with the same kind of specimens. But how can the size of a talus be compared with the size of a second phalanx? And how can we determine if the overall size of animals found at one locality was larger or smaller than at another? The Variability Size Index (VSI) is a way

Table 4. Other permanent upper cheek teeth from Ahl al Oughlam. Asterisks for dimensions at mid-crown height.

		AaO 3551 P2	AaO 3599 P2	AaO 1229 P2	AaO 2263 P2	AaO 4071a P	AaO 4071b M	AaO 37 M	AaO 1179 M?
Wear stage		2–3	2–3	2–3		[3]			
Height		32	33						
Length	Occlusal		33	32	35.8	24.7	22	23	24
Width	Occlusal	24	24	23	24.7	28 sic	24	25	23
Protocone L	Occlusal	8	8	7.8	7.9	10	9	9	8
Protocone W	Occlusal	3.6	4	4.1		5	5	5	4
Plis fossette		9	6	5		8	11	[14]	
Plis caballin		1	1	1		2			2
		AaO 1475 P	AaO 3132 P	AaO 3130 M	AaO 3555 M	AaO 1438 M			
Wear stage		2	2–3	2	2	3			
Height		42	40	44	46	21			
Length	Occlusal	26	25.1	25	25	21.6 sic			
Width	Occlusal	25	25	23	23	21.1 sic			
Length	at 2 cm	25	24	23	23.7	21.6 sic			
Width	at 2 cm	25.3	25.2	23	23	21.1 sic			
Length	at 1 cm	25	23	23		21 sic			
Width	at 1 cm	25	25	23	22	22 sic			
Protocone L	Occlusal	8	8.1	8	8	8			
Protocone W	Occlusal	4	4.1	4.2	3	4			
Plis fossette		12	20	8	14	11			
Plis caballin		2	1		1	1			
		AaO 1440 M3	AaO 3134 M3	AaO 3133 M3	AaO 3556 M3	AaO 3557 M3	AaO 3598 M3	AaO 4071c M3	AaO 4071d M3
Wear stage		0	0	1–2	1–2	2	4	3	4
Height				45	45	47	19		
Length	Occlusal						25		25
Width	Occlusal						23		22.5
Length	Mid-crown	23	23	24.5	24.5	25.1		24	
Width	Mid-crown	20	19.5	21	21	22.3		21	
Protocone L	Occlusal	7*	7.4*	9	8.2	9.1	10.1	8	11
Protocone W	Occlusal			3.2	3	3.2	4	4	4.5
Plis fossette				[9]	8	12	11	11	8
Plis caballin				1	2	3	2	1	[2]

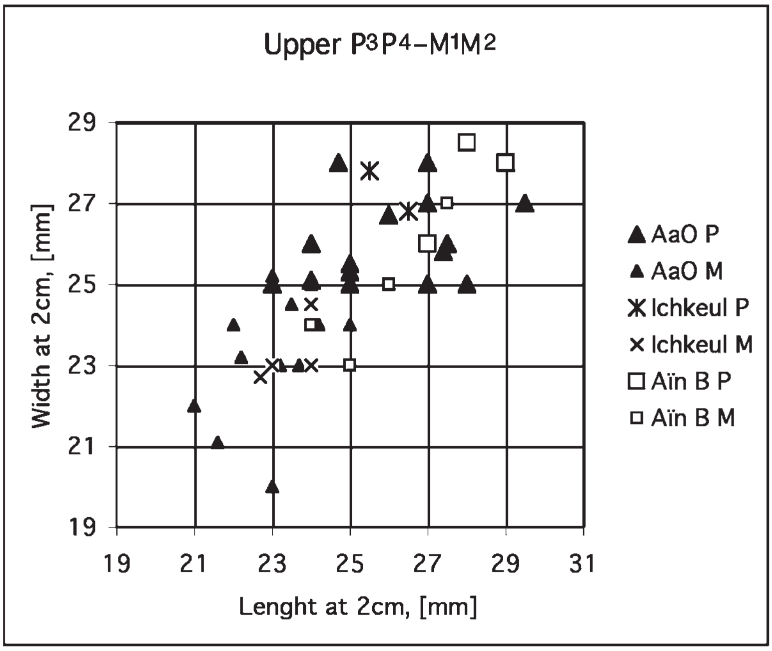

Figure 9. Scatter diagram of P3-4 and M1-2 lengths and widths of Ahl al Oughlam, Ichkeul, and Aïn Brimba.

Table 5. Permanent upper cheek teeth from Aïn Brimba.

		1958.14.173	1958.14.221	1958.14.187	1958.14.190	1958.14.190	1957.111.13
		P2	P3	P4	P4	P4	P?
Wear stage		0–1	2	1	0–1	section	2–3
Height		56	33	61	67	41	43
Length	Occlusal	40	29	29	32	30.2	[25]
Width	Occlusal	24	28	27	27	29	
Length	at 2 cm	38	29	27		28	
Width	at 2 cm	25.6	28	26		28.5	
Length	at 1 cm	39	28	26.5		27.5	
Width	at 1 cm	24.6	27	27		28.5	
Protocone L	Occlusal	[10]	10	9.9		7.9	7
Protocone W	Occlusal		5	3.8		5	4
Plis fossette			21	22		23	19
Plis caballin			2	2		1	3

		1958.14.222	1958.14.191	1958.14.191	1958.14.172	1958.14.186	1958.14.188	1958.14.189
		M?	M1	M1	M	M	M	M
Wear stage		2–3	0	section	2	1–2	1–2	2
Height		37	[72]	30	52	60	60	56
Length	Occlusal	26	29	28.5	27	27	26	26
Width	Occlusal	[26]	27	28		[26]		
Length	at 2 cm	27		27.5	25	24	25	26
Width	at 2 cm			27		26		
Length	at 1 cm	27		26	24	24	23	25
Width	at 1 cm			27.5		26		
Protocone L	Occlusal	[10]		7.3		9		
Protocone W	Occlusal			5		4		
Plis fossette		25		20	20	21		[20]
Plis caballin		4		3		1		

		1958.14.223	1958.14.192
		M3	M3
Wear stage		2	1–2
Height		38	55
Length	at midcrown	28	
Width	at midcrown	23	
Protocone L	Occlusal	10	9
Protocone W	Occlusal	3	3.9
Plis Fossette		22	[13]
Plis Caballin		2	1

Table 6. Permanent upper cheek teeth from Ichkeul.

		1950.1.123 P3	1950.1.104 P4
Wear stage		2	1–2
Height			55
Length	Occlusal	26.5	27
Width	Occlusal	26.8	25.6
Length	at 2 cm		25.5
Width	at 2 cm		27.8
Length	at 1 cm		25.1
Width	at 1 cm		28
Protocone L	Occlusal	7	11
Protocone W	Occlusal	4.8	4
Plis fossette		19	
Plis caballin		2	2

		1948.1.8 M1	1948.1.8 M1	1950.1.21 M2	1950.1.21 M2	1948.2.15 M2	1950.1.107 M2	1948.2.14 M	M
Wear stage		1	section	1–2	section	1	1–2	[2]	section
Height		59	28.5	61	41	59	55	[55]	27
Length	Occlusal	24	24	26	25.5	25	25		
Width	Occlusal	21.5	23	22.5	25	19	20.2		[22]
Length	at 2 cm			27.5	24	23	[23]		
Width	at 2 cm				24.5	22.7	[23]		
Length	at 1 cm		22.5		24	22.7			
Width	at 1 cm		22		24	23			
Protocone L	Occlusal	8	8	8	7.1	7	8.1		7
Protocone W	Occlusal	3	4.2	3	4	3	3.9		4
Plis fossette			16		21		13	[20]	>10
Plis caballin			1	1		0	2		1

		1949.1.9 M3	1949.1.9 M3
Wear stage		0	section
Height		56	27
Length	at midcrown	25	25
Width	at midcrown	23	22
Protocone L	Occlusal	10	9
Protocone W	Occlusal	3	4
Plis fossette		22	16
Plis caballin		2	3

to address these questions. Devised by archeozoologists (Uerpmann 1982; Meadow 1999), the VSI is one of the size index scaling techniques available. A sample including all the bones of a taxon is chosen as reference. Mean and standard deviation are calculated for each measurement of the sample. Comparisons are carried out using the following formula: VSI (variability size index) = $25(x–m)/s$ where s is the standard deviation of the mean (m) of the reference measurements to which another measurement (x) is being compared. The obtained values are plotted on a histogram graduated in one, two, three, or more standard deviations from the reference. As phrased by Meadow (1986), 'Using this formula, the standard dimension is set at zero; a measurement one standard deviation larger than the standard (reference) dimension will be plotted at 25, one standard deviation smaller at –25, etc'. It is recommended to use the same kinds of dimensions (widths, or depths, or lengths) for all the bones. In this study we have tried to ascertain if this technique can provide some interesting information.

1. VSI based on Höwenegg sample. The detailed description by Bernor *et al.* (1997) of the late Miocene Höwenegg sample affords the first basis of normal intraspecific variation for hipparions. Among the published measurements we have chosen to use only widths (Table 12), because they are more frequently available on fossils than lengths and depths, and because it is not recommended to combine different kinds of measurements. For the tibial diaphysis width, we have used the median of Höwenegg (44.6) instead of the mean (42.6) and we supposed a standard deviation of 2 instead of 5.61 because they appear more consistent with the rest of the data: a minimal value of 32.4 and a corresponding standard deviation of 5.61 indicate either the inclusion of a juvenile specimen or a printing error; there is no reason why the standard variation would be more than 5 for the tibia width when it comprises between 1.1 and 2.66 for other bone widths.

Equus bones do not exhibit sexual dimorphism, at least not in a marked way. There is no evidence yet that it was otherwise in hipparions (Bernor *et al.* 1997). The distribution of metrical values within a monospecific adult (epiphyses

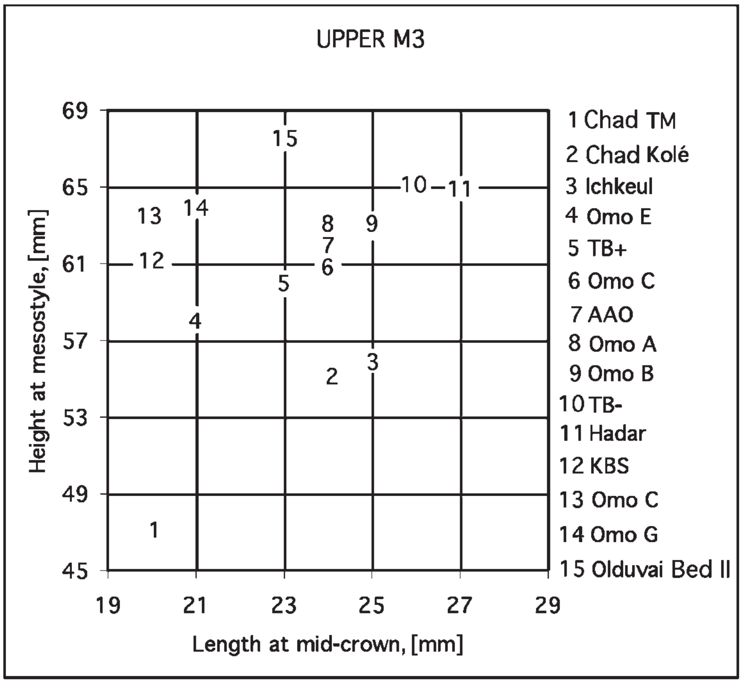

Figure 10. Scatter diagram of unworn or little worn M3 lengths and heights in various African hipparions. HI: Hypsodonty Index. 1: TM 47-101-11; HI = 220.8; 2: KL 20-98-11, HI = 235; 3: Ichkeul, HI = 224; 4: 1968-1005-38, HI = 276.2; 5: 4094, FS 751, HI = 260.9; 6: L 768-1, HI = 254.2; 7: AaO 1433, HI = 258.3; 8: 1969-108-81, HI = 262.5; 9: L 1-61, HI = 252; 10: ER 2922, HI = 250; 11: AL 58-10, HI = 240.7; 12: ER 1263, HI = 305; 13: L 724-3, HI = 315; 14: L 675-2, HI = 304.8; 15: average of Hooijer (1975), HI = 296.7.

perfectly fused) sample should be normal. In consequence, an 'abnormal' variation or distribution may reflect a long time of deposition during which a given species could have changed, or the coexistence of different taxa, or sexual dimorphism.

The AaO histogram seems, on the whole, to follow a normal distribution, centred on a peak between 50 and 75, i.e. at two to three standard deviations from Höwenegg (Fig. 12). But eight values plot between 175 and 250, evidencing the presence of surprising widths. All of them

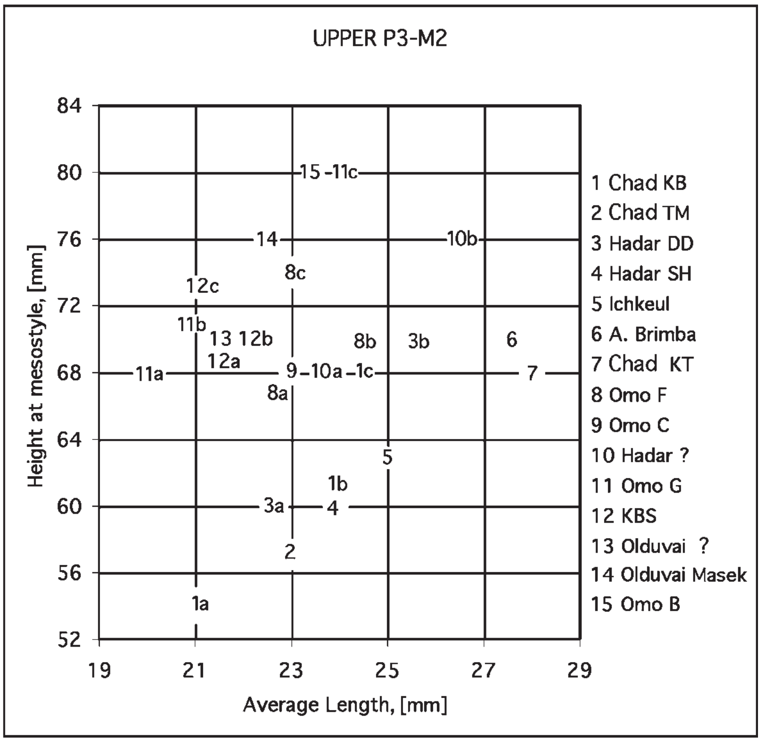

Figure 11. Scatter diagram of unworn or little-worn P3-4and M1-2 lengths and heights in various African hipparions. HI: Hypsodonty Index. 1a: KB3 98-93, HI = 257.1; 1b: KB4 96-13, HI = 254.2; 1c: KB3 97-136, HI = 277.6; 2: TM 47 101-1C, HI = 247.8; 3a: AL 155-6, HI = 264.3; 3b: AL 305-5, HI = 274.5; 4: AL 58-10E, HI = 251; 5: 1950–1-21, HI = 252; 6: 1958-14-191, HI = 254.5; 7: KT33 96-1, HI = 242.9: 8a: L 253-3a, HI = 297.8; 8b: 1972-14-108, HI = 285.7; 8c: L 398-1182, HI = 321.7; 9: L 767-1, HI = 295.7; 10a: AL 239-68, HI = 285.7; 10b: AL 288-19, HI = 286.8; 11a: F 513-33, HI = 340; 11b: L 616-62, HI = 338.1; 11c: L 627-89, HI = 333.3; 12a: ER 2263, HI = 320.9; 12b: ER 2073, HI = 318.2; 12c: ER 1231, HI = 347.6; 13: A 581, HI = 325.6; 14: 1692, HI = 337.8; 15: 1973-1958-212, HI = 340.4.

Table 7. Deciduous upper cheek teeth from Ahl al Oughlam.

		AaO 4073 dP2	AaO 4073 dP3	AaO 4073 dP4	AaO 3600 dP2	AaO 3600 dP3	AaO 1447 dP4
Wear stage		2	2	2	0–1	0–1	0–1
Height		*c.* 20	*c.* 20	*c.* 20	23	26	26
Length	Occlusal	38.0	29	29	>37	30	32
Width	Occlusal	20	21	19	*c.* 20	*c.* 20	19
Protocone L	Occlusal	8	7	7.7	9.5	10	9
Protocone W	Occlusal	*c.* 3	*c.* 3	*c.* 3			
Plis fossette		[8]	14	10			
Plis caballin		1	2	1			

		AaO 1186 dP2	AaO 3552 dP3	AaO 3546 dP4	AaO 1439 dP3	AaO 1437 dP4
Wear stage		2	2	2	0–1	0–1
Height			18	20.5	24	25
Length	Occlusal	38.0	28	29	29	30
Width	Occlusal	19	19	19.5	18	19
Protocone L	Occlusal	6	6.5	7	*c.* 8	7
Protocone W	Occlusal	*c.* 3	*c.* 2	*c.* 3		
Plis fossette		[10]	12	13		
Plis caballin		1	1	2		

		AaO 1466 dP3–4	AaO 3537 dP3–4	AaO 3538 dP3–4	AaO 3539 dP3–4
Wear stage		0–1	0–1	0–1	0–1
Height		28	26	24	25
Length	Occlusal	32.0	29	31	31
Width	Occlusal	20	19	21	22
Protocone L	Occlusal	10	8.5	9	10

are proximal widths of MC III. The preserved six distal widths of the corresponding MC III plot between 50 and 150. Thus, the asymmetry of the histogram reflects only an anatomical difference between AaO and Höwenegg MC III: in the first, the proximal epiphyses of some MC III are relatively wider.

According to the coefficients of variation, the variability of AaO is compatible with the variability of some assumed monospecific samples of *Equus,* but compared to the best samples of *Equus* (Eisenmann & David 2002; Eisenmann 2002, 2004), and *Allohippus,* the size variability at AaO is greater. Indeed, the coefficients of variation of the tali are quite bigger than in the well-represented extant *Equus grevyi* and bigger too than in the very large fossil sample of *Allohippus vireti* from Saint-Vallier (Table 13). Since the fossils of AaO are believed to have been deposited during a short period (see Introduction), and since there is no evidence for the coexistence of two species, we cannot exclude that some sexual dimorphism existed in *H. pomeli,* but this does not appear clearly on the VSI histograms.

Although much poorer than AaO's, the Hadar DD sample is interesting because it includes a nearly complete skeleton: AL 155-6. In Fig. 12, it is represented by white points. One of the largest values of AL 155-6 is, as in *H. pomeli,* the proximal MC III width (the two others are second and third phalanges widths). On the larger side of AL 155-6 plot two radii (AL 155-1 and 338-13), one distal MC III (AL 155-1), one proximal MC III (AL 116-33), and one second phalanx (Al 340–1). After consideration of the other dimensions (not included in our VSI), it appears that only the fragmentary MC III AL 155-1 (extreme point in Fig. 12) belongs without any doubt to a larger hipparion.

The recurring very large deviations of MC III proximal widths from the Höwenegg standard suggests that this old hipparion is not quite appropriate as a basis for size comparison for much younger hipparions. We have therefore tried to use *H. pomeli* as standard for further size comparisons.

2. VSI based on *H. pomeli* sample.

Using this reference (Table 12), the AaO histogram is of course 'normal' (Fig. 13). The Koobi Fora hipparions are somewhat smaller: the white ellipses indicate KBS member specimens, the two black squares correspond to tali from Chari and 'TB-?'. The Olduvai Bed II sample appears to possibly include two species: a distal MC III (DC II 52/679) seems very large.

Figure 14 shows the size differences between members A–B and G of the Omo Shungura sequence: a very small hipparion appears in member F, possibly represented later in the KBS member of the Koobi Fora Formation.

Hipparions of Hadar (Fig. 15) appear somewhat larger than those of Shungura (Fig. 14). At DD, there is an impression of three size groups, the associated bones of AL 155-6 plotting with the smallest. Using AaO as standard instead of Höwenegg (Fig. 12), AL 155-6 acquires a normal distribution. The presence of an extremely large hipparion (AL 155-1) is confirmed.

Table 8. Permanent lower cheek series or associated teeth from Ahl al Oughlam. Measurements in mm, approximate in brackets. L: length. W: width.

AaO 3180	P2	P3	P4	M1	M2	M3
Wear stage	3	3	3	3	3	3
Height	–	–	–	–	–	20
L occlusal	31.5	26	26	–	23.6	–
Ante fossette	–	9	9	7	7	8.1
Double knot	14	[17]	–	–	15.1	15.1
Post fossette	10.1	12.7	11.7	8	10	10
W occlusal	15	[16]	–	–	14	12.7
L ectostylid	3	8.1	7	+	7 & 1	4 & 1
W ectostylid	2.5	4.1	4	+	3	2.7
Protostylid	0	pli	pli	pli	pli	pli
Pli caballinid	0	0	0	–	#	0
AaO 197	**P2**	**P3**	**P4**	**M1**	**M2**	**M3**
Wear stage	1–2	1–2	1–2	1–2	1–2	1–2
L occlusal	32	25.9	25	24	24	28
Ante fossette	10	9.7	9	7.5	8	8.3
Double knot	13	16	16	15	14	12.2
Post fossette	12.7	12	12.2	10.1	10.3	10
W occlusal	12	14.2	14.5	13.5	14	13
L ectostylid	2.0	8.0	7.0	6.0	5.5 & 1	1.5
W ectostylid	1.5	4.1	4	4	3 & 1.5	2
Protostylid	0	0	0	0	0	0
Pli caballinid	0	+	0	+	0	0
AaO 1182	**P2**	**P3**	**P4**	**M1**	**M2**	**M3**
Wear stage	1	1	1	1	1	1
Height	42		61.5	52.5		60.5
L occlusal	30	27	26.1	25	24	25
Ante fossette	9	10	9	7	8.9	7.8
Double knot	13	16.1	15	15	14.5	11.5
Post fossette	14 sic	14.5	12	12.2	11.5	9
W occlusal	12	14.2	15	14	12	10.5
L ectostylid	0	present	present	–	present	0
W ectostylid	0					0
Protostylid	0	0	0	broken	0	0
Pli caballinid	+	+	0	–	+	0
AaO 2993	**P2**	**P3**	**P4**	**M1**	**M2**	**M3**
Wear stage	3	3	3	3	3	3
Height	16	17.5	–	–	–	[25]
L occlusal	31	24.5	25.1	23.5	23	28.5
Ante fossette	9	8.5	8	6	6.7	6.8
Double knot	15	16	16.6	14	15.6	13.5
Post fossette	12	12.5	13	9	10	10.7
W occlusal	14	15	17	13	14.5	14
L ectostylid	–	6	6	7	5	3.5
W ectostylid	–	4	4	4.9	4	3
Protostylid	isolated	pli	pli	pli	pli	+
Pli caballinid	0	0	0	0	0	0

CONCLUSIONS

— Although far from perfect, the use of *H. pomeli* as standard may be recommended for size comparisons of late African hipparions bones.

— There is no evidence of a marked sexual dimorphism in *H. pomeli.*

— The too frequent lack of association of bones, teeth, and skulls renders specific attribution of bones very awkward, but apart from the extremely large AL 155-1, the DD histogram is a good approximation of the size of *H. hasumense.* The latter was at least one standard deviation larger than *H. pomeli.*

Third metapodials. There are about 20 more or less complete adult MC IIIs and 35 MT IIIs, 15 of which are more or less entire (Table 14). In ratio diagrams, we use the minimal antero-posterior diameter of the medial condyle (no. 13 VE) rather than of the lateral condyle (no. 13 NY). The later was introduced only at the New York conference (Eisenmann *et al.* 1988) and most of our equid material was measured previously.

Table 9. Other permanent lower cheek teeth from Ahl al Oughlam.

	AAO 3554 P	AAO 4078 P	AAO 4072 P4	AAO 4072 M1	AAO 1435a M1	AAO 1435b M2	AAO 41 M
Wear stage	3	3	2	2	2	2	1–2
Height	15	23	[26]	[27]	34	43	
L occlusal	27.5	26	25	24	25	25.6	24
Ante fossette	10	10.5	9	7	7.3	7.7	7
Double knot	17	17	16	15	15	14	15
Post fossette	13.3	14	13.5	8.7	10.9	11.2	10.3
W occlusal	16.5	16	16	13	15	14	14
L at 1 cm	27.2	26.5	25	24	23	23	
W at 1 cm	17.7	17	15	15.5	14.9	16.5	
L ectostylid	7	2	3.5	3.5 & 1		4	6 & 1
W Ectostylid	3.7	1	2.0	2.5		2.5	3
Protostylid	pli	pli	isolated	isolated	isolated	isolated	
Pli caballinid		0	0	0	0	0	0

	AAO 3550 P2	AAO 1436 P2	AAO 3135 M3	AAO 1473 M3	AAO 3541 M3
Wear stage	4	3	2	2	3
Height	16	29	45	45	28
L occlusal	31	28.4	28	28.5	31.5
Ante fossette	7	8.4	8	8.8	8
Double knot	11.2	10	13	12.3	13
Post fossette	10.2	11.7	10.1	10	11
W occlusal	12.2	13.4	12	12.7	13
L at 2 cm			29.5	29	
W at 2 cm			12.4	12.5	
L at 1 cm			30	30	32
W at 1 cm			12.5	13	13
L ectostylid	1	0.5	2	1.5	2
W ectostylid	0.5	0.5	1	1	1
Protostylid	0	0	isolated		+
Pli caballinid	0	0		+	

Some scatter diagrams (not figured) show two sizes and/or morphologies: more or less robust, with more or less large proximal articular surfaces or distal widths. The coefficients of variation, however, are compatible with a monospecific sample. Table 15 gives the dimensions of some small and/or slender specimens of third metapodials not included in the statistical tables. They are probably subadult metapodials (like AaO-3707 and AaO-196) or juvenile.

Metacarpals. Compared with *H. mediterraneum* from the late Miocene of Pikermi (reference for the Simpson ratio diagram, Fig. 16), the AaO metacarpals are longer (no. 1), more robust (no. 3), wider at the level of the supra–articular tuberosities (no. 10), and have a more developed keel (no. 12).

Comparisons with other African hipparions are illustrated in Fig. 17. The closest resemblance is with the hipparion from Olduvai (mean of FLKN I 934, 7693, and SHK II 57/935), which is, however, more robust. From Koro Toro, Chad, one MC III (KT 96-17) is much more robust and has a more developed distal end; it falls outside the range of variation of AaO. The MC III from Ichkeul is longer than the average and seems more slender, but since it is not well preserved, most of its dimensions are uncertain. A metacarpal from Melka Kunturé, Gomboré II, seems close to those of Olduvai but is also poorly preserved. Most metacarpals from Hadar (not illustrated) are overall larger or have relatively larger distal ends (in particular the single specimen from the upper level AL 361-1, Kada Hadar member).

The development of the keel is an important character: functionally, it limits the lateral mobility of the articulation between third metapodials and first phalanges and facilitates sagittal 'pendular' movements. It is, however, difficult to quantify. To do so, Staesche & Sondaar (1979) have introduced the keel index: maximal antero-posterior diameter of the keel divided by the minimal antero-posterior diameter near the keel (percentage). Bernor *et al.* (2005) have greatly refined the estimation of keel development by also taking into account the size (scaling); in doing so, however, they were obliged to deal with relatively few specimens. We did no scaling – thus were able to use more specimens – and instead of calculating a percentage, we have considered the development of the keel as the difference between its maximal antero-posterior diameter and the minimal antero-posterior diameter of the medial condyle. When plotted versus the distal articular width of third metacarpals (Fig. 18), it appears – naturally enough – that the protrusion of the keel is related to the size of the MC III. A main group includes most of African hipparions: the relative development of the keel is roughly the same from Langebaanweg E and Olduvai (small form: l, m, n) to Olduvai (large form: o to u), including AaO, Hadar SH (d, i, j, k) and KH (b). Outside this main group, plot Omo F (5) and Roccaneyra (6) where the protrusion is maximal and more pronounced than in

Table 10. Permanent lower cheek teeth of Aïn Brimba. #: very small.

	1958.14.171 P4	1958.14.171 M1	1958.14.171 M2	1958.14.193 M2	1958.14.193 M3	1958.14.183 M2
Wear stage	0	1	0–1	1	0–1	2
Height			63		59	62
L occlusal	28	27	30	26.2	29	28
Ante fossette		10.1	11	8	8	8
Double knot		15.6	14	16	[12.5]	15.5
Post fossette		11.7	14	10.2	[9]	12
W occlusal	14	12	[11]	10.5	[8.5]	13
L at 2 cm	[28]					25
W at 2 cm						15
L at 1 cm						26
W at 1 cm						15
L first ectostylid		1		1	1, broken	1
W first ectostylid		1		1	1	1
protostylid		isolated	broken	isolated		0
Pli caballinid	1	0	1	0	1	#
	1937.11.21 P3	1958.14.175 P4	1958.14.179 M1	1958.14.184 M1	1957.11.10 M1	1958.14.183 section
Wear stage	2–3	2	2	2	2	3
Height	34	56	47	46	48	35
L occlusal	28.5	30	28	25.6	26	25.7
Ante fossette	10	14.2	7.8	8	7.7	7.8
Double knot	18.1	17	16	16	15.8	15.5
Post fossette	14.1	14.5	11	11	11.1	10.5
W occlusal	15	15	12	13.6	13	14.3
L at 2 cm	28	27	24.5	24		
W at 2 cm	16	16	14	14	15	
L at 1 cm	28	26	26	24.3	24.5	
W at 1 cm	16	16	14.3	15	15	
L first ectostylid	5.1	0.1		2	1	3.7
W first ectostylid	2.1	0.1		1	1	1
Protostylid		isolated	isolated	pli	pli	pli
Pli caballinid	1	1	1	0	0	0
	1957.11.20 P2	1958.14.229 P2	1958.14.177 P2	1958.14.178 M3	1958.14.176 M3	1958.14.174 M3
Wear stage	1–2	3–4	2–3	0–1	0–1	2
Height	44	25	37	57	60	48
L occlusal	[36]	34	34	[26]	28	30
Ante fossette	9	9	8	[8.7]	[13.5]	9
Double knot	12	14	13.1	[12.7]	[13]	14
Post fossette	15.5	15.5	15.8	[10]	[9]	11
W occlusal	13.5	13.5	14.7	[9.5]	[10.1]	11
L at 2 cm			33	30	30	30.3
W at 2 cm			13	13	13.3	12.2
L at 1 cm		33	32.8	30	30	31.1
W at 1 cm		15	13.2	13.2	12.5	13.2
L first ectostylid		2				1
W first ectostylid		1				1
Protostylid	0	0	0	not in wear	not in wear	isolated
Pli caballinid	#	0	1	1	1	0

dolichopodial hipparions (Venta del Moro, Maramena (1), Layna (2), Odessa (3), Sagajdak (4)). Minimal protrusion is found at Koro Toro, Chad (9) and in one specimen from Hadar DD2-3 (a). It is remarkable in that the keel seems relatively less developed in Hadar DD (c, e to h), and in particular less than in the contemporaneous Omo B (v, w). Mongolian (Shamar and Beregovaja) hipparions, whether more robust (*H. tchicoicum*) or more gracile (*H. houfenense*), plot with the main group. Not represented in Fig. 18, *Hipparion crassum* (Perpignan), *H. crusafonti* (Villaroya), and most of *H. heintzi* (Çalta), also plot with the main group.

Thus, it seems that the development of the keel cannot be directly related to geological age, nor to size, or gracility. Very probably, it is more related to environmental conditions that may select better adaptation to running in open landscapes, but local population idiosyncrasies cannot be excluded. It seems, therefore, risky to recognize lineages using keel development.

Metatarsals. Compared to *H. mediterraneum* (reference for the Simpson ratio diagram, Fig. 19), the AaO metatarsals are longer (no. 1), more robust (no. 3), proximally and

Table 11. Deciduous lower cheek teeth from Ahl al Oughlam. E1 and E2: first and second ectostylid. DK: Double knot.

	AaO 4070 dP2	AaO 4070 dP3	AaO 4070 dP4	AaO 2064 dP3	AaO 2064 dP4	AaO 3535 dP3
Wear stage	2	2	2	0–1	0–1	1–2
Height	–	–	–	28	34	17
L occlusal	31.5	29	31	31	34	31
Ante fossette	[9]	9	9			[8]
Double knot occlusal	12	15	15			15
Double knot maximal				[17]	[17]	
Post fossette	10.1	12.7	11.7			[11]
W occlusal	15	13	12.5			12.0
L ectostylid	1.5	3.5	2	present	present	present
W ectostylid	1	1.5	1.5			
Protostylid	0	pli	isolated	present	present	isolated
Pli caballinid	1	1	1			

	AaO 3136 dP2	AaO 3137 dP2	AaO 3169 dP2	AaO 3548 dP2	AaO 3597a dP2	AaO 4079 dP2	AaO 4080 dP2
Wear stage	1	0	0	0	0–1	0–1	0–1
Height	15	21	23	21	21	21	22
L occlusal	33	[33]	34	[34]	35.5	35	37
Ante Fossette	9						
Double knot occlusal	11	13	13	[13]	13	14	14
Double knot maximal		17	17	17.5	[17]	[19.5]	[19]
Post fossette	15						
W occlusal	11	11	11.5	10.5	11.3	13	12
Ectostylid	present		present	present	present	present	present

	AaO 2057 dP4	AaO 3138 dP3–4	AaO 3139 dP4	AaO 3140 dP3–4	AaO 3141 dP3–4	AaO 3142 dP3–4	AaO 3536 dP3–4
Wear stage	0–1	0–1	1	0–1	0–1	0	0–1
Height	[30]	27	25	26	24	26	22
L occlusal	35	[30]	32.5	31.5	31	31	31
Ante Fossette			8				
Double knot occlusal	14.5	13.5	14	14	14.5	15	15
Double knot maximal	[17]	[17]		[16]	[17.5]	[18]	
Post fossette			12				
W occlusal	10.5	10	11	10	11	11	11
top E1 from DK	11	10	3	12	8	11.5	
top E2 from DK		17	5.0			18.5	
L ectostylid maximal	6.5	6	[6.5]	9	7	6.5	
Protostylid	isolated	present	present	present	present	present	present

	AaO 3542 dP3–4	AaO 3544 dP3–4	AaO 3545 dP3–4	AaO 3547 dP3–4	AaO 3597b dP3	AaO 3597d dP4	AaO 4076 dP3–4
Wear stage	1	0–1	1	1	0–1	0–1	0–1
Height	26	26	21	23	21.5	23	27
L occlusal	[32]	32		30	[30]	[32]	31
Ante fossette			8	9			
Double knot occlusal		13	14	13.5	15	14.5	10.5
Double knot maximal	[17.5]	17	[19]	[16.5]	[17]	[18]	[16]
Post fossette			13	13			
W occlusal	11	9	11	10	11	10	9.5
top E1 from DK	11	8	5	2	10	[10]	6.5
top E2 from DK		14			17	[20]	11.5
L ectostylid maximal	8	6	[6]		7	7	6
Protostylid	present	present	present	present		present	present

distally deeper (nos. 6 & 12), and have much more developed distal widths (nos. 10 & 11). The single and incomplete MT III of Kvabebi (Vekua 1972; Alberdi & Gabunia 1985) is smaller but otherwise similar to the average of AaO; so are, to a lesser extent, the MT IIIs of Villaroya and Roccaneyra. No African Plio-Pleistocene metatarsals resemble those of AaO, the less dissimilar being those from Olduvai and Koro Toro, Chad (Fig. 20).

The scatter diagram of keel development (not figured here) carries less information than for the third metacarpals. However, another feature seems interesting because it expresses approximately the position of the lateral digits: when they are placed more ventrally, the diaphysis is narrower and deeper (Fig. 21). The deepest diaphyses are

Table 12. Statistics of Höwenegg limb bones widths from Bernor *et al.* (1997) and of *H. pomeli*. $\bar{x}$: mean, *s*: standard deviation, *n*: number of specimens, min: minimal observed value, max: maximal observed value. Tibia diaphysis, supposed: values used in this paper (see text).

Bernor *et al.* 1997	$\bar{x}$	s.e.	*n*	min	max
Humerus distal articular	70.46	2.66	13	65.3	74.1
Radius proximal maximal	69.23	1.77	13	65.8	72
Radius distal maximal	64.13	2.04	12	61.5	67.8
MC III proximal articular	39.92	1.05	16	37.7	41.9
MC III distal articular	37.09	1.6	12	33.7	39.9
PH I anterior diaphysis	29.1	1.47	12	27.1	31.2
PH II anterior diaphysis	31.85	1.17	15	30	34.5
PH III anterior articular	41.05	2.52	8	38	45
Tibia diaphysis	[42.6]	[5.61]	13	[32.4]	49.2
Tibia diaphysis	44.6	2.00	13		49.2
Tibia distal maximal	70.14	1.86	19	66.7	73.4
Talus distal articular	44.78	1.81	21	40.5	48.1
MT III proximal articular	41.77	2.09	18	37.3	46.5
MT III distal articular	37.77	1.89	23	34.9	42
PH I posterior diaphysis	30.87	1.47	12	28.1	33
PH II posterior diaphysis	31.34	1.07	11	29.2	33
PH III posterior articular	36.43	1.34	4	35	38.2

H. pomeli	$\bar{x}$	s.e.	*n*	min	max
Humerus distal articular	73.4	2.69	6	69	76.5
Radius proximal maximal	73	2.83	11	67	78.2
MC III proximal articular	46.3	2.01	20	42.5	49.6
MC III distal articular	42.0	1.19	26	39.6	44.2
PH I diaphysis	33.3	2.13	7	30	37
PH II diaphysis	37	1.75	9	35.3	40
PH III articular	42.7	2.99	13	37	48
Tibia diaphysis	47.4	2.99	10	46	53
Tibia distal maximal	70.9	2.03	8	68	73
Talus distal articular	48.5	2.35	33	43.5	54
MT III proximal articular	45.3	1.66	35	42.3	49
MT III distal articular	43.2	1.18	25	40.7	45

found in dolichopodial hipparions (Venta del Moro, Maramena (1), La Gloria (2)) but also in some specimens from Langebaanweg E and Olduvai. The widest and flattest diaphyses occur at Çalta (*H. heintzi*), Omo C (10), Hadar, and in *H. turkanense* (11). In Vallesian species, the diaphysis may be very wide and flat (Eppelsheim, 12), or much less (Esme Akçaköy). Not illustrated *H.* cf. *houfenense* of Shamar and Beregovaja and *H.* cf. *crusafonti* of Kvabebi plot with the intermediate group together with AaO.

Phalanges of the third digit: first phalanges. In most species of *Equus*, it is possible to discriminate anterior and posterior phalanges (Dive & Eisenmann 1991). This discrimination is more difficult in hipparion. Nevertheless, a scatter diagram of the proximal depth versus the distal articular width (Fig. 22) gives good results: in samples of first phalanges associated with third metapodials (Höwenegg, Hadar, Shamar, Layna, Grebeniki) or determined by Gromova (1952) (*H. elegans* from Pavlodar, *H. moldavicum*) and Gabunia (1959) (Khadjibi, Chobruchi, Kuialnik), the proximal depth is relatively larger when the phalanx is posterior. Moreover, within the same species, anterior first phalanges are usually more slender. According to these criteria, we have at AaO four anterior, and three posterior, phalanges (Table 16). The best preserved anterior phalanx (AaO 1261, Fig. 23B) is small and may belong to a not fully grown individual. On the ratio diagram (Fig. 24) it compares well with a specimen from Olduvai M-14456c (possibly Bed I), which is, however, more slender. Similar proportions are found in the much larger AL 161-1 (Hadar DD) and in the much smaller Omo 1974-263-573 (member C ?). The other anterior phalanges of AaO are larger and more robust.

One of the posterior PH Is associated with a MT III and a second phalanx (AaO-196) is badly preserved and looks very small. It could fit with the anterior AaO-1261.

On the ratio diagram (Fig. 25), AaO-2838 resembles two Tanzanian phalanges (Olduvai SHKII 1957.1165 and Laetoli M 31934) and also AL 194-2 of Hadar (DD). Specimen AaO-2844 (Fig. 23A) is more like AL 155-6 (Hadar DD).

Second phalanges. Second phalanges may be sorted into anterior or posterior by plotting the distal articular breadth versus the maximal length: posterior phalanges are relatively narrower. They are also deeper at the proximal end. According to these characters, there are four anterior and five posterior phalanges at AaO. The sample appears monospecific (Table 17).

Third phalanges. It is simple to distinguish anterior from posterior third phalanges of the same individual, for example in Hadar AL 155-6 (Table 18), the anterior being wider at the sole and having wider and more shallow articular surfaces. But the intraspecific variation is very large and assignment of a particular specimen is often uncertain in unassociated bones. At AaO (Fig. 23C,D), three third phalanges are certainly anterior and two are certainly posterior. The assignment of the rest is tentative.

Other limb bones. Compared to the extant *Equus grevyi* and the fossil *Allohippus vireti* the variation of the talus is large (Table 13; Fig. 23E), but all attempts to split the sample were unsuccessful. Measurements of other limb bones are in Table 19.

Limb bone segments. In *Equus* and *Hipparion,* the relative lengths of limb bones give useful information about cursorial abilities; information on the ground (hard or heavy) is provided by the relative width of the third phalanges (Eisenmann 1984, 1991; Eisenmann & Sondaar 1998). Schematically, third phalanges are narrow when the ground is hard; proximal limb bones are relatively short when species are cursorial. Until now there were no good data on monospecific whole (associated) skeletons of hipparions, so that in the past (Eisenmann & Sondaar 1998), ratio diagram comparisons were made with the extant *E. hemionus onager.* But now we are able to use as reference the Höwenegg sample (Bernor *et al.* 1997, and V.E. unpubl. data; Table 20). For humeri and femora, we use articular lengths; for the third phalanx, we use the solar width of the anterior phalanx; for all other bones, we use maximal lengths.

There is only one associated skeleton of African hipparion (AL 155-6 of the Denen Dora member of Hadar), presumably belonging to *H. hasumense,* and few samples rich enough for using reliable average dimensions. A ratio diagram (not illustrated) has shown no great differences between the proportions of the possible juveniles and the other bones of AaO, justifying the use of

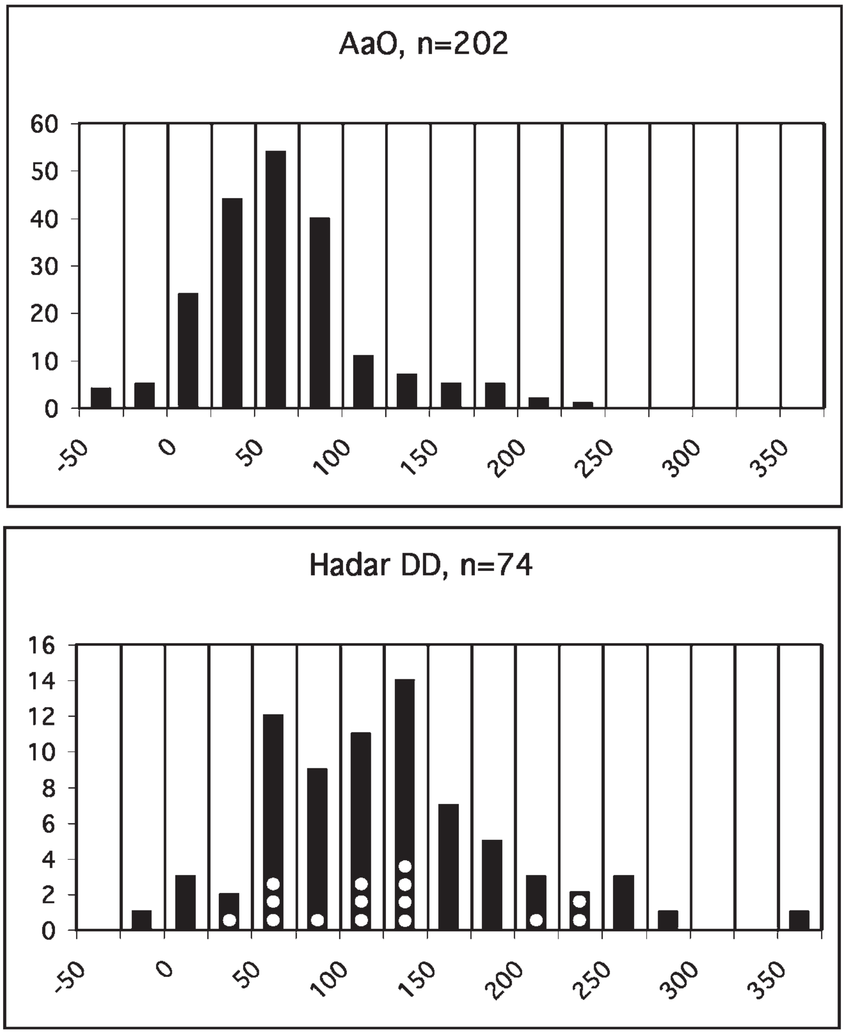

Figure 12. Variation Size Indices for AaO and Hadar DD hipparion samples, using Höwenegg as standard. *n*: number of widths. White points for AL 155-6-associated limb bones.

Table 13. Statistics for tali of the AaO sample, for the extant *E. grevyi,* and for the fossil *Allohippus vireti.* Abbreviations as for Table 12, plus c.v.: coefficient of variation (c.v. = 100 × s.e./$\bar{x}$). 1: maximal length, 2: maximal diameter of the medial condyle, 3: maximal breadth, 4. breadth of the trochlea at the apex of each condyle, 5: distal articular breadth, distal articular depth, 7: maximal medial depth.

AaO	*n*	$\bar{x}$	min	max	s.e.	c.v.
Greatest length	40	63.3	58.5	69.0	2.86	4.52
Medial length of trochlea	38	61.1	54.5	67.5	2.58	4.22
Maximal width	36	59.8	53.0	68.0	3.02	5.05
Trochlear width	40	29.6	26.6	32.0	1.43	4.83
Distal articular width	33	48.5	43.5	54.0	2.35	4.85
Distal articular depth	37	35.0	31.5	38.4	1.54	4.40
Medial depth	33	50.2	44.5	58.0	2.50	4.98
E. grevyi						
Greatest length	28	64.7	60.5	68.0	1.87	2.89
Medial length of trochlea	28	62.7	60.0	65.6	1.36	2.17
Maximal width	28	61.8	56.0	66.0	2.20	3.57
Trochlear width	28	28.9	26.0	31.0	1.59	5.52
Distal articular width	28	51.0	47.0	55.5	1.94	3.81
Distal articular depth	28	35.8	33.0	39.0	1.64	4.57
Medial depth	28	52.6	49.5	55.5	1.76	3.34
Allohippus vireti						
Greatest length	105	66.5	60	73	2.52	3.79
Medial length of trochlea	109	65.5	60	70	2.35	3.58
Maximal width	110	66.9	60	72.5	2.63	3.93
Trochlear width	114	31	27.5	34.5	1.36	4.39
Distal articular width	102	54.9	51	59.5	1.77	3.21
Distal articular depth	108	37.5	35	41	1.42	3.79
Medial depth	100	55.3	49.5	59.5	1.85	3.35

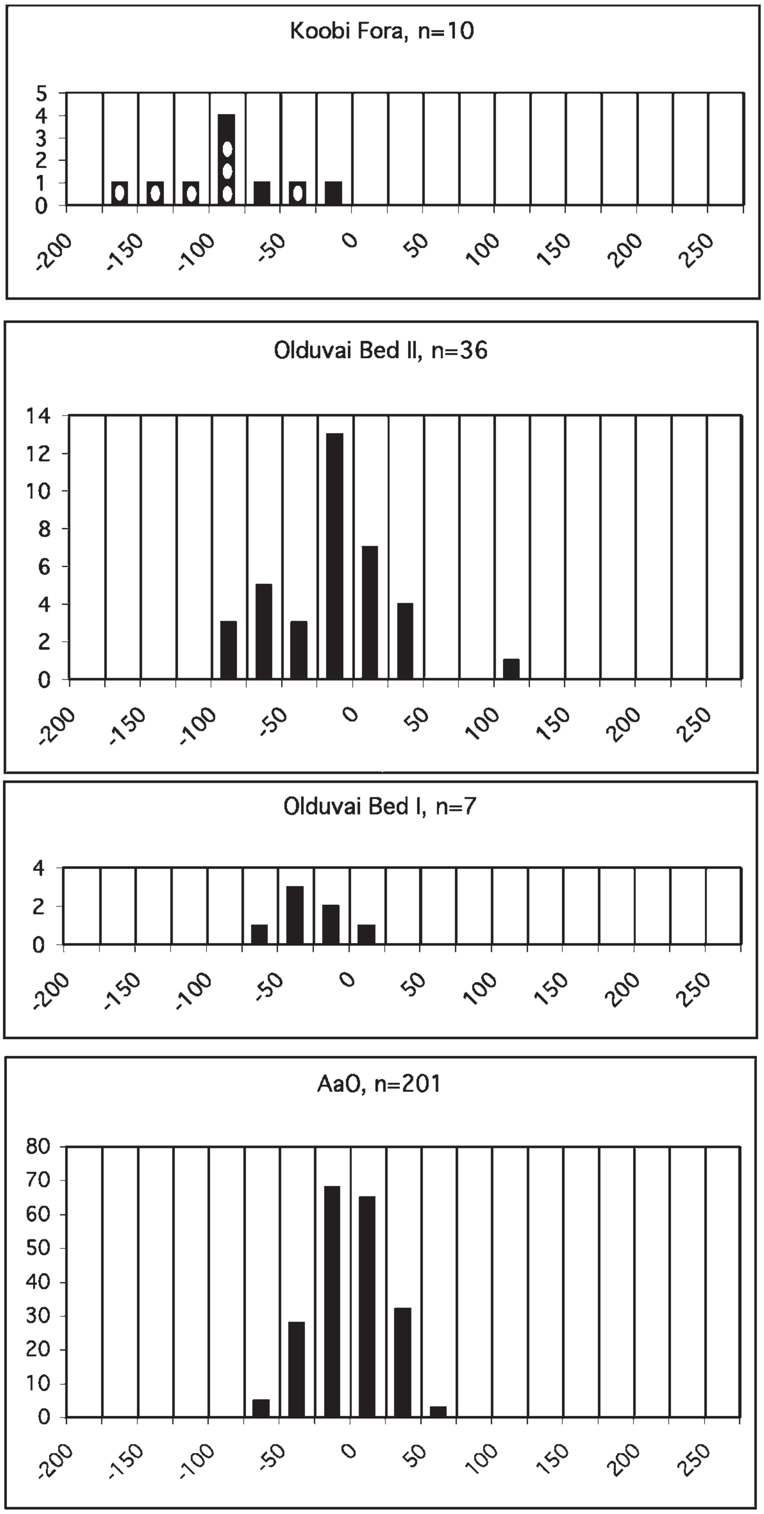

Figure 13. Variation Size Indices using AaO as standard for Olduvai Bed I, Bed II, and Koobi Fora. White ellipses for KBS member specimens.

average dimensions. Figure 26 compares *H. hasumense* AL 155-6, *Hipparion heintzi* of Çalta, the sample of Langebaanweg E, and *H. pomeli*. The very short metapodials of *H. heintzi* are a good indication of poor cursorial adaptation. By contrast, *H. hasumense* and *H. pomeli* were probably better runners. Moreover, at Höwenegg and Çalta, the femora and radii are of subequal length, while in *H. pomeli* (like in all extant *Equus*) the radius is much longer. The proportions of the Langebaanweg *E. hipparion* are similar to those of *H. pomeli.*

The cursorial adaptations of *H. pomeli* from Ahl al Oughlam agree well with the environment of the locality, where the abundance of alcelaphines and antilopines among bovids suggest an open landscape.

ADDITIONAL NOTES: *H. HENDEYI* SP. NOV. FROM LANGEBAANWEG E AND *H.* AFF. *CRASSUM* FROM KOSSOM BOUGOUDI, CHAD

Langebaanweg E

Hooijer (1976) referred to *H.* cf. *baardi* the material from

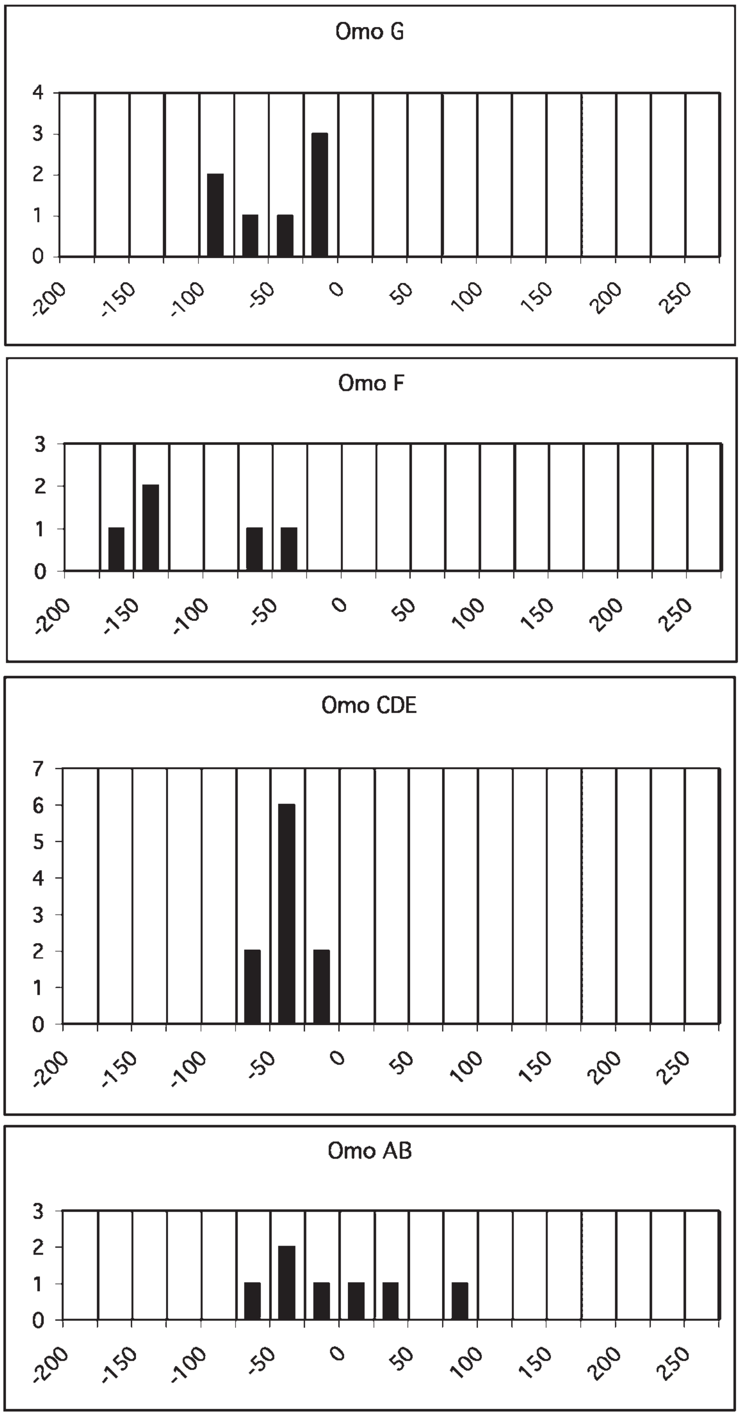

Figure 14. Variation Size Indices using AaO as standard for Shungura Formation (Omo).

Langebaanweg E Quarry, South Africa. Hendey (1978) correctly pointed that the hipparion of Quarry E was very different from *H. baardi* of Baard's Quarry and gave measurements of the lower cheek teeth. We propose to name this hipparion *H. hendeyi,* and choose as holotype the complete skull of an old female, L 22187, from Langebaanweg E, preserved in the Iziko South African Museum, Cape Town, and figured by Hooijer (1976, plate 1). The skull (Table 1) has a very long vomer–palate distance, a very faint POF, and a long and narrow muzzle; the cheek teeth of the skull are too worn to provide information on their dimensions but according to Hendey's data the lower series was about 152 mm long. On the whole, the skull resembles *H. giganteum* and *H. verae* of Grebeniki (Appendix Fig. 5), *H. moldavicum* of Taraklia, and possibly *H. feibeli* from Ekora-Kanapoi (Fig. 27). The cheek teeth of Quarry E are hipparionine, although some are hypsodont; the lower incisors are grooved (Hooijer 1976, plate 2-6; plate 8, fig. 2). The MC IIIs have well-developed keels (Fig. 18) exceptional in a species which is not dolichopodial. Two MT IIIs (L 5899 and L 21827) have very wide diaphyses and do not fit with the rest of the sample (Fig. 21).

Chad, Kossom Bougoudi 9

A fragment of skull, KB 9-97-13, dated to about 5 Ma. (Brunet *et al.* 2000), is remarkable in its very large dimensions (Table 1). The POF is situated at about 40 mm in front

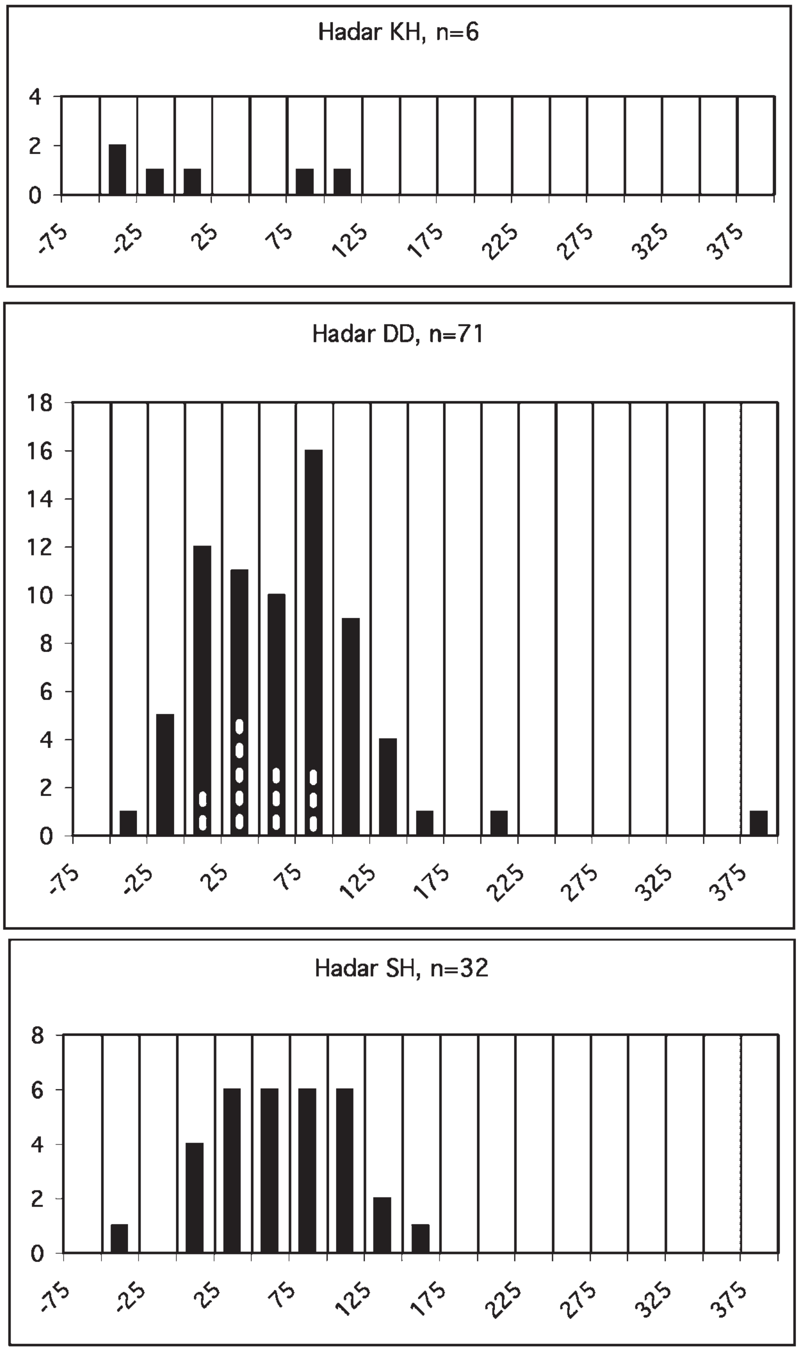

Figure 15. Variation Size Indices using AaO as standard for Hadar Formation. White ellipses for AL 155-6-associated bones.

of the orbit. The fossa is very well delimited at its anterior and dorsal borders, but not well delimited ventrally and posteriorly. The vomer–palate distance is long. The premolars and M1 are much worn; the less worn M2 and M3 are plicated.

This skull differs from *H. proboscideum* of Samos by the presence of only one POF instead of two (Koufos & Vlachou 2005), the long vomer–palate and P2–orbit distances. On the whole, it resembles best *H. dermatorhinum* from China (data Bernor *et al.* 1990; V.E., unpubl. data) and possibly *H. crassum* and *H. tchicoicum*, judging by the dimensions of the mandibles Pp 208 from Perpignan and Shamar 3381-53 (Table 2). *H. garedzicum magianense* of Sor, Tadjikistan (Zhegallo 1978) very probably belongs to the same group (Table 1; Fig. 28).

DISCUSSION

Like some other authors (Koufos & Vlachou 2005), we use *Hipparion* as a generic name for all Old World late Miocene equids without distinguishing the numerous complexes to which they may belong. We prefer also not to give specific names to isolated limb bones or teeth.

Bernor & Armour-Chelu (1999a) have presented a comprehensive overview of hipparions in general and more particularly of African forms. According to them, there were only two founding populations in Africa. The first derived from the *Hippotherium* complex, which includes (among other species) the European *H. primigenium* and *H. giganteum*, the Chinese *H. dermatorhinum*, and the African *H. africanum*. The second founding population derives from the *Sivalhippus* complex, which includes among other species, the Siwaliks *S. perimense* and the

Table 14. Statistics for third metacarpals and metatarsals from Ahl al Oughlam. Abbreviations as in Table 13.

	MC	*n*	$\bar{x}$	min	max	s.e.	c.v.
Maximal length	1	19	237.6	226	254	7.23	3.04
Minimal breadth	3	25	32.7	30.8	35	1.11	3.40
Depth at level of 3	4	22	27.6	26	30.4	1.09	3.96
Proximal articular breadth	5	20	46.3	42.5	49.6	2.01	4.33
Proximal depth	6	20	31.8	29	34.4	1.54	4.84
Distal max. supra–articular breadth	10	28	44.6	42.1	47.1	1.36	3.05
Distal max. articular breadth	11	26	42	39.6	44.2	1.20	2.85
Distal max. depth of keel	12	25	35.2	33.2	37	0.99	2.80
Distal min. depth of medial condyle	13 VE	28	28.7	27.7	30.2	0.70	2.45
Distal min. depth of lateral condyle	13 NY	5	28.7	27.7	29.5	0.73	2.55
Distal max. depth of medial condyle	14	25	30.8	29.3	33	0.84	2.74
Max. diameter of 3rd carpal facet	7	22	39.6	35.6	41.5	1.70	4.29
Max. diameter of 4th carpal facet	8	21	11.9	10	14	1.02	8.52
	MT	***n***	$\bar{x}$	**min**	**max**	**s.e.**	**c.v.**
Maximal length	1	15	282.3	277.0	288.0	3.28	1.16
Minimal breadth	3	18	32.1	30.5	34.3	0.93	2.91
Depth at level of 3	4	21	32.44	30.3	34.0	1.05	3.25
Proximal articular breadth	5	35	45.3	42.3	49.0	1.66	3.66
Proximal depth	6	30	39.0	35.5	43.2	1.49	3.81
Distal max. supra–articular breadth	10	25	47.1	44.7	50.5	1.78	3.78
Distal max. articular breadth	11	25	43.2	40.7	45.0	1.18	2.72
Distal max. depth of keel	12	26	36.9	35.1	38.7	1.03	2.8
Distal min. depth of medial condyle	13 VE	27	29.0	27.8	30.0	0.65	2.25
Distal min. depth of lateral condyle	13 NY	6	28.2	27.2	29.0	0.59	2.08
Distal max. depth of medial condyle	14	24	31.9	29.7	33.6	0.91	2.85
Max. diameter of 3rd tarsal facet	7	32	41.8	38.0	44.5	1.56	3.73
Diameter of 4th tarsal facet	8	24	10.0	8.5	11.3	0.76	7.58

Chinese *Plesiohipparion houfenense*, as well as the European *Pl. crassum* (Bernor & Armour-Chelu 1999b). Bernor & Armour-Chelu consider *S. perimense* as the sister group of *Eurygnathohippus* within which are placed *H. turkanense* and all the post-Miocene African hipparions.

In 2003, Bernor & Harris wrote that the POF of *Eurygnathohippus* aff. *feibeli* of Ekora 'suggests relationships within the *Cormohipparion-Hipparion-Hippotherium* trichotomy while *Eurygnathohippus turkanense*'s reduced POF and limb proportions suggest an alliance between *E. turkanense* and *S. perimense*. The occurrence of ectostylids in Lothagam *E. turkanense* and *E. feibeli* suggests a phylogenetic relationship exclusive of Eurasian hipparions and inclusive with Plio-Pleistocene African hipparions'.

Still more recently, Zouhri & Bensalmia (2005) made a thorough revision of Old World hipparions. They recognize four genera: *Hippotherium*, *Cremohipparion (*including *Cr. moldavicum* as a synonym of *Cr. mediterraneum), Hipparion,* and *Proboscidipparion.* The latter is subdivised into three subgenera: *Proboscidipparion, Plesiohipparion,* and *Eurygnathohippus.* They rightly point that *H. crassum* cannot be considered as a *Plesiohipparion* because of the primitive pattern of its lower cheek teeth, and rightly exclude *H. turkanense* from *Eurygnathohippus* because it has neither the typical lower cheek teeth nor the reduction of the third incisors of *Eurygnathohippus.*

1. Discussion of Bernor & Armour-Chelu (1999a) and Bernor & Harris' (2003) opinions

Our first point of disagreement concerns the definition

Table 15. Metapodials from Ahl al Oughlam. Measurements as in Table 14.

	MC AaO 194	MC AaO 2831	MC AaO 3706	MC AaO 3707	MC AaO 3725
1	230			240	
3	28.2	28.6	28.7	28.8	
4		24.3	22.4	25.5	
5	44.8		43	45.5	
6				31.8	
10				41.2	40.8
11					39.2
12				33.7	34.4
13 VE				27	27.3
13 NY				25.8	27.2
14				28	29.6
7	38		35.5	39.2	
8	10		11	10.4	
	MT AaO 196	**MT AaO 4440**	**MT AaO 1514**	**MT AaO 3725b**	
1	275				
3		29.5			
4	34.2	33.8			
5		45.7			
6		36.5			
10	42.5		44	40.8	
11	41		41	40.4	
12	33.7		35.1	34.5	
13 VE	28.4		27.8	27.9	
14	31.5		30.3	29.6	
7		42.5			
8		13.3			

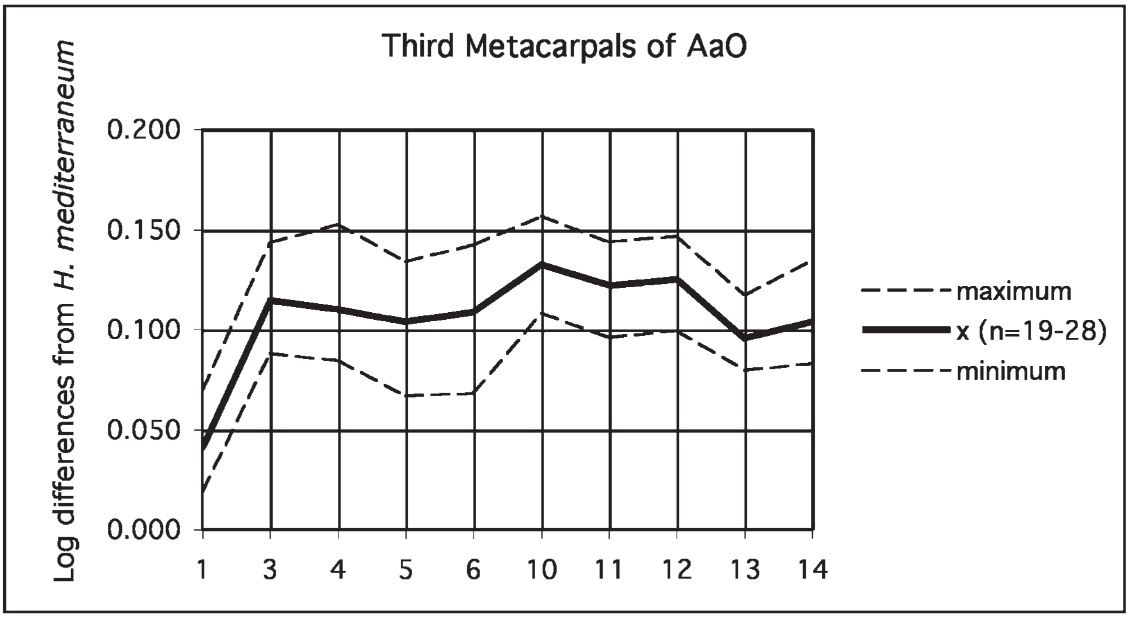

Figure 16. Ratio diagram for AaO third metacarpals maximal, average ($\bar{x}$), and minimal values. Measurements as in Table 14.

of *Eurygnathohippus.* All late hipparions – not only African – exhibit many apomorphies. But synapomorphies are not so evident.

a) The grooved lower incisors are not a synapomorphy of all African late hipparions since they are present in *H. moldavicum* (Chobruchi), *H. giganteum* (Grebeniki), *H. crassum* (Perpignan), and *H. houfenense.* On the other hand, the incisors of AL 155-6 (Denen Dora of Hadar) are not grooved, while they are grooved in AL 177-21 of the same member, and in AL 59-9B of the earlier Sidi Hakoma member. Both grooved and not grooved incisors are represented in Omo member C.

b) The cheek teeth of late hipparions present many apomorphies. Most are probable homoplasies related to grazing hard food. Such are the hypsodonty, the elongated and narrow protocones, the angular double knots, the development of protostylids, the straightening of the vestibular enamel ridges, and the development of vestibular enamel structures between protoconid and hypoconid. As already pointed out (and partly illustrated) by Forstén (1997a,b), the latter are similar in general, but different in detail. In *H. huangheense* from China (FAM 11820), a posterior pointed extension of the protoconid may be a functional equivalent of the pli caballinid/ectostylid complex. In *H. crusafonti* from Villaroya, the pointed extension of the protoconid is present but less marked than in *H. huangheense.* In *H.* cf. *crusafonti* of Kvabebi there are very well-developed plis caballinids (but no extension of the protoconid); moreover, there are well developed plis protostylids on dp2 (Fig. 29).

The only cheek tooth synapomorphy of late hipparion

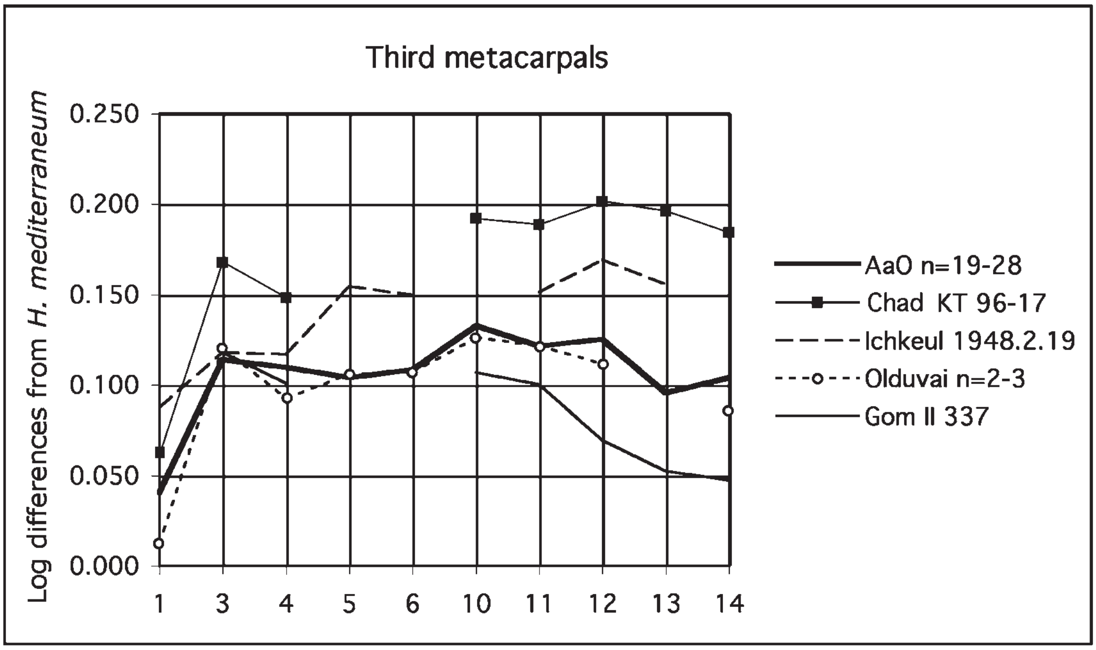

Figure 17. Ratio diagram comparing average AaO third metacarpal to metacarpals of Chad, Ichkeul, Olduvai (FLKNI 934 and 7693, SHKII 57/935), and Melka Kunturé. Measurements as in Table 14.

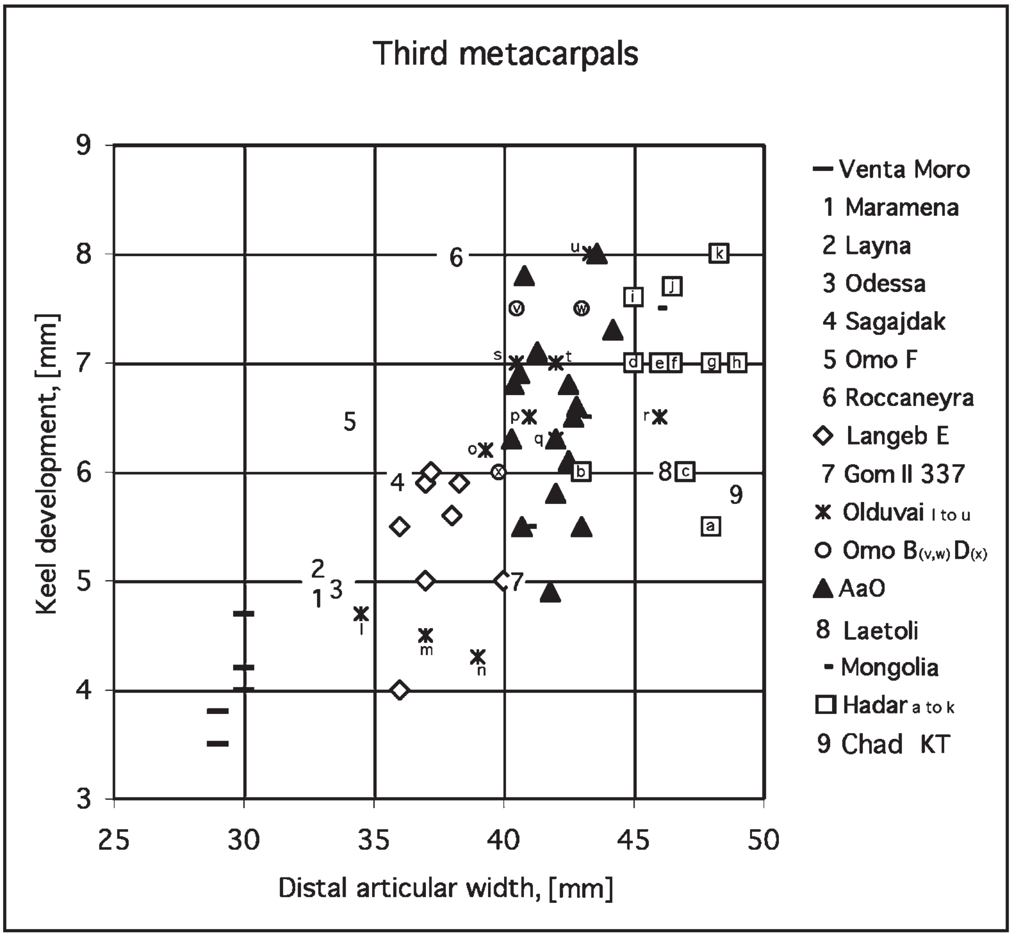

Figure 18. Scatter diagram (mm) of third metacarpal keel development versus distal articular width. Hadar: a: 116-33, DD2-3; b: 361-1, KH; c: 99-38, unknown; d: 327-14A, SH2; e: 115-6BB, DD2; f: 150–1, DD; g: 212-3, DD2-3; h: 315-9C, DD2-3; i: B 236-7, SH2-3; j: B 147-20, SH2-3; k: 107-15, SH2-3. Olduvai: l: 1963/2750, subadult, BK II; m: M 16985, unknown; n: 57/576, subadult ?, SHK II; o: 59/366, LGK; p: F 345, unknown; q: 7963, FLKN I; r: F 811, S4 1941; s: 933, FLKN I; t: 57/935, SHK II; u: 1952/307, BK II. Omo B: v: 3004-41; w: 3005-41. Omo D: x: 73-2626.

from African would be the development of ectostylids as functional equivalents of plis caballinid or protoconid extensions. But ectostylids are clearly visible on the occlusal surfaces of the molars of BMNH 26211 from Bhandar Bone Bed of Dhok Pathan (Forstén 1997b, fig. 16A). On the other hand, they are not developed in the Laetoli specimens, and in those from Baard's Quarry at Langebaanweg, and they are not expressed in *H.*

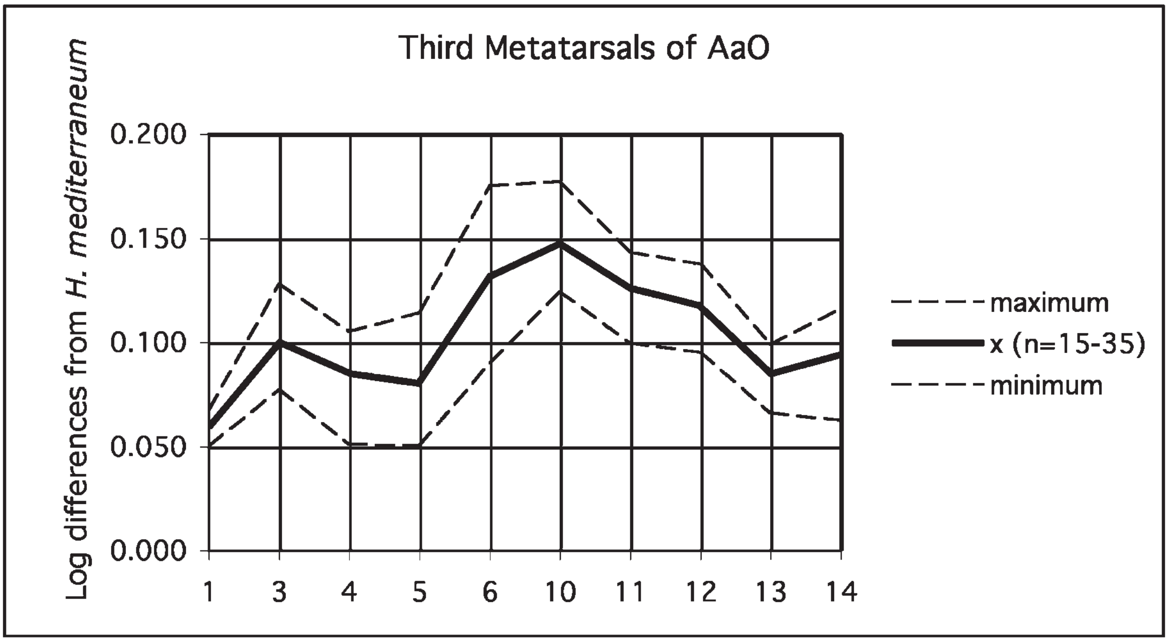

Figure 19. Ratio diagram for AaO third metatarsals maximum, average ($\bar{x}$), and minimum values. Measurements as in Table 14.

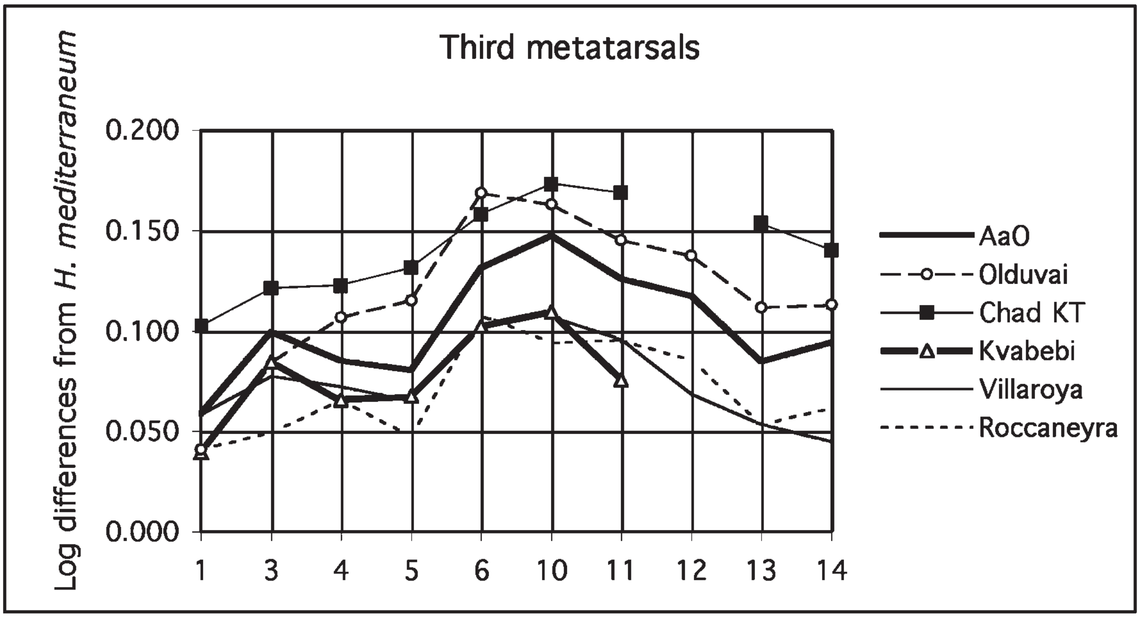

Figure 20. Ratio diagram comparing average AaO third metatarsal to metatarsals of Olduvai (BKII 1953-435, 1953-135, 1963-620; unknown 807 and 1-6), Chad KT13 (96-21, 39, 489), Roccaneyra (1948-13-11), Villaroya, and Kvabebi (KV 1082). Measurements as in Table 14.

turkanense from Lothagam Lower Nawata, appearing only in the Upper Nawata member.

c) In our opinion, the main point is the structure of the vomer and the basi-cranial 'caballine' proportions (vomer distances from the palate and the basion). They constitute solid synapomorphies for *H. afarense* and the *H. cornelianum* of East Turkana. The Chinese *H. houfenense s.s.* (type skull THP 10508) possibly had the same kind of vomer, because of its apparently long basion–vomer distance (Qiu, pers. comm.) but we are not certain of that since the skull is badly preserved. In *H. huangheense* (FAM 11820) the structure of the vomer and the

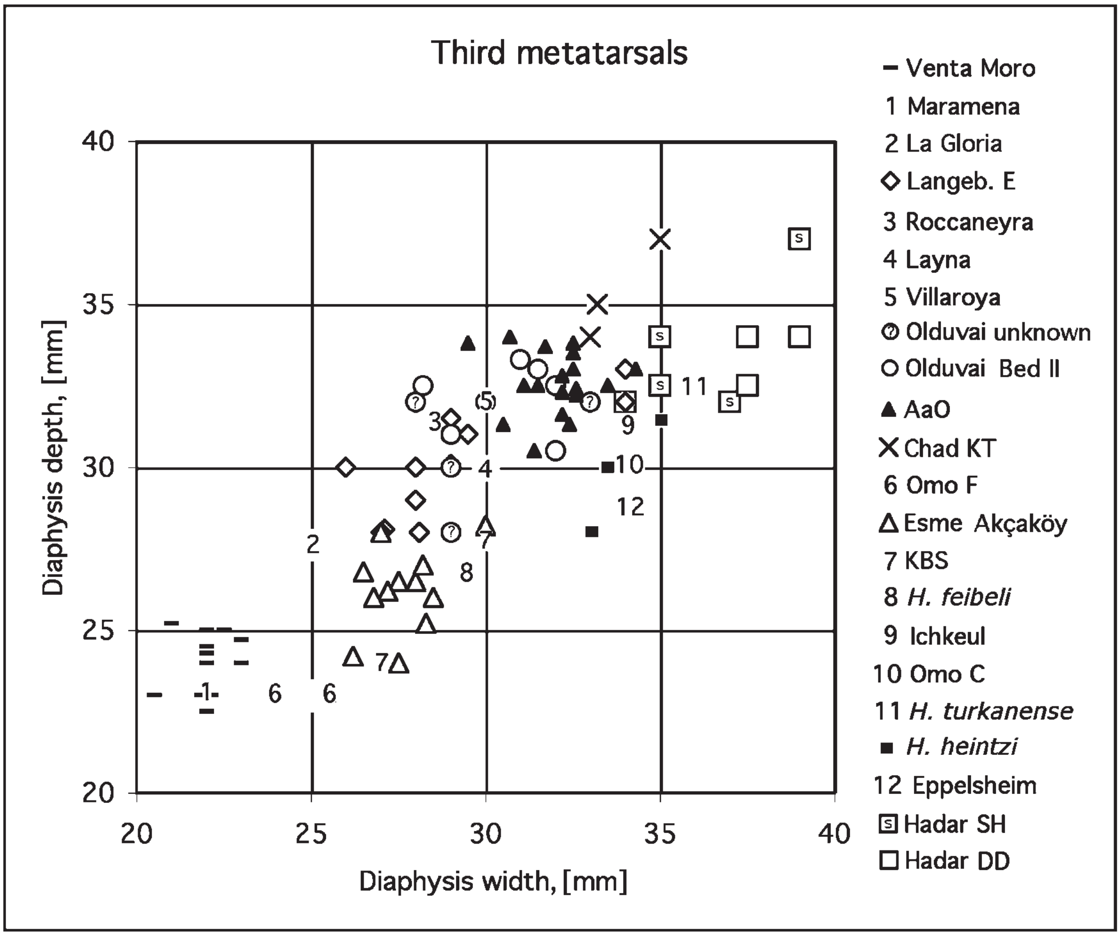

Figure 21. Scatter diagram (mm) of third metatarsal diaphysis depth versus diaphysis width.

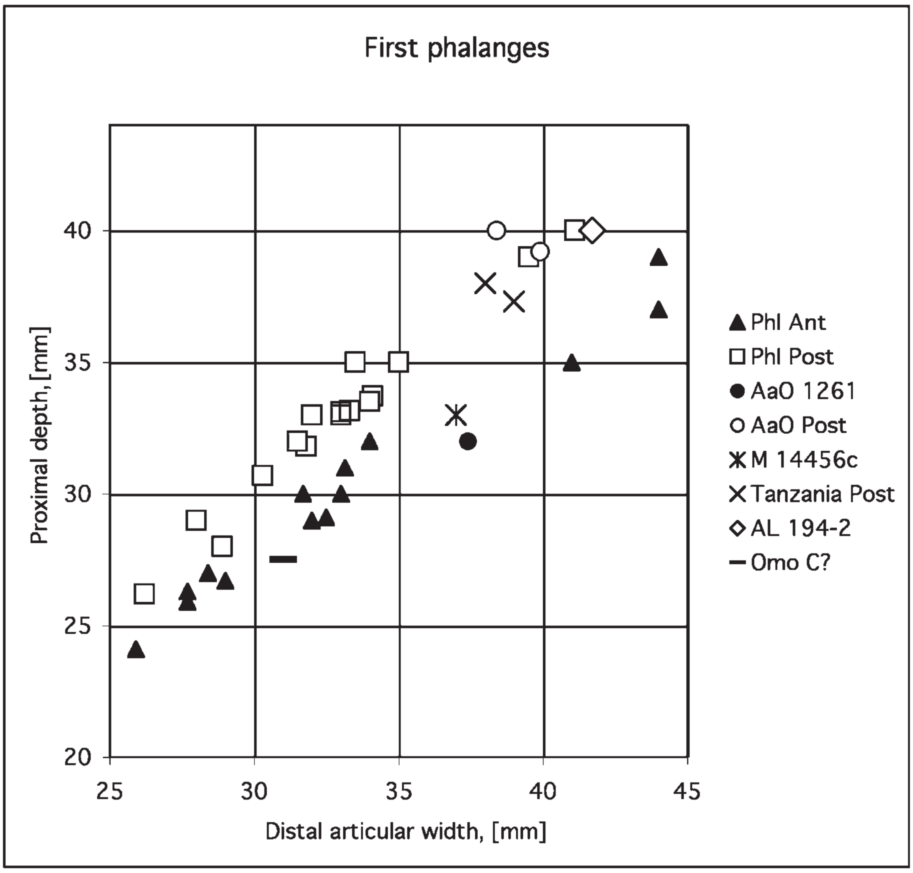

Figure 22. Scatter diagram (mm) of first phalanges of the third digit proximal depth versus distal articular width. Ant: anterior phalanges, Post: posterior phalanges. Data in Table 16.

basi-cranial proportions are uncertain owing to incomplete preparation. In *H. crusafonti* of Villaroya, the basi-cranial proportions are not known. In *H.* cf. *crusafonti* of Kvabebi, the distance from vomer to palate seems short but the morphology of the vomer and the distance between vomer and basion are unknown. When we studied the skull of *Sivalhippus perimense*, the basicranium was not fully prepared, so that information on this important point is again lacking. It is quite clear, however, that *H. turkanense* did not possess any of the basi-cranial characters shared by *H. afarense* and *H. cornelianum.*

d) Short, squarish, and broad arcades, without the reduction of I3, are not uncommon in hipparions. The best example is the well-known Greek *H. dietrichi*, but similar

Table 16. First phalanges of the third digit (PH I). W: width.

PH I		Ahl al Oughlam			Hadar DD		Omo C?	Olduvai Bed I?	Chad KT	Pikermi
	Anterior	AaO 1261	AaO 2839	AaO 3845	AL 155-6X	AL 161-1	1974.263 573	M 14456c A	13.96.42	M 47800
Maximal length	1	65.8	68.5	67.1	75	80	64	71.5	85	61.8
Minimal width	3	30	33.5	32.2	37.9	33	25	30.5	40.5	32
Maximal prox. W	4	42.8	47.7	45	52	49	36	44	57.5	45.5
Maximal prox. depth	5	32	36.4		39	37	27.5	33	43	33
Dist. supra–artic. W	7	37.4	38.8	40	44	44	31	37	48	34.7
Dist. articular width	6	36.3	39.4	38.6	45.5	44	30.5	37	48.5	35
Dist. articular depth	8				26.1				31	22.1

		Ahl al Oughlam			Hadar DD			Olduvai	Laetoli SHKII
	Posterior	AaO 2838	AaO 2844	AaO 196	AL 155-6AA	AL 161-2	AL 194-2	1957.1165	M 31934 P
Maximal length	1	67.5	70.5	62.4	70	76	72	69	67
Minimal width	3	34.2	37	32.6	38	34	36	34.2	33
Maximal proximal W	4	46.5	51.5	[43]	52	46.5	48	47.2	45
Maximal prox. depth	5	40	39.2	[32]	40	39	40	37.3	38
Dist. supra–artic. W	7	38.4	39.9	[39]	41.1	39.5	41.7	39	38
Distal articular width	6	38.8	39.9	38	43	40	41.2	39	36
Distal articular depth	8				26		28		

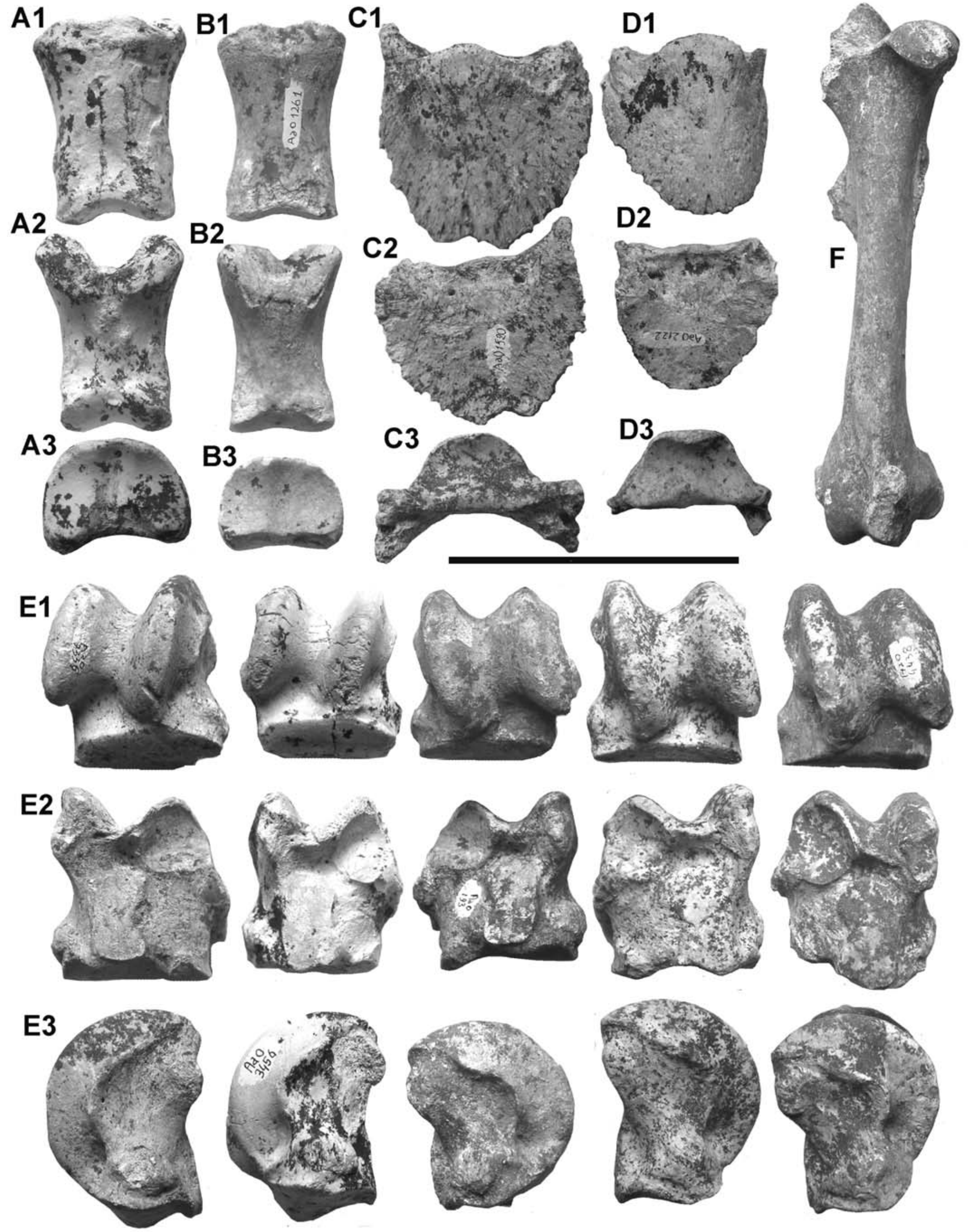

Figure 23. *Hipparion pomeli* sp. nov. from Ahl al Oughlam. **A–D**, phalanges in (1) dorsal, (2) palmar/plantar, and (3) proximal views. **A**, first phalanx AaO-2844; **B**, first phalanx AaO-1261; **C**, third phalanx AaO-1520; **D**, third phalanx AaO-2122. **E**, Astragalus in (1) dorsal, (2) plantar, and (3) medial views; from left to right AaO-3336, AaO-3456, AaO-193, AaO-1530, AaO-4438. **F**, Femur AaO-1503 in dorsal view. Scale bar = 20 cm for Fig. F; 10 cm for all others.

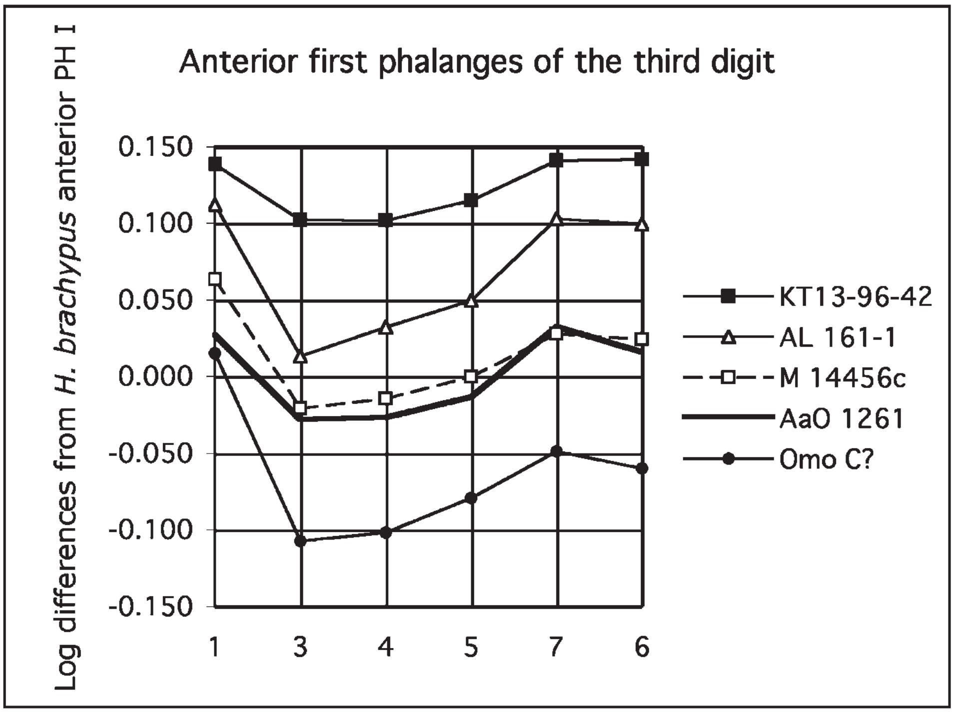

Figure 24. Ratio diagram comparing first anterior phalanges of the third digit. Data in Table 16.

morphologies may be found also in *H. prostylum* of Lubéron, and even in China (AMNH 35 B 255). This kind of structure is obviously related to grazing (Eisenmann 1998) and may well have developed in parallel in more than one lineage. But the extreme pattern, with loss of the third incisors and a broad, square incisival arcade, was achieved only by very late African hipparions (Cornelia and Olduvai, possibly East Turkana Burgi member) and seems to be the second synapomorphy. Indeed, it is this pattern that was first used to define *'Eurygnathohippus'*. *Eurygnathohippus*-like symphyses and ectostylids are not necessarily associated: ectostylids are present in *H. pomeli,* but there is no reduction of the third incisors and the incisival arcade is rounded.

In *H. houfenense s.s.* (THP 10508 and THP 10733. Qiu, pers. comm.; Qiu *et al.* 1988), the muzzle is long and narrow. *H. huangheense* (FAM 11820) is larger, and its muzzle is wider. *H. crusafonti* of Villaroya seems close to the latter species. *H.* cf. *crusafonti* of Kvabebi is smaller, with a short but not very wide muzzle (Fig. 30). *S. perimense* and *H. turkanense* have rounded and rather narrow arcades.

To summarize, in our opinion the name of *Eurygna-*

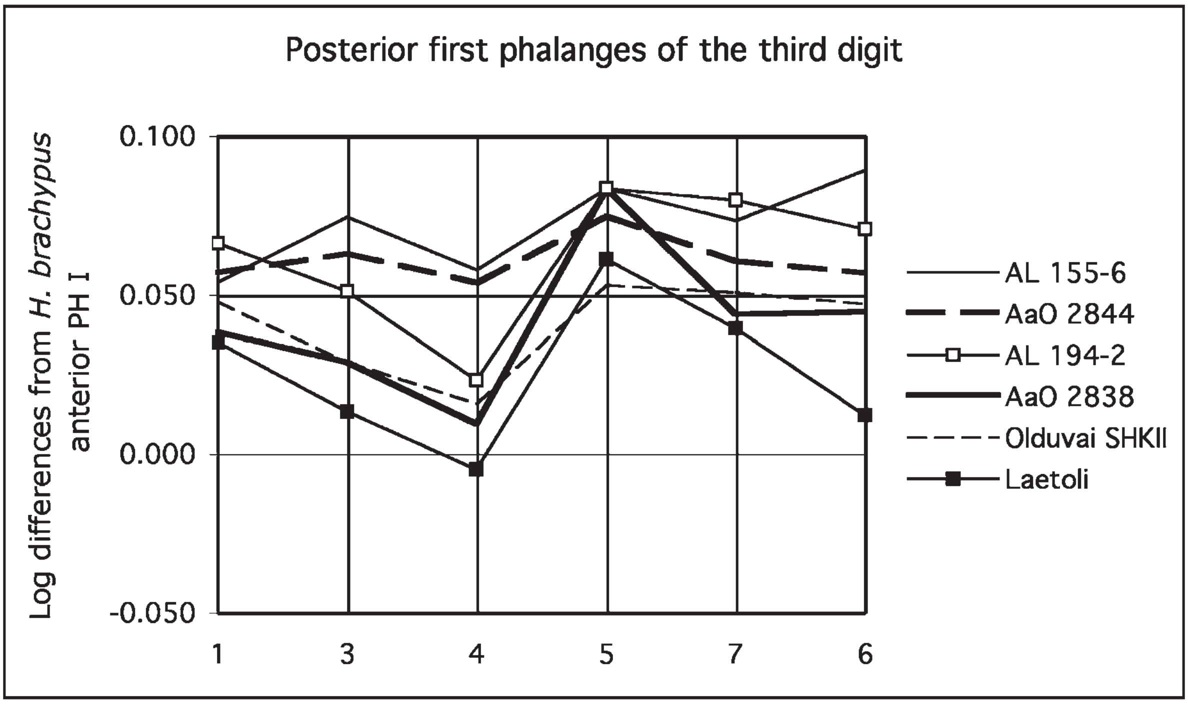

Figure 25. Ratio diagram comparing first posterior phalanges of the third digit. Data in Table 16.

Table 17. Second phalanges of the third digit (PH II).

PH II	Anterior	AaO 1536	AaO 3346	AaO 3912	AaO 4429	
Maximal length	1	42.5		44.2	45.7	
Anterior length	2	34.4	36.2		36.9	
Minimal width	3	36	[39]	37.6	40	
Proximal width	4	43	46.5		45.7	
Proximal depth	5	27.7	30.3		30.4	
Distal width	6	40.8		42.6	44.3	
	Posterior	**AaO 126**	**AaO 196**	**AaO 1268**	**AaO 2842**	**AaO 2847**
Maximal length	1	44	44.5	43.5	41.5	42.5
Anterior length	2	37	34.6	34.3	38	34.7
Minimal width	3	38.3	35.5	35.4	36.2	35.3
Proximal width	4	47	44	43.2	46	42
Proximal depth	5	32	30	30	31	27.7
Distal width	6	39.5	40	38	38.5	39.5

Table 18. Third phalanges of the third digit (PH III).

PH III		Anterior			Anterior?						
		AaO 1519	AaO 1520	AaO 3724	AaO 1547	AaO 2121	AaO 2837	AaO 2846	AaO 3371	AaO 3372	AaO 4430
Length	1		57.5			57.5	55	58	48	49.5	
Anterior length	2		66.5				57	63	58.5		
Height	3		41.8				40	43.5	40	39	
Solar width	4		70.2	74		76	65.5	66	70.3	66.5	
Articular W	5	43.8	45	46	43	48	41	42.5	43.5	44	
Articular depth	6	22.8	25.4	23.3				24.5	23.5	25.5	25
Solar circumf.	7		158			170					
		Posterior		**Posterior?**					**?**	**Anterior**	**Posterior**
		AaO 2120	**AaO 3377**	**AaO 177**	**AaO 1284**	**AaO 2122**	**AaO 2289**	**AaO 3703**	**AaO 2856**	**AL 155-6 V**	**AL 155-6 Y**
Length	1	55.5	51	50		53.5	60	54.3		68	69
Anterior length	2	58				53		56		85	71.5
Height	3	36.5	36.5			37.2		36.1		54	54
Solar width	4	64	55			54.5				82	76
Articular W	5	38	37			41.5			42	52.5	47.5
Articular depth	6		25.5		23.5	24.7				26	27.5
Solar circumf.	7									200	185

thohippus should be applied only to hipparions that present a derived basicranium, i.e. pointed vomer and long basion–vomer distance. *H. hasumense s.l.* (normal posterior border of vomer situated at subequal distances from basion and palate) is probably a sister group to *Eurygnathohippus.* Their origins are presently unknown.

Our second point of disagreement concerns the derivation of several African hipparions from *H. turkanense.*

Both *H. hendeyi* and *H. feibeli* differ from *H. turkanense* in their slender limb bones. Moreover, *H. hendeyi* (Fig. 27) strongly differs from *H. turkanense* in its very short basion–vomer and orbit–POF distances (Fig. 30, no. 4 and O–POF).

Hipparion sp. of Chad Kossom Bougoudi (Fig. 28) differs from *H. turkanense* in the presence of a POF, relatively close to the orbit (but not as close as that in *H. hendeyi*).

The derivation of *H. hasumense* from *H. turkanense* would imply a notable reorganization of the skull (Fig. 33) besides the acquisition of ectostylids. Such an evolution is possible but still hypothetical.

2. Discussion of Zouhri & Bensalmia's (2005) opinions

Our main disagreement concerns *Eurygnathohippus.* The amended diagnosis of Zouhri & Bensalmia comprises: large size, lack of POF, short naso-incisival notch, long and narrow muzzle, caballine basi-cranium, very hypsodont teeth, constant ectostylids associated with caballoid patterns in lower cheek teeth. Thus defined, *Eurygnathohippus* comprises three species: *E. libycum*, *E. cornelianum*, and *E. afarense* (including *E. hasumense* as a synonym). Zouhri & Bensalmia refer the AaO hipparion to *E. lybicum.* We think that this diagnosis is incorrect:

a) The large size is not a good character: hipparions of Shungura F member and Koobi Fora KBS member, although presumably belonging within *Eurygnathohippus* sensu Zouhri & Bensalmia, were small (Figs 13 & 14).

b) The degree of indentation of the naso-incisival incisure is defined by three points: prosthion, apex of the incisure and anteriormost point of the orbit. Length of naso-incisival notch (no. 30) is the distance between the first two; cheek length (no. 31) is the distance between the last two. The naso-incisival notch is short when it is

Table 19. Measurements of limb bones from Ahl al Oughlam.

Humerus	AaO 73	AaO 1641	AaO 1652	AaO 2194	AaO 2907	AaO 2938	AaO 3341	AaO 4069
Diaphysis width	37						27.6	38
Distal articular width	72			73	76.5	75	69	75
Distal medial depth	77.5				87		76	84
Min. trochlear height	36.3	37.2	36.6	35	37.3	34.5	31.5	38
Radius	*n*	$\bar{x}$	min	max	s.e.	c.v.	Femur	AaO 1503
Maximal length	2	304	297	311	9.9	3.26		375
Medial length	2	289	283	295	8.48	2.94		340
Diaphysis width	3	42.3	40.5	43.3	1.54	3.64		34.8
Proximal width	11	73.0	67	78.2	2.83	3.88		
Proximal articular W	9	69.5	64.8	72.1	2.12	3.04	pr.art.depth	53.7
Proximal depth	6	38.5	36.3	40	1.49	3.87		
Distal maximal width	1	65.5						94.5
Distal articular width	1	60.5						
Distal articular depth	4	34.5	32.5	36	1.48	4.3		
Radial condyle width	4	23.7	22.7	25	1	4.23		
Ulnar condyle width	2	14.5	13	16	2.12	14.63		
Tibia	*n*	$\bar{x}$	min	max	s.e.	c.v.		
Diaphysis width	10	47.4	46	53	2.99	6.31		
Diaphysis depth	8	33.5	31.4	35	1.64	4.89		
Distal width	8	70.9	68	73	2.03	2.87		
Distal depth	10	49.4	48.2	54	2.26	4.57		
Calcaneum	*n*	$\bar{x}$	min	max	s.e.	c.v.		
Proximal length	1	76.5						
Minimal width	12	21.3	17.5	23.3	1.84	8.63		
Maximal width	12	51.6	47	53.3	1.74	3.37		
Proximal width	1	35.5						
Proximal depth	1	57						
Distal depth	10	52.4	47	59.0	3.22	6.15		

smaller than the cheek length (no. 30 < no. 31). This is observed in *H. cornelianum* of Koobi Fora (Appendix Table 2) and *H. hasumense* of Olduvai Bed II (Table 1). The naso-incisival notch is long in *H. hasumense* of Hadar; the two lengths are equal in *H. pomeli* (Table 1). In consequence, the length of naso-incisival notch is not a good character for a diagnosis of *Eurygnathohippus.*

c) Figure 6 shows that the muzzle is long and narrow in *H. hasumense,* but somewhat shorter and wider in *H. cornelianum.* Thus a 'long and narrow muzzle' cannot be mentioned in a diagnosis of *Eurygnathohippus.*

d) As pointed out above, the basi-cranium of our *Eurygnathohippus* is 'hypercaballine' with a remarkably long basion–vomer distance. Moreover, the morphology of the vomer posterior border is quite peculiar in *H. afarense* and *H. cornelianum.* This is absolutely not the case of *H. pomeli* of AaO (Fig. 2, no. 4).

e) 'Very hypsodont teeth' is a vague definition. As shown in Figs 10 & 11, many teeth referred to *Eurygnathohippus* by Zouhri & Bensalmia are only moderately hypsodont, or even not hypsodont when compared with other African hipparions.

Thus, we disagree as to the validity of the genus *Eurygnathohippus* as defined by Zouhri & Bensalmia (2005), since the various species referred by them to this genus display too many and too important differences.

Another point is the inclusion of the AaO *Hipparion* in the species *H. libycum.* This species is based upon two

Table 20. Articular lengths (in mm) of Humerus (H), Femur (F); maximal lengths of Radius (R), Tibia (T), third metacarpal (MC), third metatarsal (MT), first anterior and posterior phalanges of the third digit (PH IA and PH IP); solar width of third anterior phalanx of the third digit (PH IIIA). For Höwenegg, data from Bernor *et al.* (1997), and V.E., unpubl. data.

	H	F	R	T	MC	MT	PH IA	PH IP	PH IIIA
Höwenegg	261.8	367	282.9	364.6	212.8	242.5	65.5	64.8	64.5
AL 155-6	281		332.5	392.5	267	296	75.5	70	82
Çalta	256.5	387	297.3	375	200.4	234.7	68.7	67	76
Ahl al Oughlam		331	304		237.6	282.3	68.8	68.8	74
AaO juveniles ?					230	275	65.8	62.4	
Ahl al Oughlam all		331	304		233.8	278.7	67.3	65.6	74

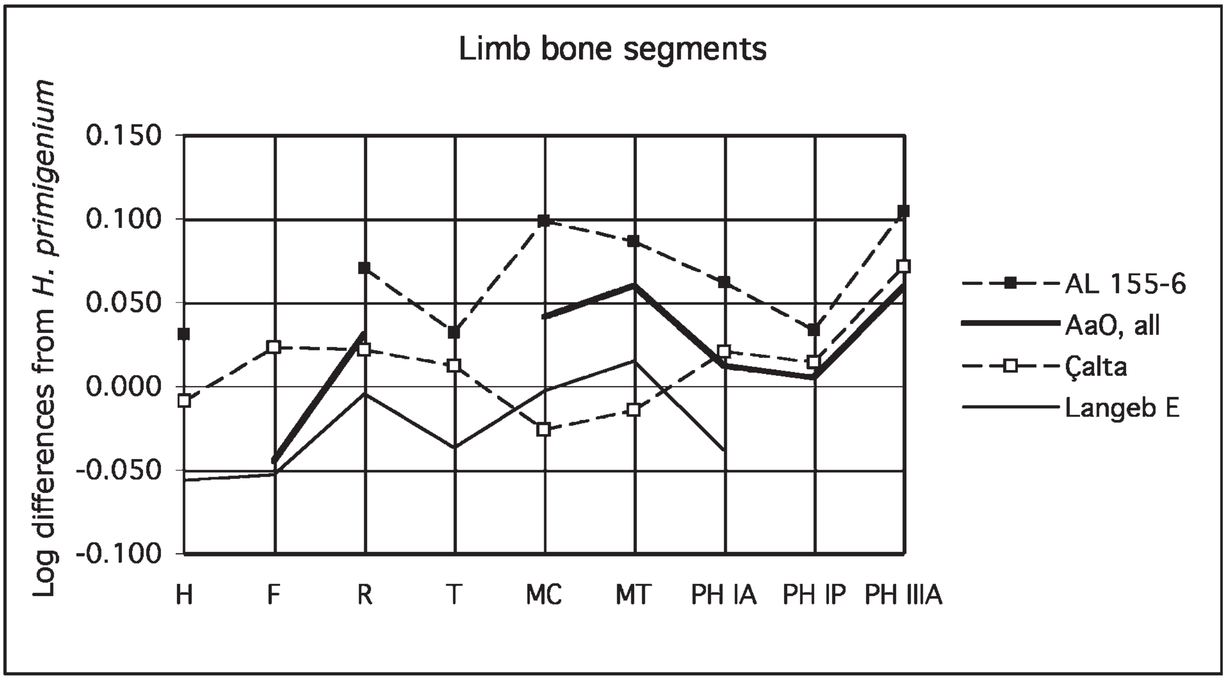

Figure 26. Ratio diagram comparing limb bone segments in hipparions. Data in Table 20.

lower premolars from Algeria, of which we hereby select the one better illustrated by Pomel (1897, plate 1, fig. 5-7) as lectotype (not holotype as stated by Zouhri & Bensalmia). Given the difficulties in *Hipparion* systematics, it is clear that this material does not allow for confident referral of any other specimen to the same species. Therefore, to avoid mixing of several unrelated species within the same species name, the name *Hipparion libycum* should be restricted to the type.

CONCLUSIONS

In our interpretation, over the last 7 Ma there were, in Africa, at least five kinds of hipparions:

— *H. turkanense* of Lower Nawata (Bernor & Harris 2003) has normal basi-cranial proportions (Fig. 33). A very faint POF is placed very far from the orbit. Resemblances between the skull of *H. turkanense* and that of *S. perimense* (AMNH 19761, formerly named *Cormohipparion antelopinum*) do exist and were illustrated by ratio diagrams a long time ago (Eisenmann 1982, fig. 5). It is quite possible that *H. turkanense* derives from *S. perimense* from which it seems to differ mainly by the lack of, or a very faintly marked, POF. But we lack information on *S. perimense* basicranial proportions. Unfortunately, we have no photographs of the Lower and Upper Nawata cheek teeth at our disposal other

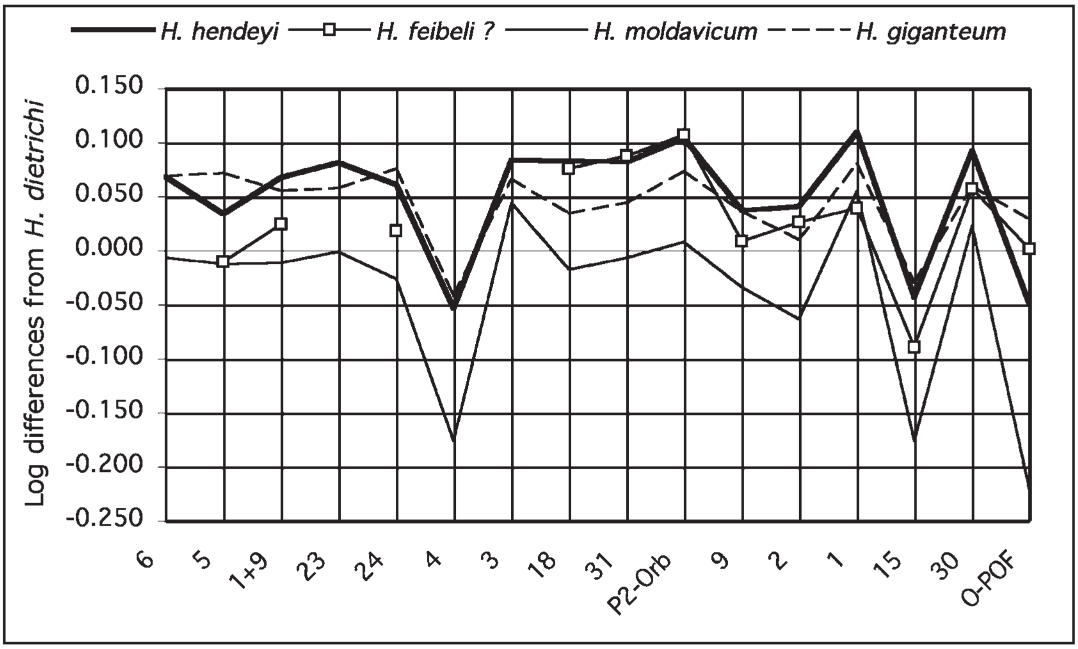

Figure 27. Ratio diagram comparing the skulls of Langebaanweg E, Ekora-Kanam, *Hipparion giganteum* of Grebeniki and *H. moldavicum* of Taraklia. Data in Table 1 and Appendix Table 2.

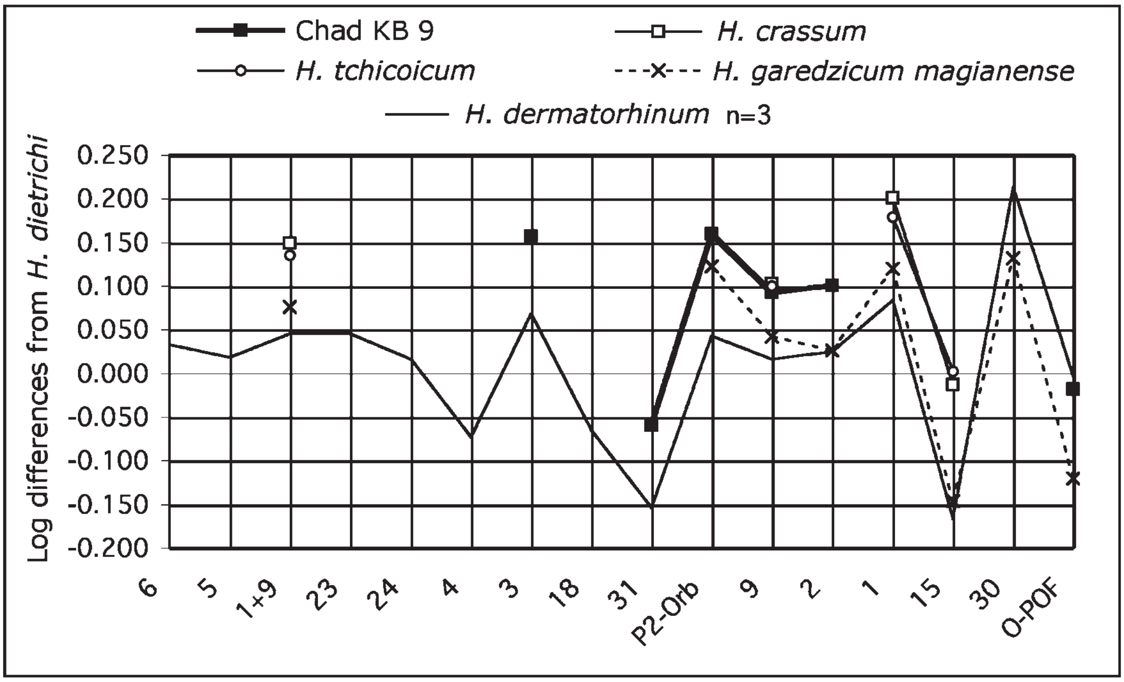

Figure 28. Ratio diagram comparing the skulls of Chad Kossom Bougoudi, *Hipparion dermatorhinum*, and *H. crassum*. Data Bernor *et al.* (1990) and V.E. unpubl. data for *H. dermatorhinum.* Other data in Tables 1 & 2.

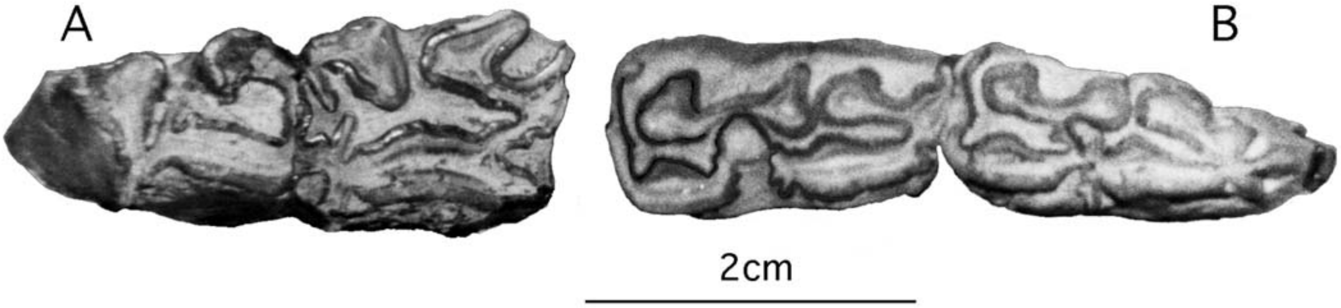

Figure 29. *Hipparion* cf. *crusafonti*, Kvabebi. **A**, dp2, **B**, m2-m3.

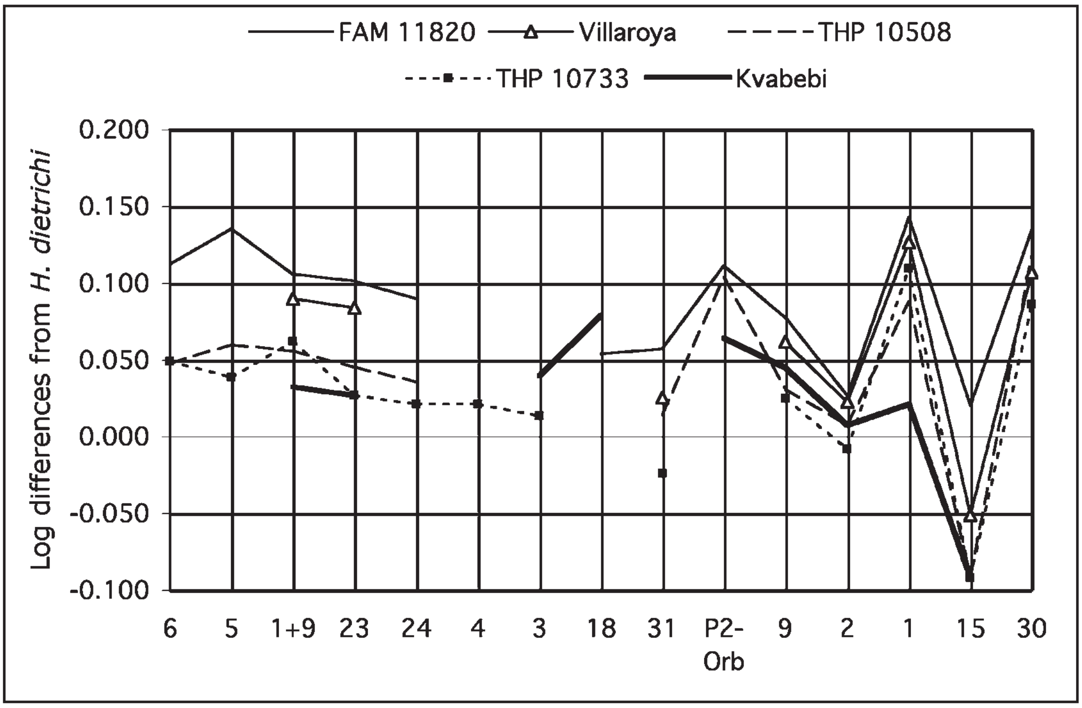

Figure 30. Ratio diagram comparing the skulls of *Hipparion houfenense s.l.*, Villaroya, and Kvabebi. Data in Table 1.

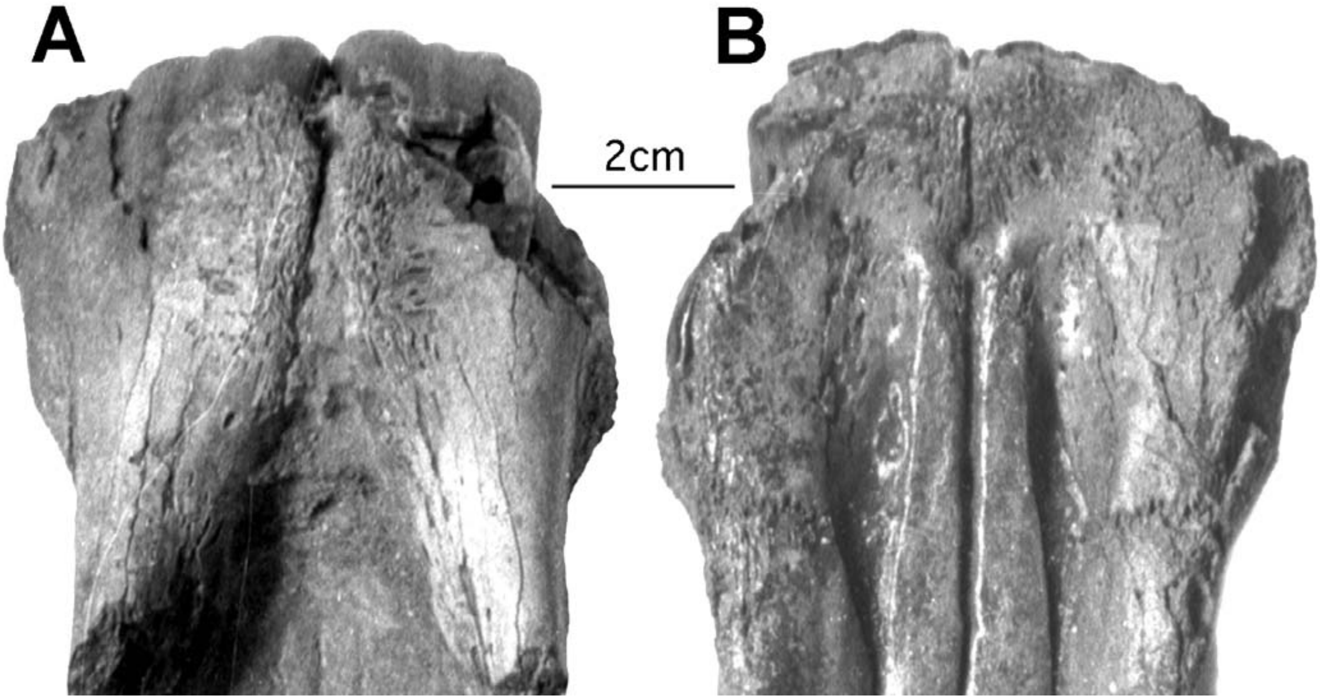

Figure 31. Muzzle KNM-ER 3539; **A**, dorsal view, **B**, ventral view.

than the very worn series from the type skull of *H. turkanense.*

— *H. hendeyi* and *H. feibeli*?. Two European skulls are similar to that of *H. hendeyi* (Fig. 27). They belong to the somewhat smaller *H. moldavicum* of Taraklia, and to *H. giganteum* of Grebeniki. They have short basion–vomer distances and narrow muzzles; the POF of *H. hendeyi,* however, is placed closer to the orbit than in *H. giganteum* and not as close as in *H. moldavicum.* The upper cheek teeth have small and rounded protocones; the lower cheek teeth are hipparionine (Hendey 1978). *H. hendeyi* cannot be derived from *H. africanum* because of its very short naso-incisival notch (Fig. 32). It may have derived from another immigrant. The skulls from Ekora and Kanam, possibly referable to *H. feibeli* but poorly known, may be akin.

— *Hipparion* sp. of Kossom Bougoudi (Fig. 28). It is represented by one of the largest skulls of hipparion. Unfortunately, the teeth are greatly worn. We do not know whether the Chad skull is derived from the *Hippotherium* complex of Bernor & Armour-Chelu (1999a) because of it resemblences with

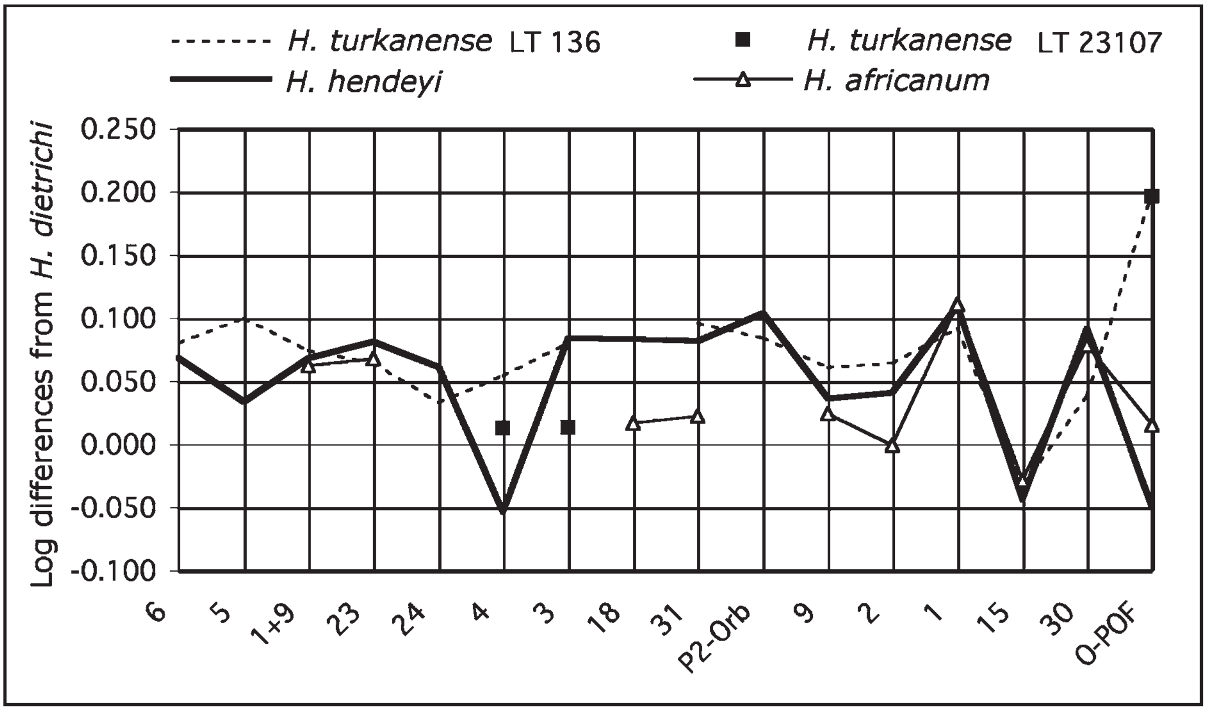

Figure 32. Ratio diagram comparing the skulls of *Hipparion turkanense, H. hendeyi,* and *H. africanum.* Data Bernor & Harris (2003) for *H. turkanense.* Other data in Table 1.

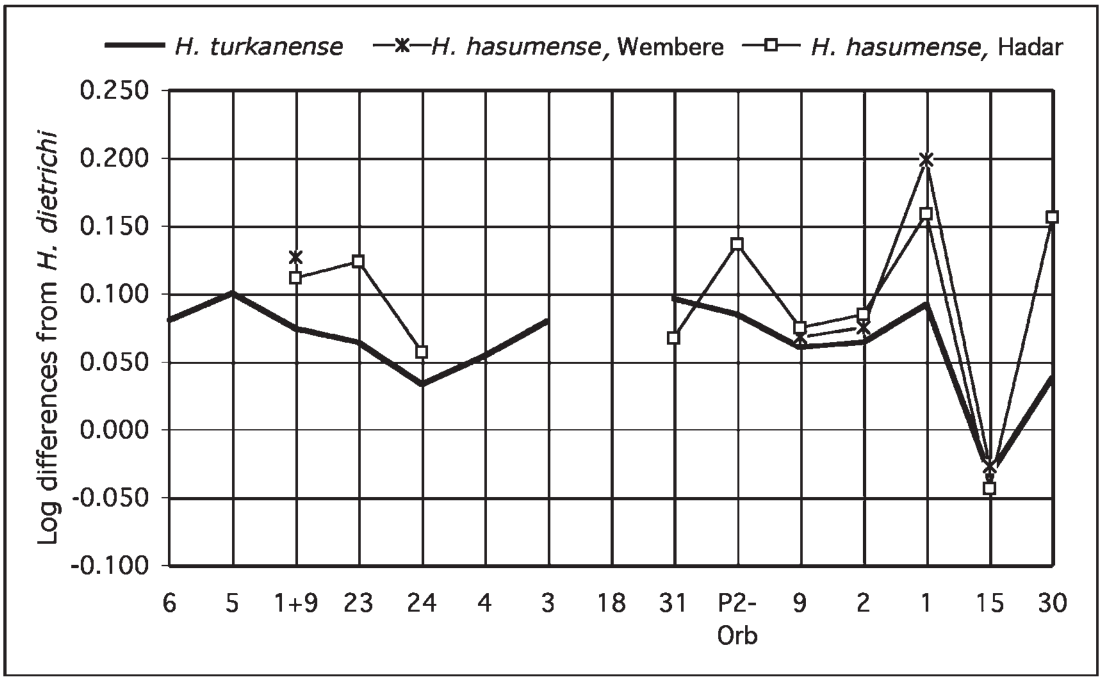

Figure 33. Ratio diagram comparing the skulls of *Hipparion turkanense* LT 136 and *H. hasumense* of Wembere Manonga WW 1528/92 (Data Bernor & Armour-Chelu 1997) and AL 340-8 of Hadar.

H. dermatorhinum in many ways, or from the *Sivalhippus* complex (Bernor & Armour-Chelu 1999b) because of its similarity to *H. crassum s.l.*

— *H. hasumense* group (Figs 2 & 3). This group displays several apomorphies: short cheek, deep naso-incisival notch, caballine double knots, isolated ectostylids and protostylids. Vomer and basi-cranial proportions are normal. The muzzle is long and narrow. We recognize it at Wembere Manonga, Hadar, Ahl al Oughlam (*H. pomeli*), and possibly Olduvai (complete but badly preserved skull BK II 2845/6).

— *H. afarense* and *H. cornelianum* (Figs 4 & 5). As already noted, the structure of the vomer is unique: the acutely pointed vomerian incisure is associated with 'hyper-caballine' basi-cranial proportions. The muzzle is short and wide. Other apomorphies are like those in *H. hasumense.*

It is quite probable that *H. afarense* was the ancestor of the true *Eurygnathohippus* for two reasons: 1) the skulls AL 363-18 of *H. afarense* and KNM ER 3539 of *H. cornelianum* are quite similar; 2) KNM ER 3539 is about 1–2 years old by *Equus* standards (Klingel & Klingel 1966); at that age the permanent I1 (contra Bernor & Armour Chelu 1999a) are erupting and they can perfectly be seen on this skull because the DI1 are lost; an unerupted right I2 may be seen for the same reason, and there is no room for an I3 other than a very reduced one (Fig. 31).

Bernor & Armour-Chelu (1999a) believe that the preceding forms may derive from *H. turkanense,* which they consider as an *Eurygnathohippus*, sister group to *S. perimense.*

In our opinion, the derivation of *Eurygnathohippus* from *H. turkanense* is, for the moment, an assumption based more on the belief that there were no other immigrations of hipparions into Africa than on osteological evidence.

If the Pliocene African hipparions are not descended from *H. turkanense,* they must have an Eurasian origin, and have immigrated into Africa around the Mio-Pliocene boundary (Fig. 34). This period documents indeed a major turnover in African mammalian faunas, mostly by local evolution from local forms. However, there are also some newcomers. In North Africa, the Messinian crisis prompted some faunal exchanges across the Gibraltar straits; they are best known for rodents, but probably involve also canids, and it is likely that a better knowledge of North African Mio-Pliocene large mammals would increase the list. Other taxa of Eurasian origin, arriving in Africa at this time are the Camelidae, first known from the early Pliocene of Chad, and perhaps *Giraffa* and some carnivores: the ursid *Agriotherium,* the hunting hyena *Chasmaporthetes,* and the mustelid *Plesiogulo.* The list is not long, but demonstrates that North–South migrations were possible at that time. The presence at Kossoum Bougoudi, Chad, of a huge hipparion with a very well developed fossa could also result from a migration, possibly of a kind of *H. crassum.*

We are grateful to J. Hassar Benslimane, former head of the Institut National des Sciences de l'Archéologie et du Patrimoine, Rabat, for allowing us to work on the hipparions from Ahl al Oughlam, a locality excavated as part of the 'Programme Casablanca' led by F.Z. Sbihi-Alaoui and J-P. Raynal. We thank also M.T. Alberdi, J. Brink, M. Brunet, Y. Coppens, L.K. Gabunia, A. Gentry, PH. Haarhof, J.M. Harris, D. Johanson, W. von Koenigswald, R. Leakey, C. Smeenk, R. Smith, A.K. Vekua, V.I. Zhegallo, for their trust and help in accessing material, as well as to J. Brink, J.M. Harris, A. Monguillon and M. Pickford for discussions and sharing of information. We also thank the reviewers whose suggestions and criticism led to many improvements in the manuscript.

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ABBREVIATIONS

AaO	Ahl al Oughlam
Hadar DD	Hadar Formation, Denen Dora member
Hadar KH	Hadar Formation, Kada Hadar member
Hadar SH	Hadar Formation, Sidi Hakoma membe
POF	pre-orbital fossa
L	length
W	width

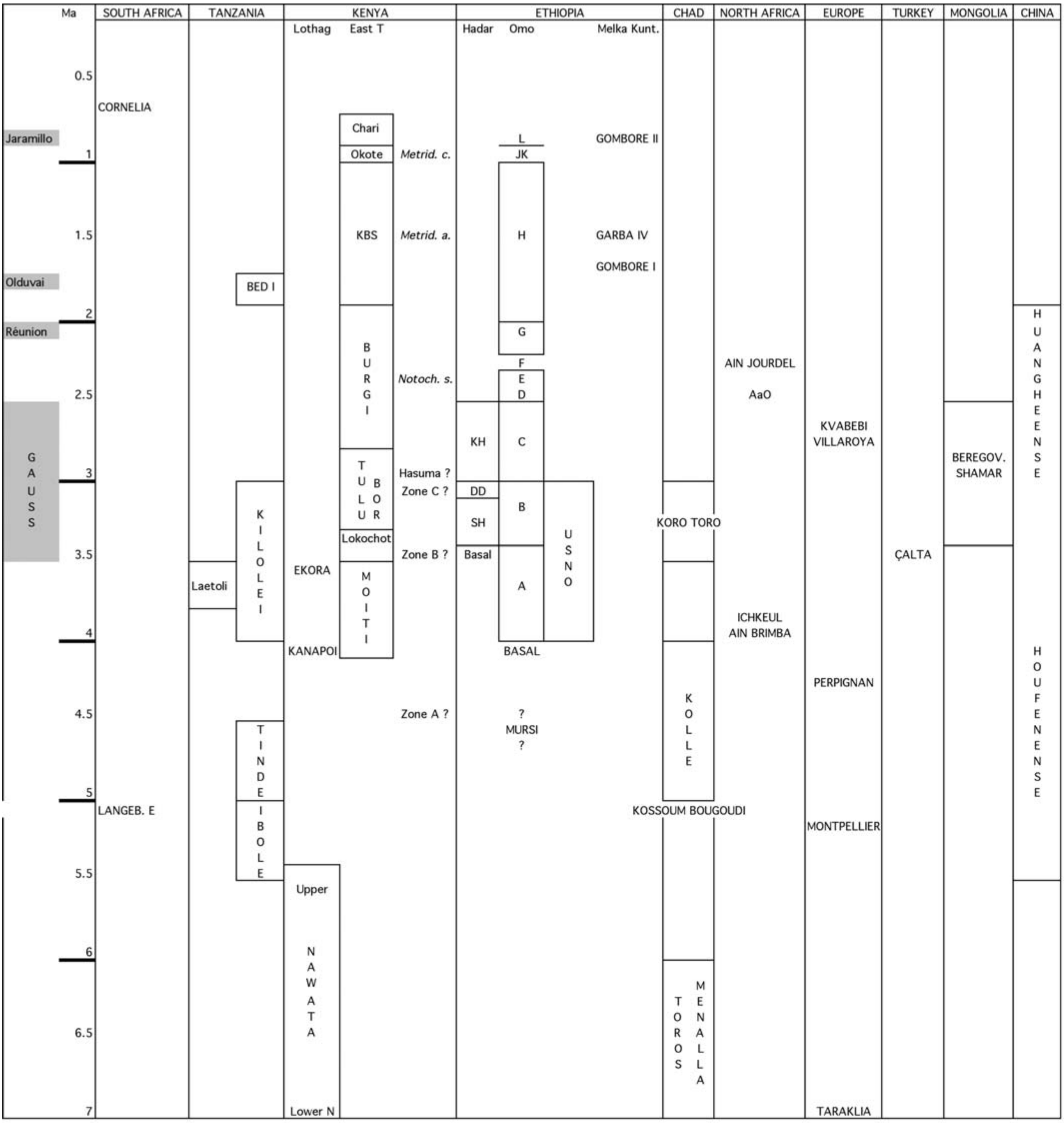

Figure 34. Schematic chronology of some hipparion-bearing late Cenozoic Old World localities.

MC III	third metacarpal
PH I	first phalanx of the third digit
PH II	second phalanx of the third digit
PH III	third phalanx of the third digit
MT III	third metatarsal.

Measurements are in millimetres.

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APPENDIX

Juvenile skulls

Well-preserved skulls are rare. It is frustrating when they belong to juvenile animals, and thus cannot be directly compared to adults. It may, however, be possible to 'extrapolate' the juvenile dimensions to adult ones. We have tried to do so by applying what we know about the skull growth of extant *Equus* species.

Four species were considered: Grevy's zebra, Plains zebras, Hemiones, and Przewalski's horses. Comparison was made between average adult skulls and juvenile skulls of different ages by calculating the percentage rate of 'growth' of the latter. Appendix Table 1 gives the percentages of growth of the dimensions used in our ratio diagrams. The choice of dimensions was made to adapt to more-or-less complete fossil material. Thus, some are simple measurements while others are sums of segments. Most were defined in Eisenmann *et al.* (1988). Appendix Fig. 1 illustrates the values of the percentages of growth in the considered extant species.

Samples of adult skulls were chosen to correspond as much as possible to the available (always poor) juvenile samples. For instance, only adult *E. burchelli* from Etosha Pan were used because the best sample of juvenile skulls comes from Etosha Pan. For adult skulls, means were calculated from *c.* 60 *E. grevyi* (but cheek and naso-incisival notch lengths are known only from five specimens), and *c.* 60 hemiones (excluding hemippes, kiangs, and Mongolian hemiones), 22 to 31 *E. przewalskii,* and 15 to *E. burchelli.* Juvenile samples vary from one age group to another.

The juvenile skulls we examined (Appendix Table 2) are: KNM ER 3539 from East Turkana, BM 5465, and BK II 283 from Olduvai (*H. cornelianum*); KNM EK 4 from Ekora and BM 15906 from Kanam West (*H. feibeli* ?).

One–two years. Juvenile samples consist of 9 *E. grevyi,* 9–10 *E. burchelli,* 6–11 *E. hemionus,* and 7–13 *E. przewalskii.*

Naturally, the highest percentages concern the 'growth' of the cheek teeth, since there are only three decidual teeth instead of six adult. The smallest percentages concern the growth in length of the muzzle. Obviously, skulls of different species grow in different ways. In *E. grevyi* the muzzle width grows less than in other species while the length of the naso-incisival notch seems to increase more. On the whole, however, the concordance seems good enough to justify tentative reconstructions of juvenile skulls.

A perfectly preserved juvenile skull (KNM ER 3539) was found under the KBS Tuff in East Turkana. It was illustrated in Eisenmann (1976, Plate 3). The M1 had begun to wear, the M2 were not erupted. In *Equus,* that would indicate an age of between one and two years. The following ratio diagram (Appendix Fig. 2) compares dimensions of the juvenile skull with tentative reconstructions of its adult state according to the *Equus* species growth. It shows that most of predicted adult dimensions are similar but notable interspecific differences appear in the width of the muzzle.

The use of *Equus* skulls as the basis for a reconstruction of an *Hipparion* skull may appear rash and untestable. We can, however, somehow 'test' the (accuracy of) extrapolation of KNM ER 3539 by comparing it with the adult skull of *H. afarense* AL 363-18 (Eisenmann, 1976, Plate 2). The obvious resemblances on the next ratio diagram (Appendix Fig. 3) make our reconstruction credible. The adult skull ER 3539, when adult, would probably have looked like *H. afarense,* possibly slightly smaller and with longer teeth and palate. The muzzle would have been at least 70.4 mm wide (according to the *E. grevyi* model), possibly as wide as, but no more than, 91.7 mm (*E. przewalskii* model), more probably about the calculated average (81 mm) which is close to the actual width of *H. afarense* (80 mm).

About one year. Juvenile samples consist of one *E. grevyi,* six *E. burchelli,* 2–5 *E. hemionus,* and five *E. przewalskii.*

The juvenile skulls KNM EK 4 from Ekora and BM 15906 from Kanam West are about one year old (unerupted M1). They both have a POF and have also the same dimensions of the deciduous series. We suppose that they belong to the same species. The various possibilities of adult state are represented in Appendix Fig. 4. Their overall concordance justifies the use of an average adult state (Appendix Fig. 5).

One of us has already pointed that the Ekora skull may well belong to the small hipparion of Lothagam (Eisenmann 1995). If so, our reconstruction gives an idea about the adult skull of *H. feibeli* (Bernor et Harris 2003). According to our results, the *H. feibeli* skull most resembles *H. verae* and *H. giganteum* of Grebeniki (as seen on the ratio diagram Appendix Fig. 5), and *H. hendeyi* (Fig. 24).

From Olduvai, there is another fragmentary skull of about one year old, BM 067/5465. Although perhaps slightly younger than KNM ER 3539, it has larger dimensions. Otherwise it does not seem much different. Unfortunately the vomer–basion distance is uncertain. Two alternatives were used (Appendix Fig. 6). It appears that BM 5465 had relatively smaller teeth than KNM ER 3539 but probably belonged also to *H. cornelianum.*

About three years. Juvenile samples consist of 1–15 *E. grevyi,* 4–7 *E. burchelli,* 5–10 *E. hemionus,* and 3–8 *E. przewalskii.*

A fragmentary juvenile skull from Olduvai Bed II, BK II 283, was illustrated by Hooijer (1975, Plates 9–10). P4 and M3 are erupting, which would point in *Equus* to an age of around 3 years. The skull is particularly interesting because it has well preserved frontals. The reconstructions based on our modern models differ but slightly. Like in BM 5465, the teeth are relatively small. We refer it also to *H. cornelianum* (Appendix Fig. 6).

The real (juvenile) and extrapolated 'adult' values are in Appendix Table 2.

Skull-mandible dimensions

Another question concerns the relationship between mandible and skull dimensions, in particular muzzle lengths and widths.

Muzzle lengths. We have calculated the regression line for skull versus mandible dimensions in 83 modern horses (Appendix Fig. 7). The correlation R^2 is 0.88. The skull muzzle length = (0.963 × mandible muzzle length) + 15.8. The Hadar skull of *H. hasumense* AL 340-8 is associated with a mandible. The mandible muzzle length is about 130 mm, the skull muzzle length is about 140 mm. The muzzle length of the mandible AL 177-21 (also from DD) is the same; according to the regression, the skull muzzle length would have been 141.2 mm, i.e. close to the actual length in AL 340-8. For the mandible of *H. cornelianum* KNM ER 1626 (muzzle length 115 mm), the corresponding skull dimension would have been 126.7 mm. For the mandibles of *H. crassum* P. 208 and of *H. tchicoicum* (muzzle lengths 144 and 136 mm), the corresponding skull dimensions would have been 154.8 and 147 mm.

The regression of mandible versus skull dimensions is: mandible muzzle length = (0.910 × skull muzzle length) + 1.022.

Muzzle widths. We calculated the regression lines for skull versus mandible dimensions and of mandible versus skull dimensions in modern equids with broad muzzles to match the broad muzzled African hipparions. The sample comprises 32 horses and 29 kiangs (Appendix Fig. 8). The correlation R2 is 0.80.

- Skull muzzle width = (0.729 × mandible muzzle width) + 21.823.
- Mandible muzzle breadth = (1.097 × skull muzzle width) – 11.959.

In the first scatter diagram (Appendix Fig. 8) are plotted the real values for the associated skull and mandible AL 340-8 of *H. hasumense* and the values estimated from the mandible and from the skull. The real AL 340-8 plots far from the regression line, with an actual skull muzzle 57 mm wide instead of the calculated 61.2 mm. This is probably because it is very old and slightly crushed (Eisenmann 1976, plate 1).

In the same diagram are plotted the values for *H. hendeyi* of Langebaanweg E. The skull L 22187 is old, and its muzzle width is 57 mm, giving 50.6 mm for an estimated width of the mandibular muzzle. On the normal mandible L 20553 the muzzle width is 56 mm giving 62.7 mm as the probably normal skull width.

In Appendix Fig. 9 are plotted the estimations for the skull muzzle widths of AL 177-21 (62.7 mm), Omo 18-1968-363, KNM ER 1626 (73.6 mm), 324 (64.1 mm), and 1221 (67 mm), Olduvai 067/5344, Melka Kunturé Garba IVD 6767, and Cornelia COR 679 (74 mm).

In Appendix Fig. 10 are plotted the estimations for the mandibular muzzle widths of AL 155-6 (53.9 mm), AL 363-18 (64.8 mm), AL 142-18 (68.1 mm), Olduvai BK II 2845/6 (56 mm) and BK II 264 (71.4 mm), WW 1528/92, AaO 3647 (53.9 mm), Lothagam LT 136 (54.7 mm), KNM ER 3539, and Kanam BM 15906.

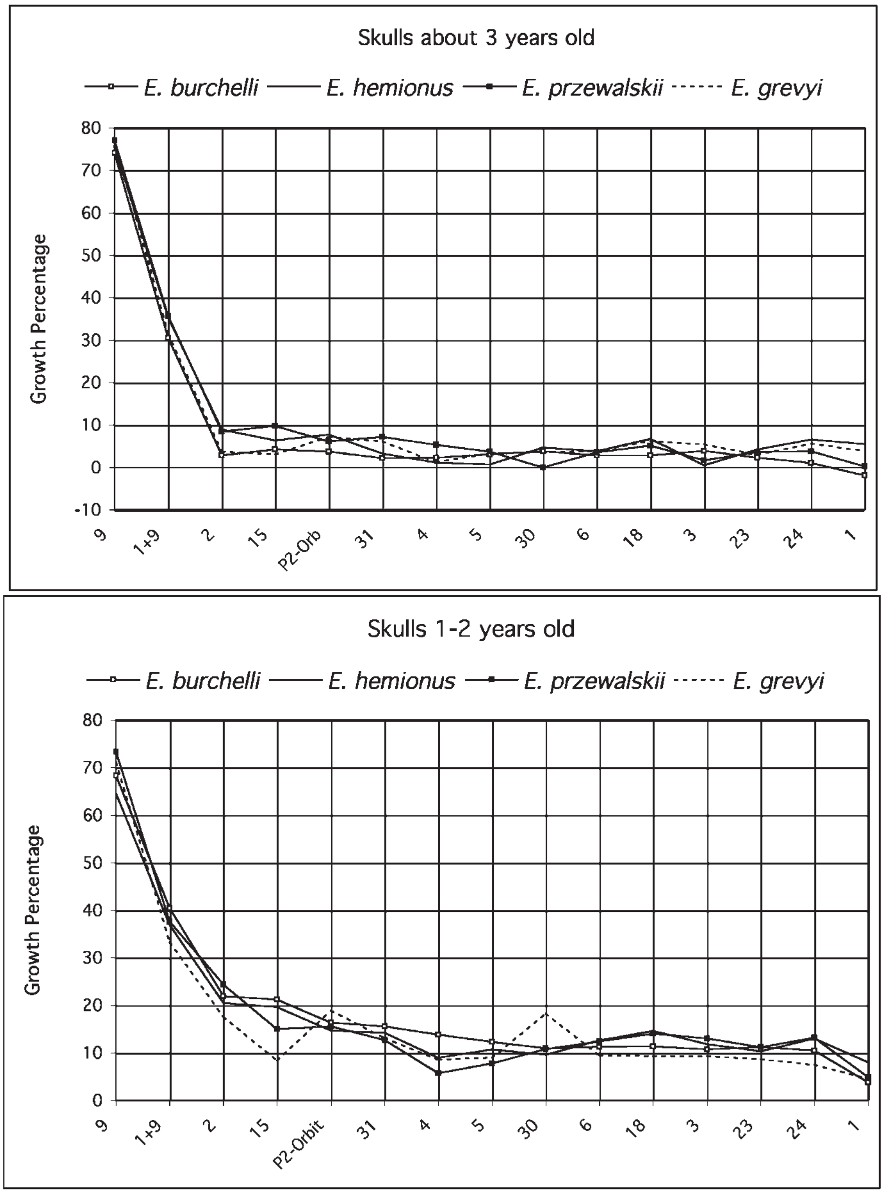
Not plotted estimations for *H. crassum* and *H. tchicoicum* are in Table 2.

Appendix Table 1. Percentage of growth of extant *Equus* species.

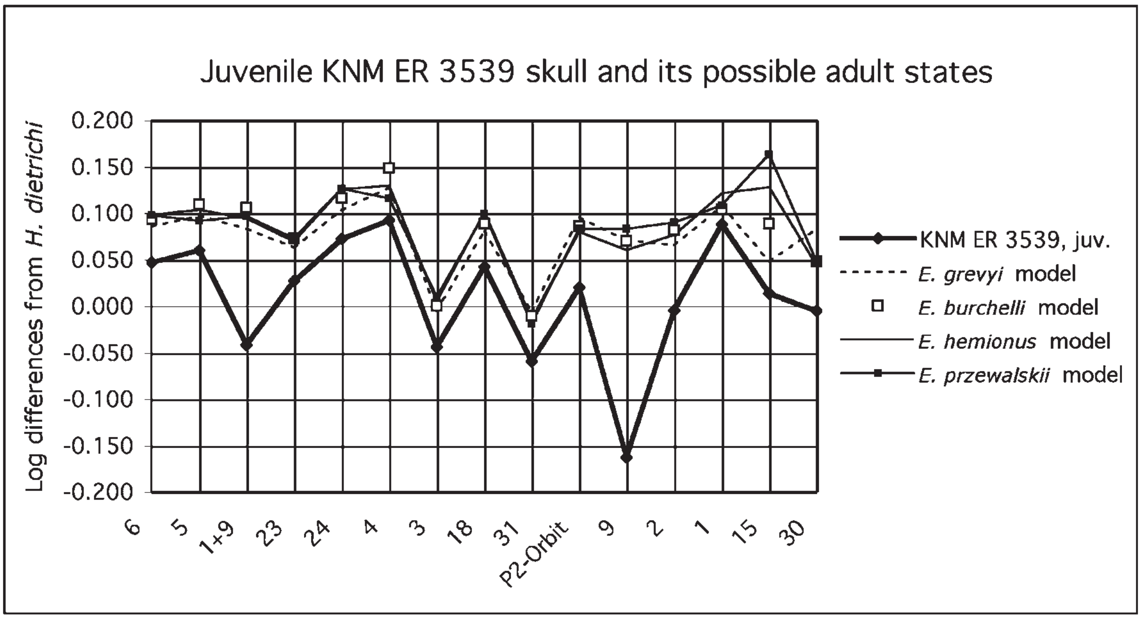
		E. grevyi	*E. burchelli*	*E. hemionus*	*E. przewalskii*
	adults	n = 5–60	n = 15	n = 58–59	n = 22–31
	around 3 years	n = 1–15	n = 4–7	n = 5–10	n = 3–8
Basilar length	6	3.8	2.8	3.8	3.5
Postpalatal length	5	3.3	3.1	0.7	3.6
Muzzle + cheek teeth L	1+9	31.5	30.5	35.3	35.6
Anterior ocular line	23	3.0	2.3	4.2	3.6
Posterior ocular line	24	5.6	1.0	6.6	3.8
Postvomerine length	4	1.2	2.3	1.1	5.3
Vomerine length	3	5.4	3.9	0.5	1.7
Frontal width	18	6.2	2.8	6.7	5.1
Cheek length	31	6.1	2.2	3.3	7.2
P2–Orbit	P2–Orbit	7.2	3.7	7.7	6.1
Cheek teeth length	9	77.4	74.1	75.6	77.2
Palatal length	2	3.7	2.8	8.9	8.3
Muzzle length	1	3.9	–1.9	5.5	0.2
Maximal muzzle width	15	3.1	4.2	6.4	9.8
Length of narial opening	30	3.5	3.8	4.7	–0.1
	1 to 2 years	n = 9	n = 9–10	n = 6–11	n = 7–13
Basilar length	6	9.4	11.3	12.6	12.4
Postpalatal length	5	9.0	12.3	10.7	7.8
Muzzle + cheek teeth L	1+9	33.3	40.4	36.9	37.6
Anterior ocular line	23	8.7	11.2	10.3	11.2
Posterior ocular line	24	7.4	10.5	13.0	13.2
Postvomerine length	4	8.5	13.8	9.0	5.7
Vomerine length	3	9.3	10.7	11.8	13.0
Frontal width	18	9.3	11.4	14.6	14.1
Cheek length	31	13.1	15.6	14.2	12.7
P2–Orbit	P2–Orbit	18.9	16.4	14.7	15.6
Cheek teeth length	9	71.2	68.3	64.6	73.3
Palatal length	2	17.6	21.9	20.5	24.4
Muzzle length	1	4.6	3.8	8.0	4.9
Maximal muzzle width	15	8.4	21.2	19.6	15.0
Length of narial opening	30	18.3	11.0	9.6	10.8
	around 1 year	n = 1	n = 6	n = 2–5	n = 5
Basilar length	6	16.3	17.9	18.7	21.5
Postpalatal length	5	15.0	17.5	15.0	16.9
Muzzle + cheek teeth L	1+9	32.1	36.2	39.3	42.5
Anterior ocular line	23	14.0	17.3	15.0	20.1
Posterior ocular line	24	12.7	13.7	18.7	25.0
Postvomerine length	4	3.7	16.5	12.0	9.8
Vomerine length	3	29.0	18.6	24.1	26.2
Frontal width	18	14.8	16.9	23.0	25.6
Cheek length	31	22.3	22.8	20.0	21.2
P2–Orbit	P2–Orbit	32.0	22.8	22.9	31.5
Cheek teeth length	9	59.1	67.4	68.7	75.2
Palatal length	2	36.8	32.4	27.3	33.6
Muzzle length	1	9.1	10.3	12.8	11.2
Maximal muzzle width	15	23.1	21.0	23.4	33.0
Length of narial opening	30	21.0	16.4	20.1	29.0

Appendix Table 2. Measurements in mm of juvenile hipparion skulls.

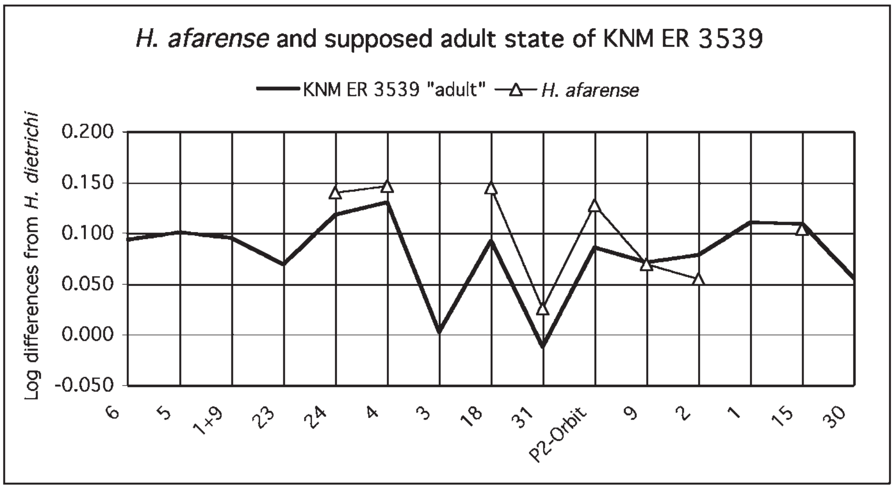
		H. feibeli ?		*H. cornelianum*		
		Ekora *c.* 1 year KNM EK 4	Kanam W *c.* 1 year BM 15906	Koobi Fora Burgi 1–2 years KNM ER 3539	Olduvai BK II *c.* 1 year BM 067/5465	Olduvai BK II *c.* 3 years BK II 283
P2 – Orbit				146		170
Muzzle length	1		96	119		
Palatal length	2	87		110		
Vomerine length	3			85	95	
Postvomerine length	4			128	[139]	
Postpalatal length	5	[165]		210	[234]	
Basilar length	6			430		
Lacteal premolar length	7	86	86	96	100	[90]
Choanal length	10	[57]		62	65	
Minimal choanal width	11	[25]		35	[35]	
Maximal choanal width	12	[37]	[31]	39	[43]	
Minimal muzzle width	14		29	49		
Muzzle width at I3	15		41	[65]		
Length of temporal fossa	16	65				
Frontal width	18	[150]		180	[180]	215
Bizygomatic width	19			[180]		[200]
Basioccipital width	21	[87]				
Anterior ocular line	23			320		
Posterior ocular line	24	148		197	[190]	
Facial height	25		76	88		
Cranial height	26	82		83	105	
Ant–post. orbital diameter	28	51		57	56	
Vent–dors. orbital diameter	29	51		[48]	50	
Length of naso-incisival notch	30		[110]	120		
Cheek length	31			130		
Orbit to preorbital fossa (POF)	32	45				
Length of POF	33	61				
POF to foramen infraorbitale	34	43				
Height of POF	35	34				
POF to facial crest	36	29				
For. infraorb. to alveol. border	37	40				
POF to alveolar border	38	67				



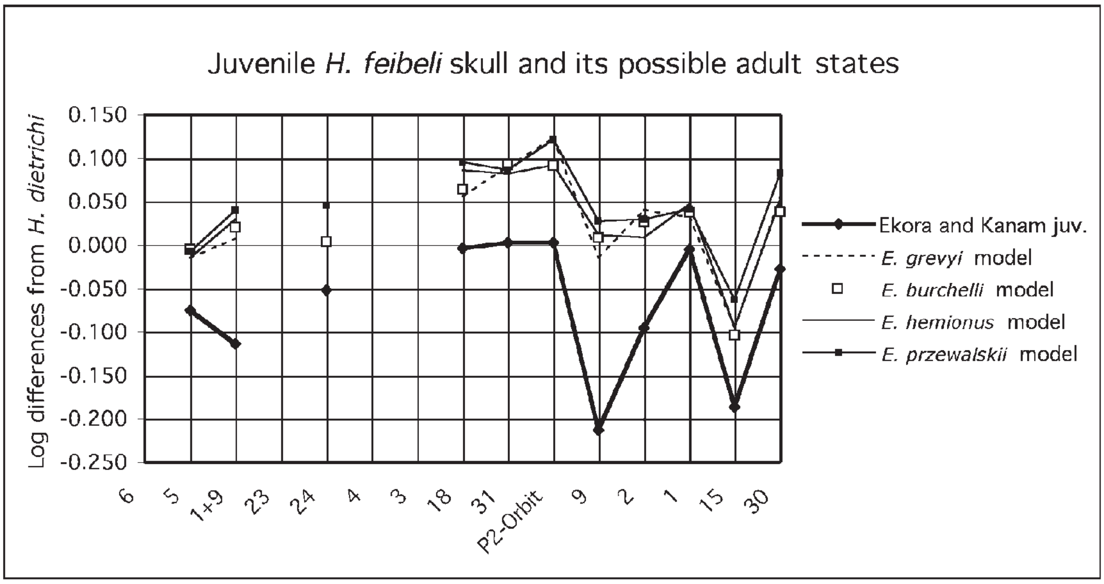
Appendix Fig. 1. Percentage of growth of extant *Equus* species. Measurements defined in Appendix Table 1.



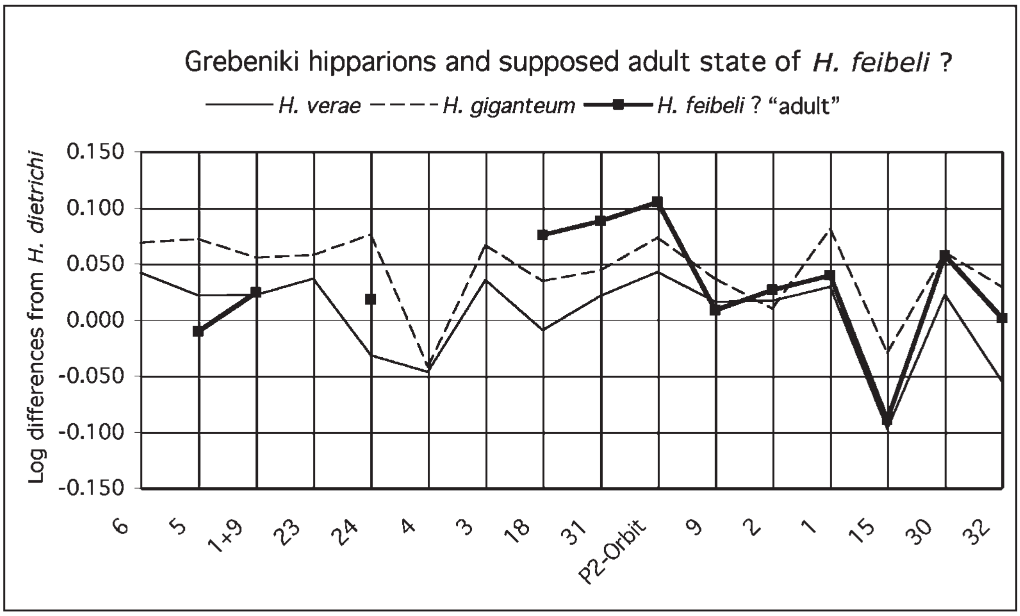
Appendix Fig. 2. Ratio diagram of *H. cornelianum* juvenile skull from Koobi Fora, Burgi and its adult dimensions according to the growth of extant *Equus* skulls.



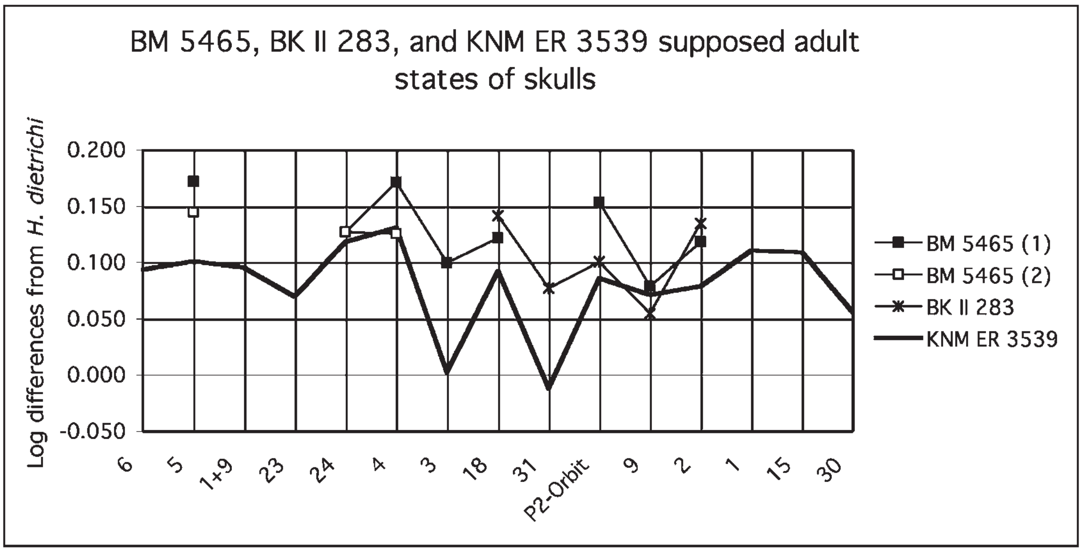
Appendix Fig. 3. Ratio diagram of *H. cornelianum* skull supposed adult dimensions compared to the adult *H. afarense.*



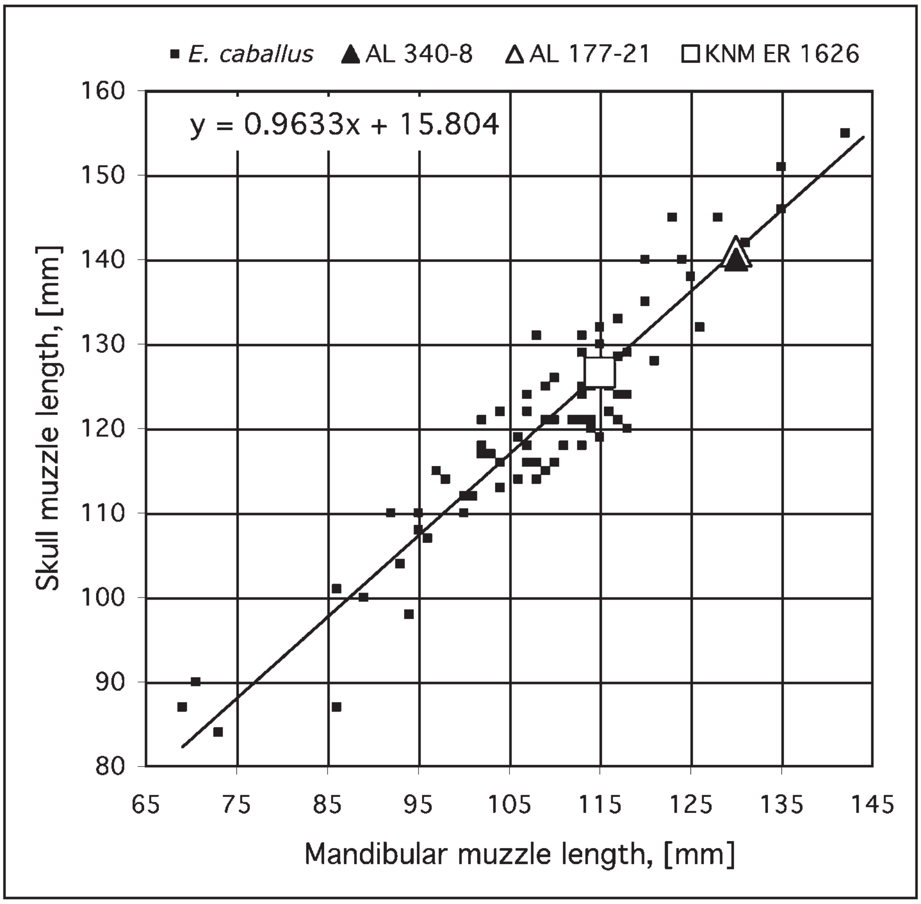
Appendix Fig. 4. Ratio diagram of *H. feibeli* ? juvenile skulls from Ekora and Kanam and its adult dimensions according to the growth of extant *Equus* skulls.



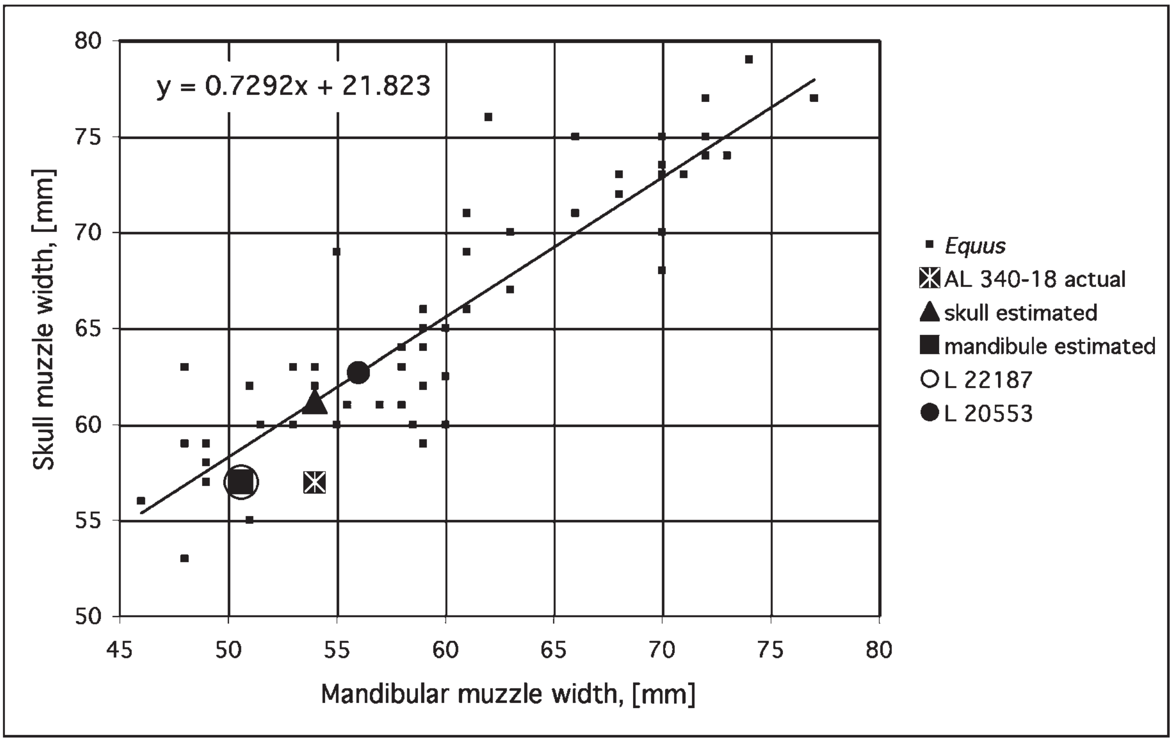
Appendix Fig. 5. Ratio diagram of *H. feibeli* ? skull supposed adult dimensions compared to the adults *H. verae* and *H. giganteum* of Grebeniki.



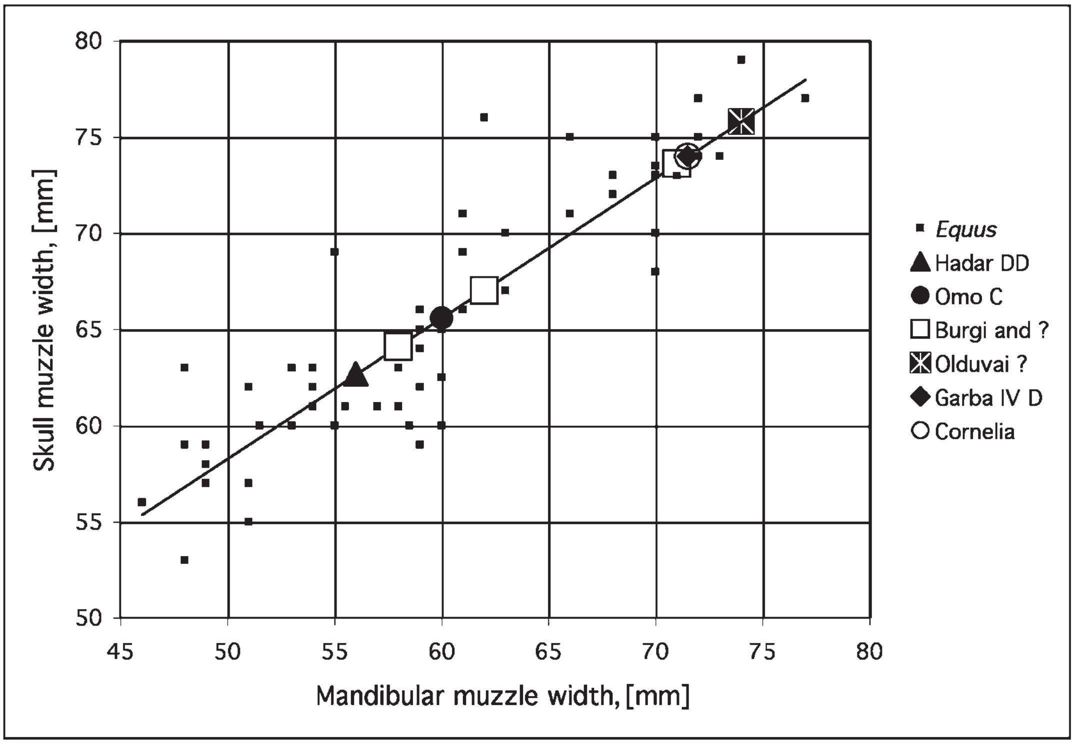
Appendix Fig. 6. Ratio diagram of supposed adult dimensions of *H. cornelianum* from Koobi Fora, Burgi and Olduvai Bed II.



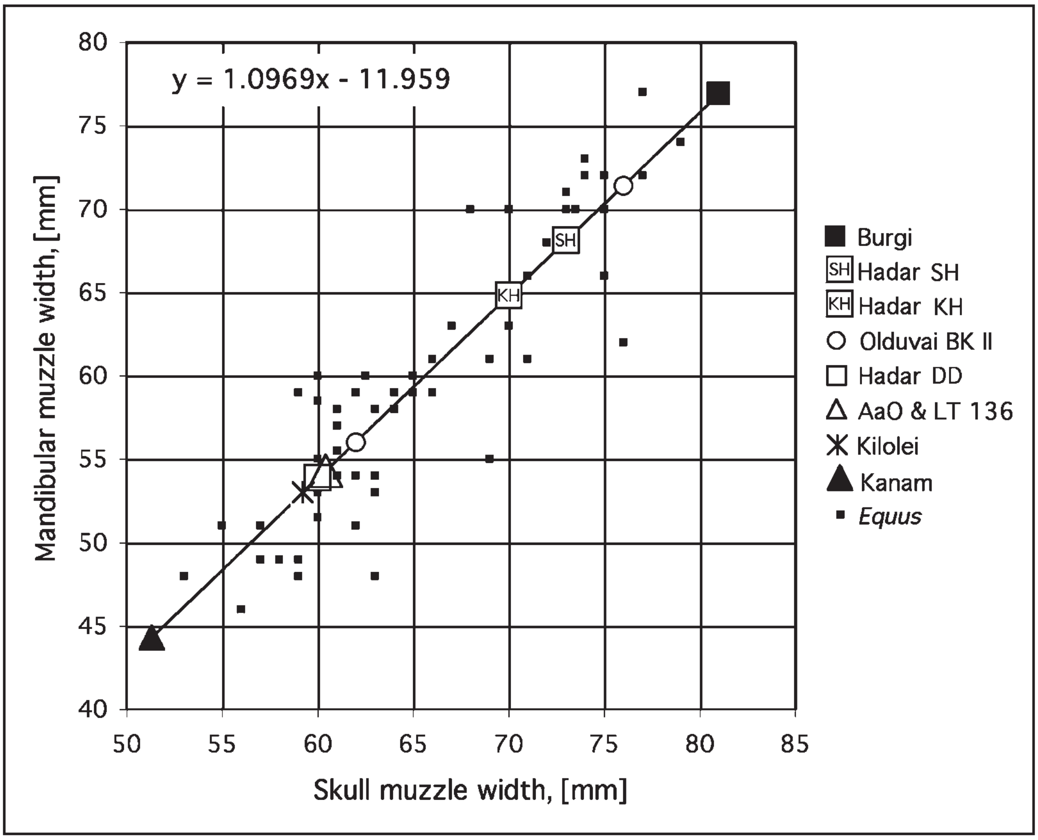
Appendix Fig. 7. Scatter diagram and regression of the skull muzzle length on the mandibular muzzle length.



Appendix Fig. 8. Scatter diagram and regression of the skull muzzle width on the mandibular muzzle width.



Appendix Fig. 9. Scatter diagram and regression of other skull muzzle widths on other mandibular muzzle widths.



Appendix Fig. 10. Scatter diagram and regression of the mandibular muzzle width on the skull muzzle width.

A sabre-tooth felid from Coopers Cave (Gauteng, South Africa) and its implications for *Megantereon* (Felidae: Machairodontinae) taxonomy

Adam Hartstone-Rose[1*], Darryl J. De Ruiter[2], Lee R. Berger[3] & Steven E. Churchill[4]

[1]*Department of Biological Anthropology and Anatomy, Box 90383, Duke University, Durham, North Carolina 27708, U.S.A.*
E-mail: ah7@duke.edu

[2]*Department of Anthropology, Texas A&M University, College Station, 77843, U.S.A.*
E-mail: deruiter@tamu.edu

[3]*Institute of Human Evolution, University of the Witwatersrand, Johannesburg, 2050 South Africa.*
E-mail: bergerl@geosciences.wits.ac.za

[4]*Department of Biological Anthropology and Anatomy, Duke University, Durham, North Carolina 27708 U.S.A.*
E-mail: churchy@duke.edu

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Metrical and morphological analysis of a new sabre-tooth felid mandible recovered from the Plio-Pleistocene hominid-bearing site of Coopers, South Africa, indicates that it can be assigned to the genus *Megantereon,* though it is by some measures the smallest individual of this taxon yet described. Comparison of morphological variability within this genus to that found within four extant, medium-sized felid species (*Acinonyx jubatus*, *Neofelis nebulosa*, *Panthera pardus* and *P. uncia*) and the extinct genus *Smilodon* (sister taxon of *Megantereon*) provides confirmation of the suggestion by Martínez-Navarro & Palmqvist (1995, 1996) that *Megantereon* is a geographically polymorphic genus comprised of at least two species: *M. cultridens* (Cuvier, 1824) of North America and Europe and *M. whitei* (Broom, 1937) of Africa and Europe.

Keywords: sabre-tooth, Plio-Pleistocene, palaeontology, carnivore.

INTRODUCTION

The early history of systematics research on the genus *Megantereon* led to a proliferation of specific names for morphologically similar specimens, many of which came from geographically and temporally proximate sites. Various sabre-tooth cats that fit the general description of the genus *Megantereon* have been assigned, over the last two centuries, to at least 11 species: *Megantereon cultridens* (Cuvier, 1824), *M. megantereon* (Croizet & Joubert, 1828), *M. falconeri* (Pomel, 1853), *M. sivalensis* (Falconer 1868), *M.* (*Machairodus*) *nihowanensis* (Teilhard de Chardin & Piveteau, 1930), *M. hesperus* (Gazin, 1933), *M.* (*Felis*) *whitei* (Broom, 1937), *M.* (*Machairodus*) *inexpectatus* (Teilhard de Chardin, 1939), *M.* (*Felis*) *gracile* (Broom & Schepers, 1946), *M. eurynodon* (Ewer, 1955) and *M. ekidoit* (Werdelin & Lewis, 2000). While the naming of new species still occasionally occurs, most recent works have seen this material as falling into three or fewer species (Ficcarelli 1978; Turner 1987, 1997; Martínez-Navarro & Palmqvist 1995, 1996; Sardella 1998; Palmqvist 2002).

Martínez-Navarro & Palmqvist (1995, 1996) suggest that the genus *Megantereon* contains up to three distinct species, including a predominantly African group for which the nomen *M. whitei* (Broom, 1937) is available. Four features distinguish the African clade: relatively small lower premolars; a diastema between the third and fourth lower premolars; relatively small carnassials (P^4 and M_1); and a relatively vertical mandibular symphysis (Martínez-Navarro & Palmqvist 1995). Specimens from several earlier Pleistocene localities of southern Europe (Spain and Greece) align themselves with the African taxon (Martínez-Navarro & Palmqvist 1995, 1996). Recently recovered specimens from Africa, as reported here and by Werdelin & Lewis (2000), support the existence of a distinct African species of *Megantereon,* and contribute to an African sample size large enough for statistical analysis.

We report here on a mesial fragment of a left mandible (CD 5997: Fig. 1), provisionally attributed to the Plio-Pleistocene sabre-tooth felid genus *Megantereon* (Berger *et al.*, 2003), from the site of Coopers Cave (26°00′46″S, 27°44′45″E), Gauteng Province, South Africa. This is the most complete mandibular specimen recovered from the Witwatersrand Basin, and the only one from this region that preserves the anterior chin and alveolar morphology.

Morphometric analysis of fossils attributed to *Megantereon,* along with four medium-sized extant felid species and one other extinct felid genus (*Smilodon*) allows an assessment of the number of morphologically distinct groups contained within the genus *Megantereon,* and of the claim for a distinct African species (*M. whitei*).

Diagnosis of Megantereon. *Megantereon,* a member of the family Felidae, subfamily Machairodontinae, is a genus of sabre-tooth felids found in Africa, Asia, Europe and North America. Unpublished body mass estimates based on the Orce and Dmanisi specimens suggest that *M. cultridens* weighed approximately 100 kg, about the size of a living Jaguar, *P. onca* (Palmqvist, pers. comm.). Based on its limb proportions, *Megantereon* is believed to have been a

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*Author for correspondence.

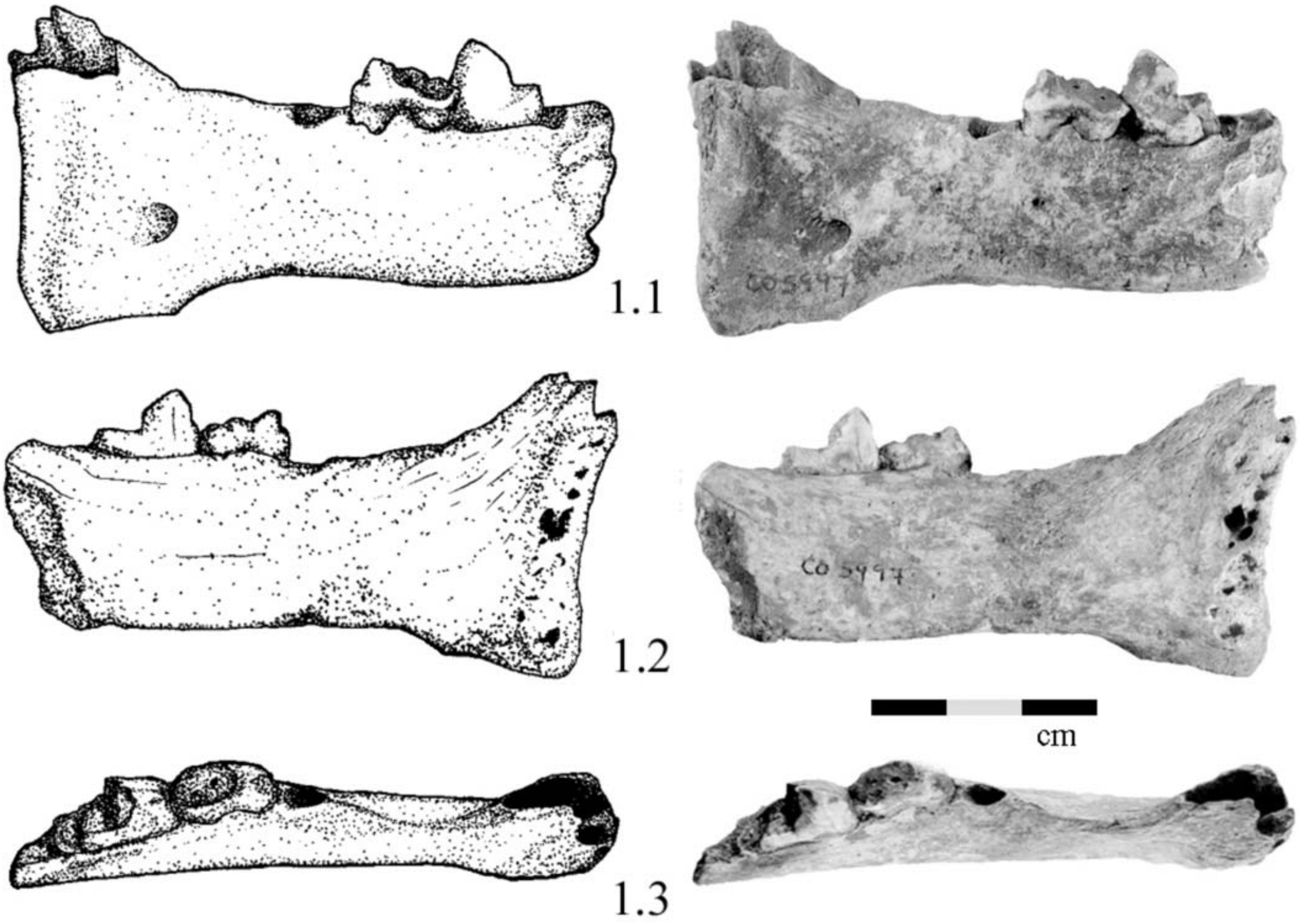

Figure 1. Lateral (**1.1**; mesial is left, superior is up), medial (**1.2**; mesial is right, superior is up) and occlusal views (**1.3** mesial is right, lateral is up) of CD 5997. Photographs and drawings by A.H-R.

partially arboreal carnivore occupying a closed forest niche (Marean 1989; Lewis 1997). Turner (1987: 1266) offered this diagnosis:

> A medium-sized, sexually dimorphic cat; short, high skull, triangular in profile with convex dorsal outline; extended glenoid apophysis; limbs and feet short and powerful, the forelimbs more so than the hindlimbs; tail reduced in length; upper canines elongated, compressed and curved; crenulations absent on all teeth; long post-canine diastema; upper and lower second premolars lost; upper and lower third premolar present and functional but very variable in size; P^4 protocone developed but variable in size; M^1 present but reduced; P^3–M^1 backward raking; main cusp of P^4 high crowned; M^1 lacking talonid or metaconid, paraconid shorter than protoconid and forming a relatively acute angle with it; mandible with short coronoid process, strong and vertical symphysis with enlarged flange extending well below the ventral margin of the horizontal ramus; single large mental foramen.

Berta & Galliano (1983) also note that *Megantereon* differs from *Smilodon* (namely *S. populator*) in its relatively smaller size, relatively larger mandibular flange and lack of canine serrations, among other less noticeable traits. It is generally accepted that *Megantereon* is more primitive than *Smilodon* as its upper and lower incisors are less enlarged and procumbent, and its upper canines are less enlarged than its larger sister genus (Berta & Galliano 1983; Turner 1997).

MATERIALS AND METHODS

Coopers Cave is situated approximately 45 km northwest of Johannesburg (Gauteng Province, South Africa), within the Cradle of Humankind World Heritage Area between the well-known fossil hominin-bearing sites of Sterkfontein and Kromdraai. The site presents a series of collapsed and deroofed breccia caves designated Coopers A, B and D. Renewed excavations in 2001 into *in situ,* decalcified sediments at Coopers D have produced a rich and varied faunal assemblage, including abundant carnivore material, dated on biostratigraphic grounds to between 1.6 and 1.9 million years ago (Mya) (Berger *et al.* 2003). It is from this deposit that CD 5997 is derived.

CD 5997 is compared with congeneric specimens, and the variation in *Megantereon* is compared to that found between the extinct genus *Smilodon* and four extant felid species: *Acinonyx jubatus* (cheetah), *Neofelis nebulosa* (clouded leopard), *Panthera pardus* (leopard) and *P. uncia* (snow leopard) (Tables 1, 2 & 3). The comparative extant felid species were chosen because they represent medium-sized cats – ranging from 20 kg (*N. nebulosa*) to 90 kg (*P. pardus*) – corresponding with the body size range

Table 1. Sample sizes of fossils and casts, by curatorial institution, of extinct felid study group examined in person.

Genus	Actual fossils	Casts	Total	Held at
Smilodon	5	6	11	AMNH
African *Megantereon* (excluding CD 5997)	3 (South African)		3	TM
		1 (East African)	1	AMNH
Non-African *Megantereon*	1	6	7	AMNH
	1 (type of *M. cultridens*)		1	NHM
CD 5997	1	0	1	WITS
Total	11	13	24	

AMNH: American Museum of Natural History, New York.
TM: Transvaal Museum, Pretoria.
NHM: Natural History Museum, London.
WITS: University of the Witwatersrand, Johannesburg.

Table 2. Sample sizes by sex of extant felid study group. All specimens held at AMNH.

Species	Males	Females	Unrecorded sex
Acinonyx jubatus	7	4	2
Neofelis nebulosa	2	1	3
Panthera pardus	8	5	0
P. uncia	3	3	2

Table 3. Country of origin of the *Panthera pardus* study group. All specimens held at AMNH.

Continent	Country	
Africa	Democratic Republic of Congo	5
	Tanzania	3
	Malawi	1
Asia	China	1
	India	3

of *Megantereon* (Turner 1997; Palmqvist, pers. comm.). *P. pardus* is particularly useful for comparison because, like *Megantereon,* it is found over a wide, multi-continental, geographic range (Table 3). The much larger fossil form *Smilodon* was chosen as the extinct comparison group because it is one of the closest related taxa to *Megantereon* and it is very well represented in the fossil record. All data – from both extinct and extant forms – were collected on adult individuals by AHR or incorporated from published literature (Ficcarelli 1978; Berta & Galliano 1983; Martínez-Navarro & Palmqvist 1995; Werdelin & Lewis 2000; Qiu *et al.* 2004). All comparative data on the extant felids were collected at the American Museum of Natural History. The data on the extinct genera were collected in various institutions on either actual fossils or museum quality casts (Table 1).

The taxonomic attribution, geological age (for fossil specimens) and sex (for extant specimens) were recorded for each specimen. Table 4 lists the morphometric variables that were collected wherever possible from each specimen. Where possible, measurements were taken on the left side of the mandible. All tooth measurements were taken at the alveolar margins (see Ficarelli 1978). This substantially increases the number of measurements available on many of the fossils (since many of the teeth are broken away or lost postmortem), including the CD 5997 mandible, which adds to the statistical robusticity of the analysis.

Published dental measures include crown dimensions (Werdelin & Lewis 2000; Martínez-Navarro & Palmqvist 1995; Berta & Galliano 1983; Ficcarelli 1978) and estimates or alveolar dimensions (Berta & Galliano 1983; Martínez-Navarro & Palmqvist 1995). To assess the validity of combining these different forms of data, we have evaluated each of the five specimens that overlap in our data sample and in the data sample used by Martínez-Navarro & Palmqvist (1995). For the 18 values that could be thus compared the average difference between our alveolar measurements and the reported crown measurements is 3.59% (S.D. 5.31%) (Table 5) which is similar to empirically derived intraobserver error taken on a single structure (see references in White 1991). While these forms of error may be additive (thus further reducing their accuracy), considering the relatively small size of the measurements and the accuracy of the measuring equipment, we regard this difference as negligible. One tooth (the M_1 of KA 64) gave particularly aberrant results in this comparison: our mesiodistal measurement is 7.3% lower than that of Turner (1987) and our buccolingual measurement is 21.34% higher. We believe that this outlier is due to a thick layer of Glyptal preservative which leaves the lingual border of the mandibular premolar-molar row difficult to measure. Though additional preparation has partially alleviated this problem, it is perhaps wise to view all measurements of these teeth with caution. If this single tooth (M_1 of KA 64) is excluded from our analysis of the difference between our measurements and those analysed by Martínez-Navarro & Palmqvist (1995), then the overall average percentage difference is reduced to 2.25% with a standard deviation of just 2.85% (Table 5).

RESULTS

Preservation of the specimen

CD 5997 consists of an apparently undistorted, 81.3 mm long mesial segment of an adult left mandibular corpus (Fig. 1). The dentary is not fused at the symphysis. Distally, the specimen is broken perpendicular to the occlusal plane approximately 9 mm distal to the distal margin of the M_1 alveolus. Also missing is the inferior-most margin of the mandibular flange, the missing portion measuring approximately 16 mm proximodistally

Table 4. Measurements taken (mm) to the nearest 0.1 mm.

Abbreviation	Definition	CD 5997	African and early European *Megantereon* group – including CD 5997 **Mean** (range*, *n*)	Late European, North American and Asian *Megantereon* group **Mean** (range*, *n*)
I1 BL	Buccolingual (BL) width and mesiodistal (MD) length, measured at the alveolar margins, of all lower teeth (I_1, I_2, I_3, C_1, P_3, P_4, M_1). The left side was used when available.	**3.8**	**4.7** (3.8-5.7, 3)	**8.1** (1)
I1 MD		**1.2**	**2.9** (1.2-5, 3)	**4.4** (1)
I2 BL		**5.9**	**5.7** (5.5-5.9, 3)	**7.9** (1)
I2 MD		**2.6**	**3.5** (2.6-4.3, 3)	**6.2** (1)
I3 BL		**5.9**	**6.4** (5.9-6.9, 3)	**9.3** (1)
I3 MD		**4.3**	**5.0** (4.3-5.8, 4)	**8.2** (1)
C BL		**9.5**	**9.2** (7.8-10.9, 4)	**11.5** (10-15, 9)
C MD		**8.7**	**7.0** (5.1-9.8, 5)	**8.0** (6.5-11.4, 7)
P3 BL		**2.8**	**3.7** (2.8-4.5, 6)[†]	**5.4** (4-6.6, 15)
P3 MD		**4.7**	**5.7** (4.7-6.9, 7)[†]	**9.9** (7-12.7, 16)
P4 BL		**6.2**	**6.9** (4.5-10.1, 9)	**8.4** (6.6-10.5, 19)
P4 MD		**13.9**	**13.9** (6.3-17.5, 9)	**18.9** (15.7-21.5, 21)
M1 BL		**8.7**	**8.9** (8.1-11.2, 9)	**9.8** (7.8-13, 19)
M1 MD		**16.8**	**17.9** (16.8-19.3, 9)	**21.5** (18.2-26, 20)
IC row	Incisor-canine row width measured from interdentale to the lateral most margin of the canine alveolus.	**13.3**	**17.7** (13.3-22.2, 2)	**28.3** (1)
PM row	Premolar-molar row length measured from the mesial margin of P_3 to the distal margin of M_1	**37.6**	**40.4** (37.1-44.7, 5)	**49.7** (47.3-50.9, 6)
CP diast	Canine-premolar (post-canine) diastema length measured from the mesial margin of P_3 to the distal margin of C_1	**24.4**	**32.6** (24.4-36.9, 3)	**24.9** (21.7-28.2, 2)
Symph height	Maximum symphyseal measurement. (Instrumentally determined.)	**36.9**	**43.4** (36.9-49.9, 2)	**35** (1)
Symph depth	Maximum symphyseal depth perpendicular to maximum symphyseal height.	**10.2**	**14.5** (10.2-18.9, 2)	**15.6** (1)
Ant P3 height	Maximum measurement of corpus in the coronal plane perpendicular to the long axis of the corpus mesial to the P_3 (instrumentally determined).	**23.2**	**24.3** (23.2-25.3, 2)	**27.1** (22.3-30.4, 3)
Ant P3 width	Maximum width of corpus in the coronal plane perpendicular to the 'Ant P3 height' measurement mesial to the P_3	**10.8**	**10.5** (10.2-10.8, 2)	**13.3** (9.1-16, 5)
Post M1 height	Maximum measurement of corpus in the coronal plane perpendicular to the long axis of the corpus distal to the M1 (instrumentally determined).	**24.6**	**27.3** (24.6-30, 2)	**30.9** (26.7-37, 4)
Post M1 width	Maximum width of corpus in the coronal plane perpendicular to the 'Post M1 height' measurement distal to the M1.	**11.0**	**12.1** (11.0-13.3, 2)	**13.3** (9.7-16.5, 5)

*Owing to the small sample sizes, ranges were used instead of standard deviations.

[†] Not including KNM-ST 23812, which reportedly exhibits agenesis of the P_3 (Werdelin & Lewis 2000). If this specimen were included here (as 0 in both measurements), the means would be reduced to 3.2 and 5.0 for the buccolingual and mesiodistal measurements, respectively.

by 6.8 mm mediolaterally and <2 mm superioinferiorly. Except for this small flake, the dentary is complete, from the distal break to the symphysis.

The incisors, canine and third premolar are missing post-mortem and their alveoli are encrusted with a thin (<0.1 mm) layer of sediment, indicating that the teeth were lost prior to fossilization. The fourth premolar is broken distal to the mesial accessory cusp and is sheared buccodistally. The carnassial (M_1) is similarly broken: the posterior half of the tooth is also sheared buccodistally, leaving intact only the paraconid. It does not appear that the shearing of these teeth is the result of natural occlusal wear, as none of the South African *Megantereon* specimens exhibit a wear pattern as extensive as this. However, it is possible that some or all of the breakage of these teeth occurred during the life of the animal and were modified by occlusal wear. Further analysis of the tooth damage and wear is warranted.

Taphonomy

The distal break displays gouge marks consistent with chewing by hyenas. In addition to the gnaw marks of a large carnivore at the proximal break, there are smaller tooth marks over much of the mandible, and dozens of

Table 5. Comparison of our alveolar measurements with the crown measurements used by Martínez-Navarro & Palmqvist (1995).

Specimen	Measurement	P3 MD	P3 BL	P4 MD	P4 BL	M1 MD	M1 BL
USNM 12614	Our measurement					19.75	8.03
	Berta &Galliano (1983)					19.80	8.50
	% Difference					**–0.25**	**–5.69**
KA 64	Our measurement			17.47		18.22	11.15
	Turner (1987)			17.00		19.60	9.00
	% Difference			**2.73**		**–7.30**	**21.34**
TM 856	Our measurement	6.85	3.89	14.78		17.65	8.62
	Turner (1987)	6.60	3.90	14.50		17.60	8.50
	% Difference	**3.72**	**–0.26**	**1.91**		**0.28**	**1.40**
STS 1588	Our measurement			13.49	7.10	19.29	8.45
	Turner (1987)			13.30	6.90	19.30	8.30
	% Difference			**1.42**	**2.86**	**–0.05**	**1.79**
ER 793	Our measurement			14.67	5.72	17.05	8.08
	Turner (1987)			14.40	6.40	17.10	8.10
	% Difference			**1.86**	**–11.22**	**–0.29**	**–0.25**
Average % difference	**3.59**						
S.D.	**5.31**						
Average % difference – KA64 M1	**2.25**						
S.D.	**2.85**						

round holes of differing sub-millimeter diameters perpendicular to the surface of entry (possibly representing insect activity).

Description

The morphology of CD 5997 is like that of other sabre-tooth cats, though it is relatively small in comparison with other members of *Megantereon,* an already relatively small sabre-tooth felid (Table 4). It has a long diastema between the highly reduced and laterally compressed mandibular canine and the reduced third premolar. It also has an exaggerated mandibular flange that extended below the ventral border of the symphysis with a marked antero-ventral ridge (Fig. 1). This mandibular flange, a feature for which the function is still unknown, is one of the most diagnostic characteristics of *Megantereon* in that it is larger than that found in most other Machairodonts (Emerson & Radinsky 1980). The mandibular flange of CD 5997 extends on the ventral border of the corpus inferior to and just posterior from the anterior-most projection of the anterior-most alveolar margin of the incisors (between I_1 and I_2) and continues posteriorly to approximately the midpoint between C_1 and P_3. It extends below the ventral border of the corpus about 7mm, but if its ventral-most aspect were intact, it probably would have extended 10 mm or so ventrally. The mandibular flange has a strong dorsoventral ridge marking its anterior margin, and lies predominantly lateral to the midline in the anterior view (not shown), extending below the level of the symphysis.

The symphysis itself is relatively long (Table 4), extending from the incisal alveoli superiorly, and extending inferiorly below a line representing the continuation of the ventral border of the corpus (Fig. 1). It is nearly vertically oriented and is highly pitted with symphyseal interdigitations. CD 5997 thus preserves a relatively complete, unbroken, hemimandibular symphysis (with only slight surface abrasion).

There is no indication that the masseteric fossa projects anteriorly to the distal margin of M_1. Nor is there any indication of notable grooves along the inferomedial surface of the corpus as has been described for specimens of '*M. hesperus*' (Berta & Galiano 1983).

As noted above, all of the teeth except for P_4 and M_1 have fallen out, and the remaining ones are so worn or damaged as to render their analysis difficult. Based on alveolar dimensions, the incisors appear to have been relatively small, mesiodistally compressed and slightly crowded. Based on the depth of the alveoli, they do not appear to have been very high-crowned. However, the canine alveolus is very deep which suggests that the canine was relatively substantial. It too was probably laterally compressed. The alveolus of the P_3 is sufficiently encrusted (see above) so as to render its analysis difficult. However, it appears to have contained a tooth with the largest root being distal, the second largest root being mesial.

The P_4 and M_1 are broken and worn (see above). The P_4 displays an elliptical occlusal outline and marked bulging of the enamel above the cervicoenamel junction. The occlusal outline of the M_1 is longer and more rectangular. The paraconid bears a sharp distal margin indicating the typical felid carnassial notch.

Taxonomic affinities of CD 5997

CD 5997 can be identified as *Megantereon* based on both quantitative and qualitative evidence. Though the specimen is overall the smallest in our sample other than that from South Turkwel, which was not viewed in person (Table 4), it falls within or very close to the *Megantereon* range in all measures of shape (Table 6). Qualitatively, the specimen clearly comes from a small-bodied sabre-tooth

Table 6. Shape derivatives of measurements taken. Shape = BL/MD

Abbreviation	CD 5997	African and early European *Megantereon* group **Mean** (Range*, *n*)	Late European, North American and Asian *Megantereon* group **Mean** (Range*, *n*)
I1	**3.3**	**2.1** (1.1–3.3, 3)	**1.8** (1)
I2	**2.3**	**1.7** (1.3–2.3, 3)	**1.3** (1)
I3	**1.4**	**1.3** (1.2–1.4, 3)	**1.1** (1)
C	**1.1**	**1.3** (1.1–1.7, 4)	**1.4** (1.1–1.6, 7)
P3	**0.6**	**0.6†** (0.6–0.8, 5)	**0.6** (0.4–0.8, 15)
P4	**0.4**	**0.5** (0.4–0.7, 9)	**0.4** (0.4–0.5, 19)
M1	**0.5**	**0.5** (0.4–0.6, 9)	**0.5** (0.4–0.5, 19)
Symph (height/depth)	**3.6**	**3.1** (2.6–3.6, 2)	**3** (1)
Ant P3 (height/width)	**2.1**	**2.4** (2.1–2.7, 2)	**2.4** (1.9–2.8, 3)
Post M1 (height/width)	**2.2**	**2.25** (2.24–2.25, 2)	**2.2** (1.9–2.3, 4)

*Owing to the small sample sizes, ranges were used instead of standard deviations.

†Not including KNM-ST 23812, which reportedly exhibits agenesis of the P_3 (Werdelin & Lewis 2000).

felid with reduced premolars, an increased post-canine diastema and the diagnostic ventral mandibular flange. Again, though it is relatively small in many, though not all, respects, CD 5997 appears to exhibit typical *Megantereon* morphology.

Metric comparisons

Only the premolar-molar row dimensions provided sample sizes large enough for multivariate analysis. All of the seven original variables (mesiodistal and buccolingual measurements from each of the three teeth, as well as the entire premolar-molar row length) and the four variables extrapolated from that data (tooth shape = mesiodistal/buccolingual index for each tooth, tooth row compression = sum of mesiodistal measurements of the three teeth/premolar-molar row length) show segregation to varying degrees, consistently separating the fossils into at least two *Megantereon* populations with the Plio-Pleistocene African and Dmanisi specimens and the early Pleistocene fossils from Greece and Spain grouping separately from all others (Tables 4 & 6). The two measurements of the third premolar (Figs 2 & 3) along with the premolar-molar row length (Fig. 4) are particularly useful in making this distinction, as there is almost no overlap between the two populations in these variables, as indicated by Martínez-Navarro & Palmqvist (1995, 1996). The degree of separation between the two *Megantereon* populations, in terms of these three variables, is not only highly significant ($P < 0.01$ in two-tailed *t*-tests) in each of the cases, but is more extreme than the degree of separation between all other felid taxa examined (with the exception of premolar-molar row length for *Neofelis* and *Smilodon*, these latter taxa being also the most disparate in overall body size).

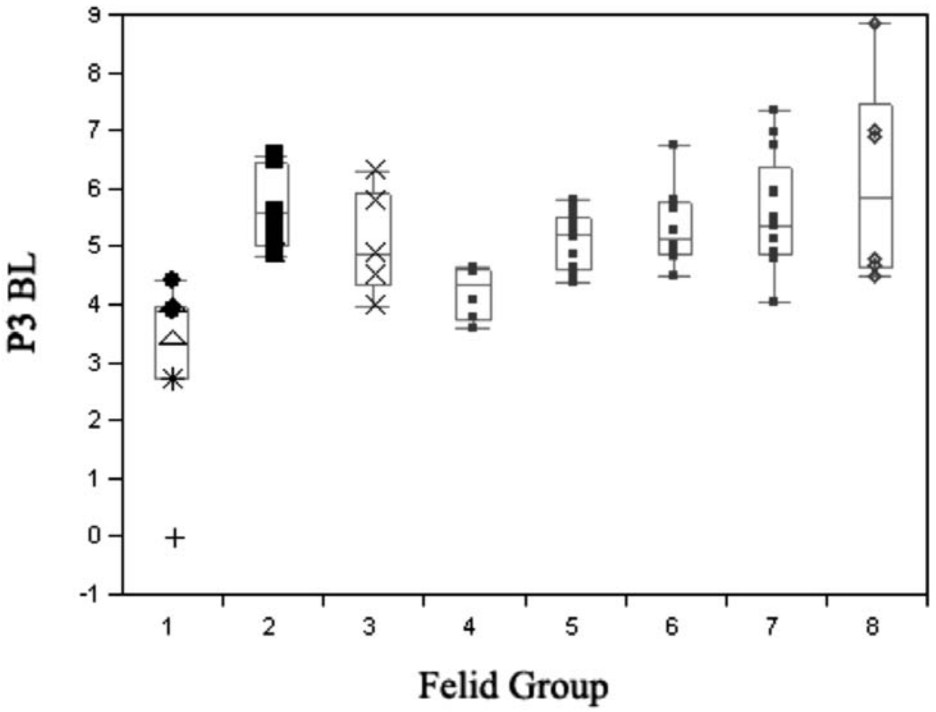

Figure 2. Box plots of third premolar buccolingual measurement by genus/species group. Legend: Group 1 = African and Early European *Megantereon*, 2 = North American and Late European *Megantereon*, 3 = Asian *Megantereon*, 4 = *Neofelis*, 5 = *Acinonyx*, 6 = *Panthera uncia*, 7 = *P. pardus*, 8 = *Smilodon*. Asterisk = CD 5997, triangles = Early European *Megantereon*, '+' = South Turkwel *Megantereon*, closed circles = other African *Megantereon*.

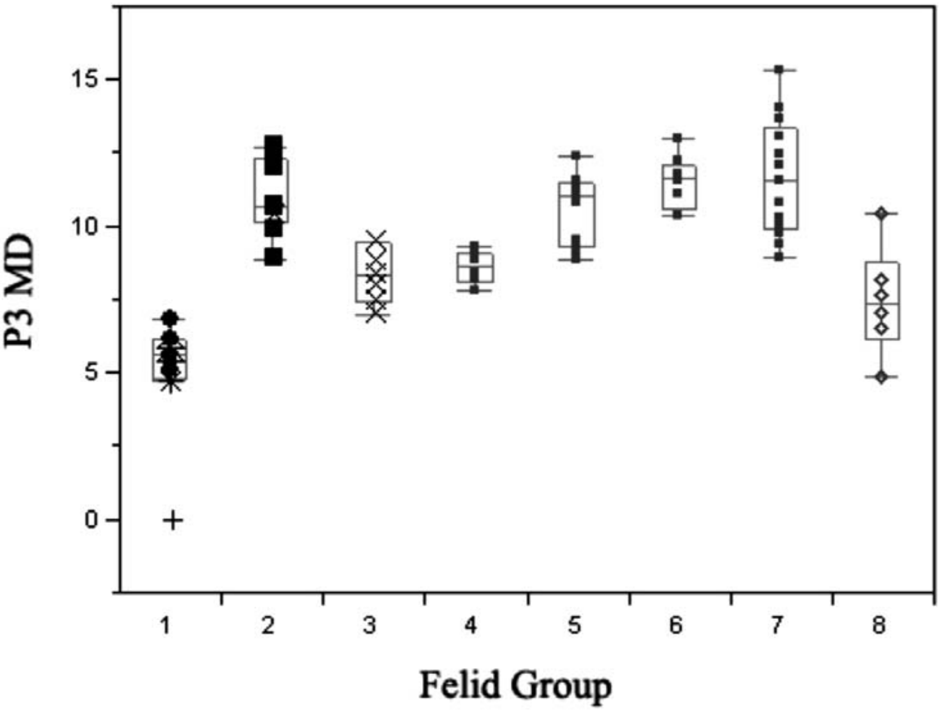

Figure 3. Box plots of third premolar mesiodistal measurement by genus/species group. Legend as in Fig. 2.

Likewise, a principal components analysis of the premolar-molar row variables (the six mesiodistal and buccolingual alveolar measurements of the premolars and molar) yields similar results (Figs 5 & 6). Given the positive factor loadings of the metric variables in the first principal component (Fig. 5, Table 7), which accounts for 62.58% of the variation within the total sample, this component may be interpreted as a size vector which is predominantly driven by the P_4 and M_1 dimensions. Generally the first principal component accounts for size variation, as is the case in our sample, and it often contains less information about systematic/phylogenetic relationships than do later components that examine more detailed shape relationships within the data. However, size should not be neglected, because differences in gross size are important in the identification of many felids (which can vary tremendously in size but conservatively in shape). As shown in Figure 5, the first principal component (PC1) separates the two groups of *Megantereon* (with the Asian specimens possibly as a third distinct grouping). The difference in the mean of PC1 scores between the African/ Early European group and Late European and North American *Megantereon* is significant ($P < 0.01$) based on a two-tailed *t*-test. The Asian specimens group with the

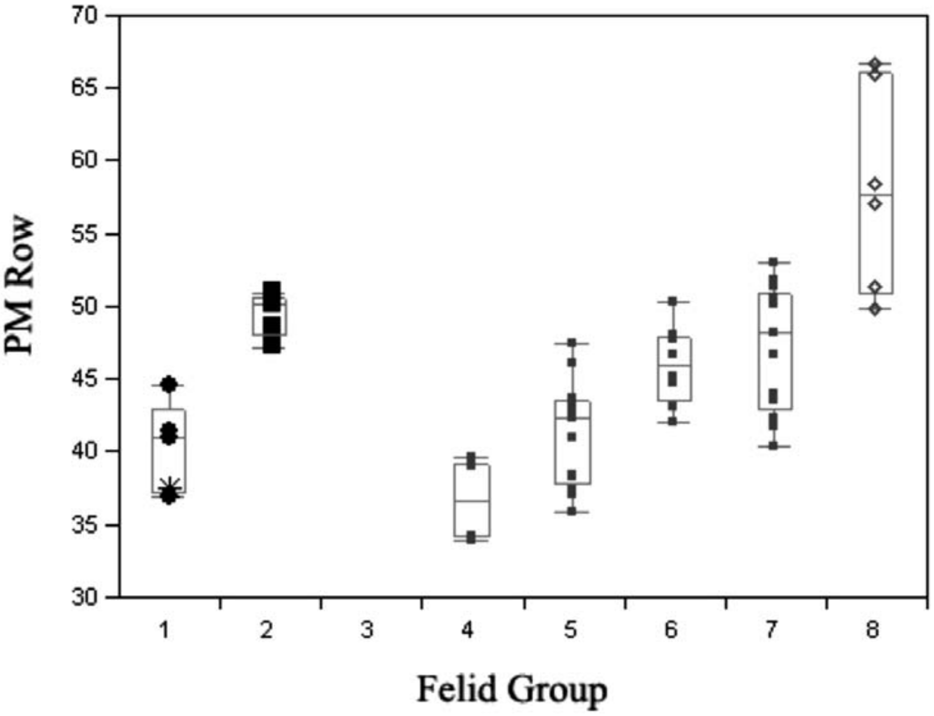

Figure 4. Box plots of premolar-molar row length by genus/species group. Legend as in Fig. 2.

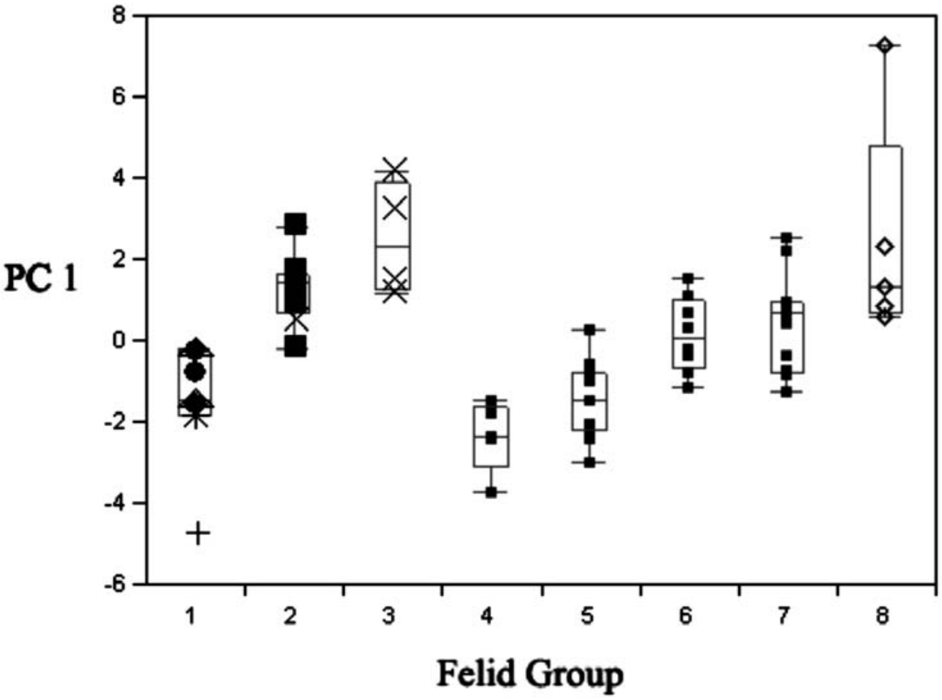

Figure 5. Box plots of the first principal component by genus/species group. Legend as in Fig. 2.

Later European group for this variable.

The same findings obtain with the second principal component (PC 2: Fig. 6) which accounts for 25.90% of the variation within the total sample and separates the two *Megantereon* groups ($P < 0.01$) as well. Based on variable loadings (Table 7), principal component two reflects an inverse relationship between the mesiodistal and buccolingual lengths of P_3 and M_1. Interestingly, in terms of PC2 (Fig. 6), the African/Early European group of *Megantereon* clearly clusters with the *Smilodon* specimens (see discussion). They also group statistically with the Asian specimens for this variable.

Table 7. Principal components on correlations of all felid groups sampled.

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
Eigenvalue	3.75	1.55	0.30	0.18	0.12	0.10
Percentage	62.58	25.90	4.93	2.97	1.99	1.63
Cum. percentage	62.58	88.48	93.41	96.38	98.37	100.00
Eigenvectors						
P_3 BL	0.36	0.47	-0.68	-0.38	0.17	0.07
P_3 MD	0.14	0.74	0.37	0.48	0.27	0.02
P_4 BL	0.47	0.06	0.55	-0.51	-0.28	0.37
P_4 MD	0.49	0.01	-0.09	0.27	-0.59	-0.57
M_1 BL	0.44	-0.34	0.18	-0.11	0.69	-0.41
M_1 MD	0.44	-0.34	-0.22	0.53	0.05	0.60

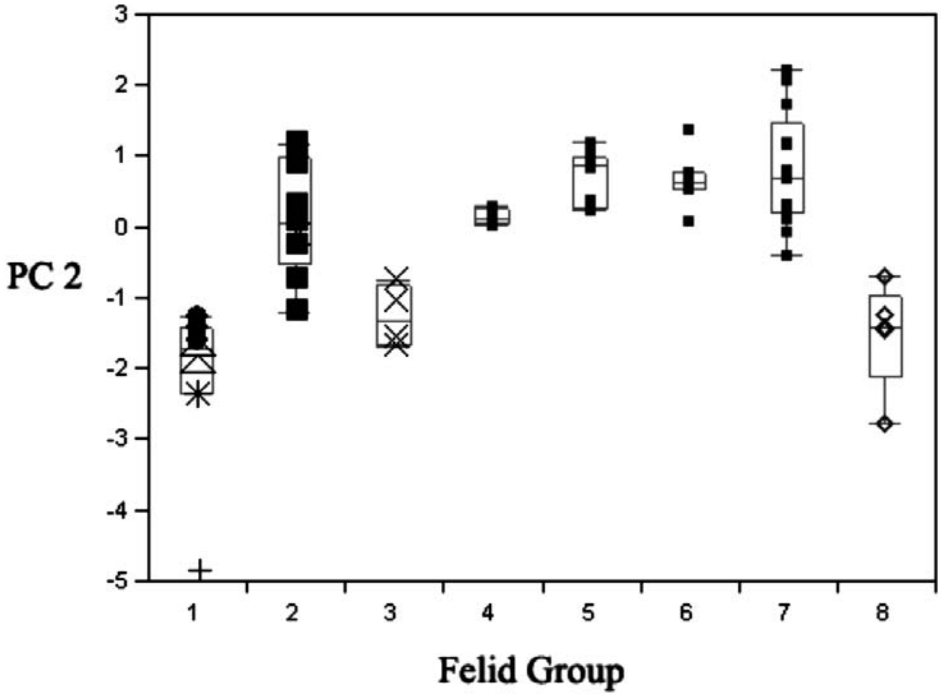

Figure 6. Box plots of the second principal component by genus/species group. Legend as in Fig. 2.

The other principal components, accounting for the remaining 11.52% of the variation within the premolar-molar data, do not show any consistent patterns of separation between any of the study groups. These components have eigenvalues of less than one (Table 7) and thus can be interpreted in terms of random variation. The first two principal components clearly separate the specimens of *Megantereon* into at least two distinct groups, as do the univariate analyses. In fact, the divergence displayed by these combined analyses is greater than most of the differences evident between the means of the extant felid groups. Based on the clear separation of the *Megantereon* groups (African/Early European vs Late European/North American) as seen in the significant *t*-tests for the raw variables and principal component scores, we reject the null hypothesis that *Megantereon* is monomorphic (and by inference, monospecific). The Asian specimens may represent a third species given that they are statistically distinct from the African/Early European group in the first principal component, and the Late European/North American for the second principal component (see discussion). While the specimen from South Turkwel is the most metrically unique among the genus, until further specimens are described that are morphologically and metrically similar, it cannot be statistically determined to represent a new species.

DISCUSSION

The nomen *Megantereon whitei* (Broom, 1937) has taxonomic precedence, and we therefore agree with Martínez-Navarro & Palmqvist (1995) that the evidence warrants a resurrection of this taxon to accommodate an African/Early European group. The Late European/North American group should maintain its designation as *Megantereon cultridens* (Cuvier, 1824). This Late European/North American group probably contains multiple species as Martínez-Navarro & Palmqvist (1996) suggest (with the Asian specimens making a likely bid for separation); however, the present analysis cannot resolve this issue.

Might the size differences between the groups represent sexual dimorphism? The variation between the two *Megantereon* groups is similar to that between the two sexes of leopard (*P. pardus*) – the most sexually dimorphic extant taxon examined – for most premolar-molar row bivariate comparisons, although principal components analysis reveals a substantial degree of metric variability in terms of size and shape for *Megantereon*, greater than for any living felid species. However, we feel it is improbable that only males would have been recovered in one geographic sample and only females in the other. In fact, assuming random sampling of the *Megantereon* populations in each region, there is an exceptionally remote chance of getting a distribution as or more extreme than that observed (eight of eight African specimens being of the small sex and 10 of the thirteen non-African specimens being of the larger sex) assuming an even sex ratio. Though it could be argued that there is some agent in Africa that has accumulated only females and some agent outside of Africa that has selected mostly males, we find this possibility unlikely. Thus, despite the similarity to sexual dimorphism in leopards, it is improbable that sexual dimorphism accounts for the differences between the *Megantereon* populations.

Might the variation in the sample be a result of polytypism normally found in a widely dispersed species? For the morphological traits that we analysed, which clearly separate the *Megantereon* sample, the *P. pardus* sample – which also ranges across Africa and Eurasia – does not cluster into geographically distinct groups.

In almost all analyses of premolar-molar row measurements (e.g. Figs 2–6), the East African *Megantereon* from East Rudolf, the Greek *Megantereon* from Appolonia (Martínez-Navarro & Palmqvist 1996), the Spanish *Megantereon* from Venta Micena (Martínez-Navarro & Palmqvist 1995) and the Dmanisi *Megantereon* from Georgia (Vekua 1995) fall within or close to the range of the African group, indicating that *M. whitei* is the most appropriate identity for these specimens based on current evidence.

Likewise, the Kenyan specimen from South Turkwel (Werdelin & Lewis 2000) is either in the range of, or smaller than the other *M. whitei* specimens in terms of the key variables that warrant the splitting of the genus into an African and non-African species. It must be acknowledged that the morphological features used by Werdelin and Lewis (2000, 2002) to classify the South Turkwel specimen into its own species were not addressed in this paper, and thus all that we can say is that it falls within the range of the African population in terms of the features that we analysed, as suggested by Palmqvist (2002) (but see also Werdelin & Lewis 2002). Thus, while our analysis suggests that *M. whitei* encompasses all African specimens of *Megantereon* and those from Georgia, Greece and Spain, and the other *Megantereon* specimens included in our study should maintain their designation as *M. cultridens*, other non-metric features may be invoked to further parse the sample into more species.

We would like to thank the American Museum of Natural History, the Natural History Museum (London) and their staffs, the University of the Witwatersrand and the Transvaal Museum and its staff (especially Stephany Potze) for granting us access to the collections. We would also like to thank Blair Van Valkenburgh and Lars Werdelin for comments on an earlier draft of this paper and especially Paul Palmqvist for comments and data. Funds were provided by Duke University's Undergraduate Research Support Office, Howard Hughes Program and Department of Biological Anthropology and Anatomy; the Palaeo-Anthropology Scientific Trust (PAST); the National Geographic Society; and the Wenner-Gren Foundation (grant 6914 to D.J.D.). We also thank the South African Heritage Resource Agency for Permits to excavate and the Fossil Trackers team for assistance in the excavations.

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Description of an anomalous tortoise (Reptilia: Testudinidae) from the Early Holocene of Zimbabwe

Donald G. Broadley*

Research Associate, Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe

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An anomalous subfossil tortoise is described from a Holocene cave deposit at Pomongwe in the Matobo Hills, southwest Zimbabwe (Carbon 14 date 9400 ±100 yrs BP). This specimen appears to be unique in its truncated and depressed anterior carapace with loss of the normal second peripheral, but agrees with *Kinixys* Bell and *Impregnochelys* Meylan & Auffenberg in having numerous auxiliary scales. It may lack the carapacial hinge of *Kinixys.* The epiplastron appears most similar to that of a female *Chersina angulata* Gray.

Keywords: *Kinixys spekii* (?), Testudinidae, osteology, Holocene, Zimbabwe, Africa.

INTRODUCTION

The extensive deposits in Pomongwe Cave in the Matobo Hills were excavated in 1960/61 (Cooke 1963). Beneath a superficial layer of dust (Level 1) was a thin deposit of red soil (Level 2), which had been imported during the 1920s by the current curator in an attempt to stabilize the white ash (Level 3) on the floor of the cave for the benefit of visitors to the cave paintings. The bone recovered from Level 3 included many fragments of tortoise bones (Brain 1981), some identified as *Stigmochelys* (ex *Geochelone*) *pardalis* and *Kinixys spekii* (Broadley 1993, 1997), but eight more or less complete bones possibly represent an undescribed taxon. Tortoise bones from later excavations in the same cave (Walker 1995) were also examined, but did not yield additional material of this unusual form. As no further excavations are planned in this cave, it was decided to describe this tortoise on the basis of the limited available material.

MATERIALS AND METHODS

Comparative material of all African tortoise species except *Geochelone sulcata* (Miller) was available in the Herpetology Department of the Natural History Museum of Zimbabwe in Bulawayo (NMZB) (see Appendix 1). Nomenclature for bones and epidermal shields follows Zangerl (1969), while nomenclature for limb bones follows Walker (1973). In the figures, thin black lines denote bone margins, sutures and fractures, while thick white (subfossil) or black (other genera) lines denote sulci between epidermal shields.

SYSTEMATIC PALAEONTOLOGY

Order Testudines Linnaeus, 1758 (=Chelonii Brongniart 1800)
Suborder Casichelydia Gaffney, 1975
Infraorder Cryptodira Cope, 1868
Superfamily Testudinoidea Batsch, 1788
Family Testudinidae Batsch, 1788
Subfamily Testudininae Batsch, 1788

Genus (?) *Kinixys* Bell, 1827

Type species: *Kinixys castanea* Bell (=*Testudo erosa* Schweigger 1812), by original designation.

(?) ***Kinixys spekii*** Gray, 1863: 381, Figs 1–4

Locality and horizon. Pomongwe Cave, Matobo National Park, southwest Zimbabwe. Excavated by C.K. Cooke in 1960/61. Level 3 (Pomongwe Industry), Carbon 14 dated at 9400 ± 100 yrs BP (Cooke 1963), i.e. early Holocene. These bones are stained red-brown, so were presumably at the surface of Level 3 in contact with the red soil of Level 2.

Diagnosis. This specimen differs from all known forms of Testudinidae in the truncated anterior carapace with apparent fusion of the second and third peripherals, the third marginal scute is restricted to the dorsolateral surface of the carapace and the peripheral bone shows clear sulci demarcating three axiliary scales (submarginals of Loveridge & Williams 1957) on its anteroventral surface (Fig. 1). The epiplastron most closely resembles that of a female *Chersina angulata* (Fig. 2), but is truncated laterally, while the upper surface is slightly concave in cross-section instead of sloping steeply away towards the hyoplastral suture. The gulars may have been even longer than in *Chersina.* However, it should be noted that elongate thickened epiplastra are even better developed in male *Kinixys erosa,* although in this case they are deeply forked (Loveridge & Williams 1957: fig. 49; Broadley 1997: fig. 5).

Material. NMZB 14473A, an almost complete right second + third peripheral, with associated first costal (NMZB 14473B), and NMZB 14473C, a partial right epiplastron; NMZB 14473D, a complete fourth neural; NMZB 14475A, a right humerus, lacking the head, and NMZB 14475B , a right femur lacking the head. NMZB 14471A, outer portion of a left hypoplastron (level 2); NMZB 14474, right costal 8 (level 1).

Description

The most diagnostic bone (NMZB 14473A) apparently represents the fused second + third peripherals, with a distinct angular 'shoulder'. This bone has maximum dimensions of 26 mm long by 22 mm wide (Fig. 1A,C). The

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*Present address: Biodiversity Foundation for Africa, P.O. Box FM 730, Famona, Bulawayo, Zimbabwe. E-mail: broadley@gatorzw.com

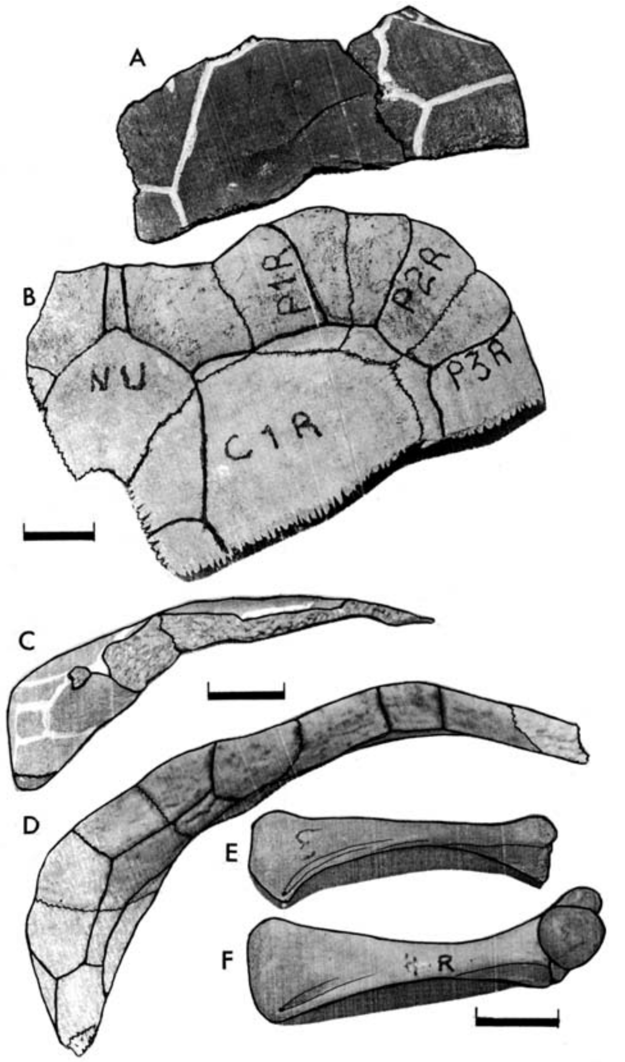

Figure 1. (?) *Kinixys spekii,* NMZB 14473A+B: **A**, dorsal and **C**, anterior views of right peripherals 2 + 3 and right costal 1; **E**, dorsal view of right humerus to show ectepicondylar fossa (note white spot in the shadow below it). *Kinixys spekii*: NMZB 8847: **B**, dorsal and **D**, anterior views of nuchal, right costal 1 and right peripherals 1–3; **F**, dorsal view of right humerus of NMZB 11925. Scale bars = 1 cm.

sulci marking the lateral margins of the first pleural cross the inner anterior corner, and wedge into the inner posterior corner to meet the sulcus separating the second and third marginals. The rounded anterior edge of the bone is bordered by two large axillary scales, with a smaller rectangular one wedged between them and the second marginal, which is dorsally subtriangular in shape. On the inner anterior edge of the bone is a small projection terminating in a sutural face quite distinct from the adjacent one to accommodate the first peripheral, suggesting the presence of an independent epithecal ossification. The internal suture with the hyoplastral buttress apparently terminated at the point where the first and second peripherals meet the first costal. The African species showing least anterior expansion of the first three peripherals is *Psammobates oculiferus,* but the form of the enigmatic peripheral of this specimen seems closest to *Kinixys.*

The associated first costal (NMZB 14473B) is subrectangular and has a maximum width of 38 mm and length of 22 mm (Fig. 1A,C), the bone is very thin. The sulci marking the borders of the first and second vertebrals cross the

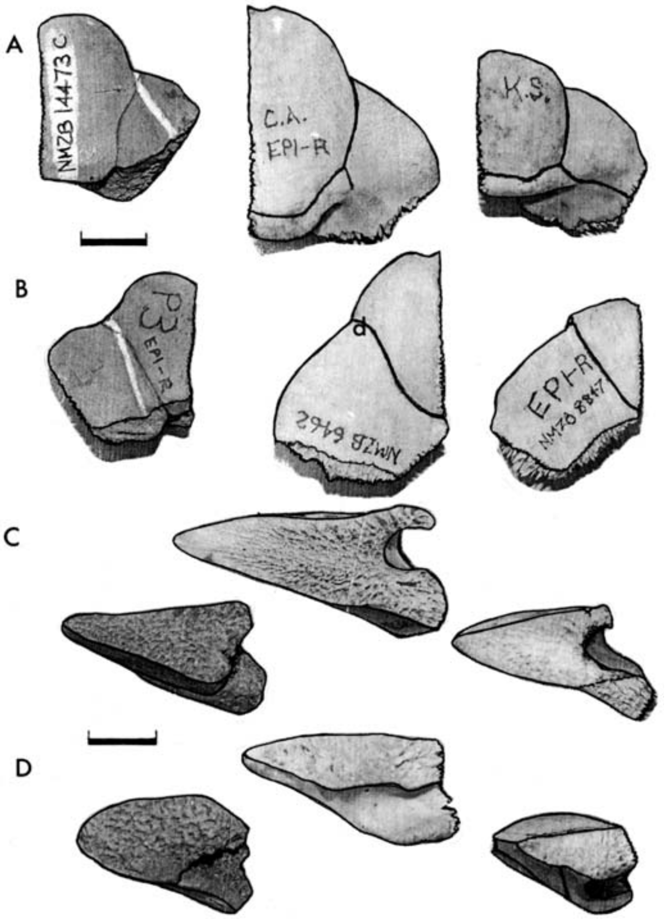

Figure 2. Right epiplastron of, from left to right: (?) *Kinixys spekii* NMZB 14473C; *Chersina angulata* NMZB 6492; *Kinixys spekii* NMZB 8847. **A**, dorsal views; **B**, ventral views; **C**, interepiplastral suture; **D**, epiplastral/hyoplastral suture. Scale bars = 1 cm.

dorsal third. A shallow depression marks the areolus, a curved groove extends from it laterally to the second marginal and a shallower one extends anteriorly to the first marginal. The intact suture between the peripheral and the first costal indicates that the carapace was strongly depressed.

The partial epiplastron (NMZB 14473C) is 25.5 mm wide, with a lip 26.5 mm long and 13 mm deep, but the bone is broken caudad, so it is not known if there was a posterior excavation of the epiplastral lip (Fig. 2). The dorsal surface is slightly concave mesially. Ventrally the gular sulcus diverges towards the gular/hyoplastral suture, suggesting that it will reach the entoplastron.

The hexagonal fourth neural (NMZB 14473D) is the same size and shape of the corresponding bone of *Kinixys spekii,* but dorsally it has shallow depressions on each side of the midline, while ventrally the vertebral scar is weak.

A right humerus (NMZB 14475A) lacks the head (estimated length 44 mm, Fig. 1E). It resembles that of *Kinixys spekii,* with a well-defined fossa culminating in a foramen, but the bone is more slender (maximum width at distal end 11 mm, maximum width of shaft 3.5 mm) than a comparable sized *K. spekii* humerus from the same level (12.8 and 4 mm, respectively). It also differs in having a sharp keel lateral to the ectepicondylar fossa and also a pronounced ventral keel.

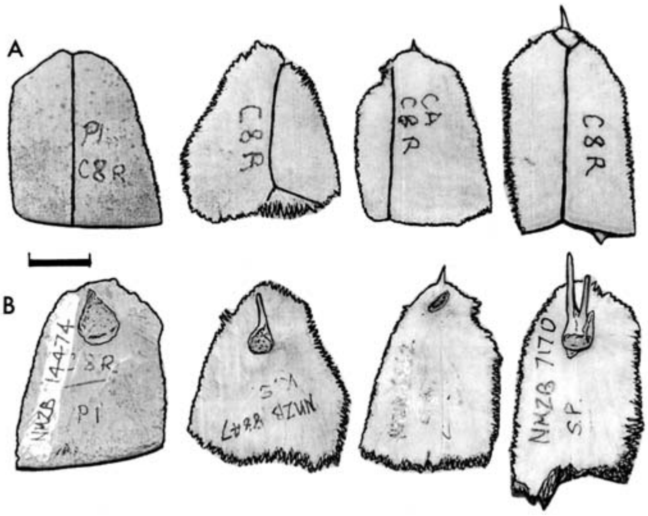

Figure 3. Right costal 8 of, from left to right: (?) *Kinixys spekii* NMZB 14474; *Kinixys spekii* NMZB 8847; *Chersina angulata* NMZB 6492; *Stigmochelys pardalis babcocki* NMZB 7170. **A**, dorsal views; **B**, ventral views. Scale bars = 1 cm.

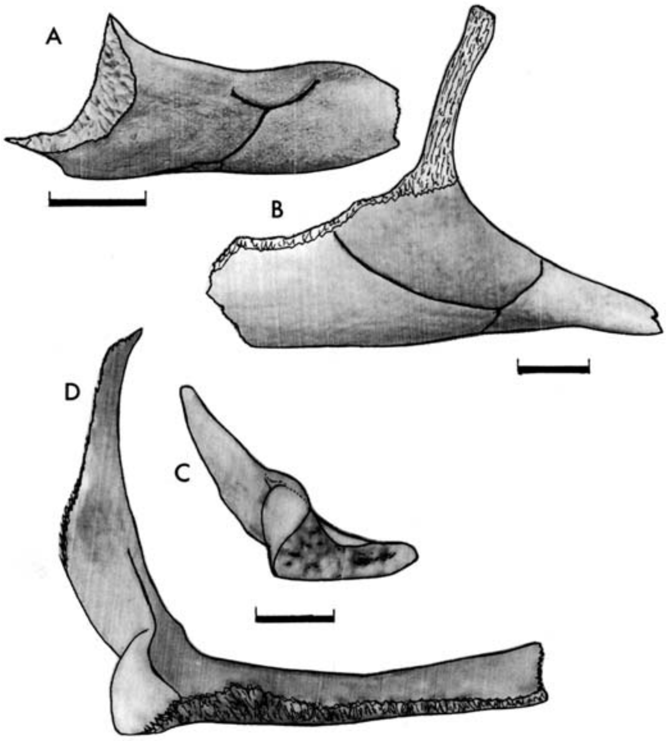

Figure 4. (?) *Kinixys spekii* NMZB 14471A, outer portion of left hypoplastron: **A**, lateral view: **C**, rear view. *Kinixys spekii* NMZB 8847, left hypoplastron: **B**, lateral view, **D**, rear view. Scale bars = 1 cm.

A right femur (NMZB 14475B) lacks the head and is shorter than the humerus. It resembles that of *K. spekii*, but the tibial condyle is wider, while the dorsal surface lacks the shallow terminal depression of the latter species.

Right costal 8 NMZB 14474 (Level 1), height 30 mm, width at lower edge 25 mm (Fig. 3). The sulcus between the fourth pleural and fifth vertebral is straight, the suture between costals 7 and 8 is gently curved and that between costal 8 and the suprapygal is straight. The subtriangular iliac scar is quite large. The lower edge shows a smooth curve but is somewhat worn (?from use as a scraper), but the costo-peripheral suture may not have closed.

Outer posterior portion of left hypoplastron NMZB 14471A (Level 2), height 18 mm (Fig. 4). There is no development of the long incurving buttress beneath the hinge found in *Kinixys spekii*, instead the superior projection slopes steadily outwards and posteriorly the outer margin of bone bordering the xiphiplastron is much higher.

This specimen was initially suspected to represent a new genus and species, but because it was sympatric with *Kinixys spekii*, there remains the possibility that it represents a highly anomalous specimen of the latter species, which it resembles in size. I described a Recent specimen of *Pelusios sinuatus* which had numerous fusions of bones in both carapace and plastron, resulting in an almost circular shell, but this terrapin was caught as an adult and lived for many years in captivity (Broadley 1997b). So the truncated anterior carapace may not have been a major handicap to the 'mongrel' Matobo tortoise.

PALAEOECOLOGY

The habitat in the vicinity of Pomongwe cave has been illustrated by Brain (1981: fig. 24). It is an extensive area of rugged granite hills with intervening areas of woodland and very limited areas of grassland (Walker 1995: plates 2–5). The tortoises eaten by the Stone Age people and represented in the cave deposits are *Stigmochelys pardalis* and *Kinixys spekii.*

The only tortoise carapace examined which shows a suggestion of a 'shoulder' on peripherals 2 and 3 is from the steppe tortoise *Testudo horsfieldi,* which has a broad, somewhat depressed shell, but not truncated anteriorly. However, it seems that the 'shoulder' may be better developed in the 'saddlebacked' races of *Chelonoidis nigra* on the Galapagos Islands. A photograph of the adult male holotype of *C. n. hoodensis* (Van Denburgh 1914: plate 53, fig. 2) shows this well (see also Pritchard 1979: 340). The raised anterior carapace and narrow anterior plastron give the saddleback tortoises more freedom for their forelimbs and neck, allowing them to negotiate rugged terrain, as illustrated by a photograph of an adult *C. n. ephippium* on Pinzon (= Duncan) Island (King 1968: 17). Molecular data indicates that *Chelonoidis* is sister to *Kinixys* (Le *et al.* 2006). Gerlach (1999) has shown that the saddleback giant tortoise, *Aldabrachelys arnoldi,* of the Seychelles shows adaptations of the deep jaw and humerus musculature enabling it to browse efficiently. An extinct saddleback giant tortoise, *Cylindraspis vosmaeri,* is also known from Rodrigues, the easternmost of the Mascarene Islands (Bour 1984), so the saddleback adaptation can appear in unrelated giant tortoises inhabiting isolated islands which lack predators.

The present specimen differs from all the saddlebacked giant tortoises in its small size, depressed carapace and African mainland distribution. The reduced anterior carapace and plastron could have made this tortoise more agile and fast moving in a rocky habitat. It may have had a life style similar to that of *Malacochersus tornieri,* spending most of the time wedged in rock crevices and emerging for short spells of activity in the vicinity of its retreat (Ireland & Gans 1972). This unusual specimen apparently belongs in the *Chelonoidis/Kinixys* clade (Le *et al.*, 2006),

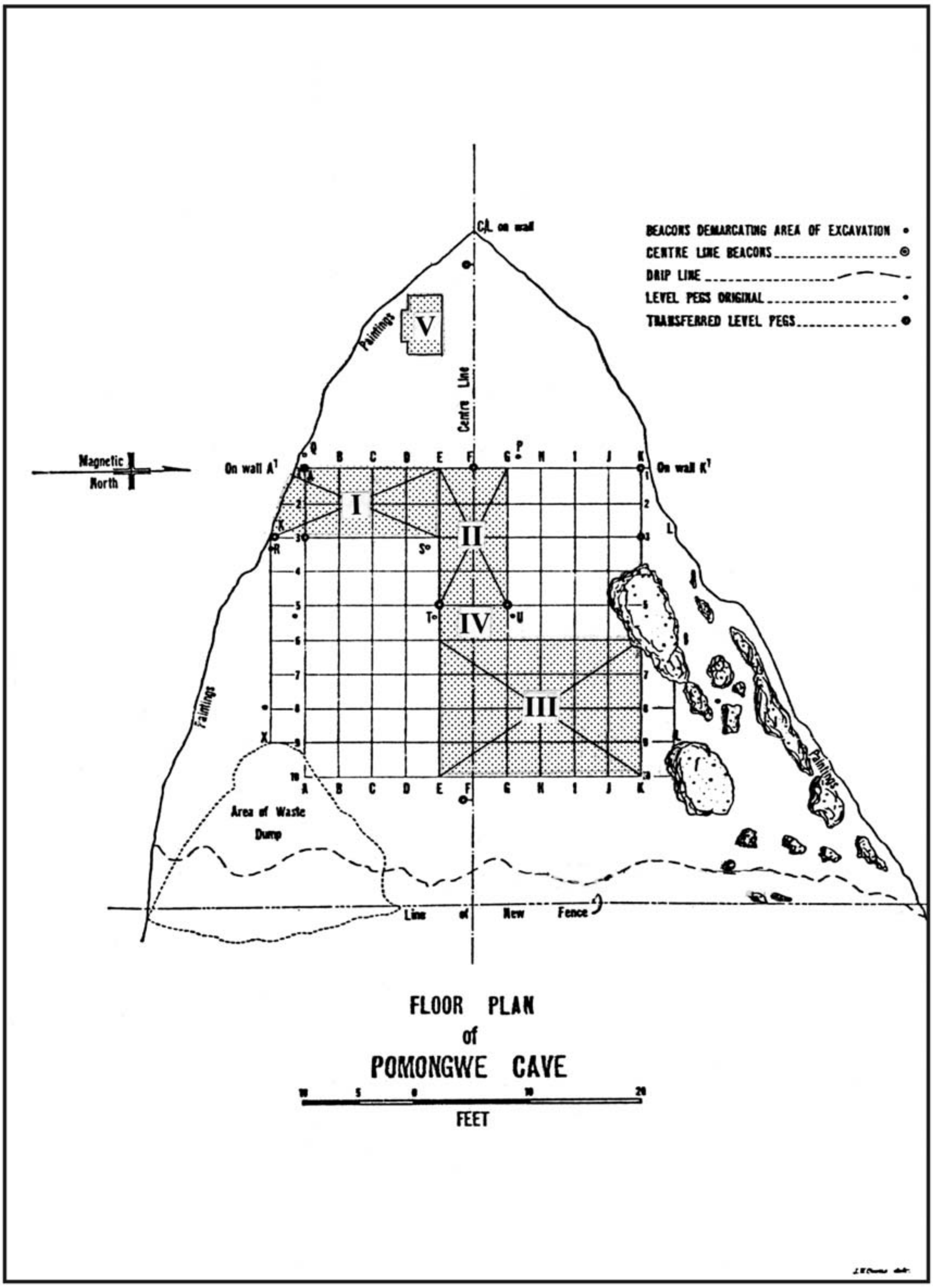

Figure 5. Floor plan of Pomongwe Cave (modified from Cooke 1963: fig. 1). The excavated areas are stippled. Trenches I to III were excavated by Cooke in 1960/61 and trenches IV and V by Walker (1995). The grid is of one metre squares.

having numerous axillary scales like the latter genus and *Impregnochelys* of the Miocene of Africa (Meylan & Auffenberg 1986).

DISCUSSION

C.K. Brain analysed the 17 756 bone fragments from C.K. Cooke's excavations at Pomongwe Cave in 1960/61 and recorded a total of 1357 fragments of tortoise carapace and plastron (Brain 1981: table 9). Of these, 321 fragments came from level 3, and apart from the six bones that are assigned to the specimen under consideration, I have assigned 55 fragments to the leopard tortoise *Stigmochelys pardalis* (the genus *Stigmochelys* Gray was reinstated by Lapparent de Broin, 2000) and 24 to *Kinixys spekii,* the remainder are unidentified. Two additional bones assigned to the unusual specimen came from levels 1 and 2, but may have been brought towards the surface by burrowing rodents or beetles. The fact that the eight diagnostic bones are in relatively good condition suggests that they were not subject to trampling on the open floor of the cave, but may have been excavated from among the boulders of the rock fall to the right of the cave (Fig. 5). If in the future a fresh excavation is made between the end of Cooke's Trench III and the rock fall, more of the missing bones of the carapace and plastron may be found. It is also possible that this tortoise was not eaten, but took refuge between the rocks during a drought and died there, which would also account for the bones not being scattered. The corner of the metre square J6 where this strange tortoise may have been found is illustrated in Cooke (1963: plates XIX A & B). Bone is not normally preserved in the acidic granite-derived sand of the Matobo Hills, so tortoise bones are only likely to be found in dry caves.

I am indebted to C.K. ('Bob') Brain (Transvaal Museum) for painstakingly sorting the thousands of bone fragments excavated in Pomongwe Cave by Cran Cooke in 1960/61. I am grateful to the late Barbara Bennefield, who prepared most of the comparative skeletal material used in this study prior to her untimely death in 1986. I also thank John and Moira FitzPatrick for photographing the bones and making the prints from which the images in Figs 1–4 were prepared. Robert Drewes (California Academy of Sciences) kindly supplied me with photographs of the type material of *Chelonoidis nigra hoodensis* (Van Denburgh). I thank Peter Pritchard and Bill Branch for their advice regarding the interpretation of this strange tortoise.

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APPENDIX 1. Comparative material.

Kinixys natalensis, NMZB 11071, Weenen Nature Reserve, KwaZulu-Natal, South Africa
Kinixys spekii, NMZB 8847, Majoda, Zimbabwe
Kinixys spekii, NMZB 11925, Matobo National Park, Zimbabwe
Kinixys belliana, NMZB 12078, Gonarezhou National Park, Zimbabwe
Kinixys nogueyi, NMZB 9708, Ngaoundere, Cameroon
Kinixys erosa, NMZB 9894, Lolodorf, Cameroon
Kinixys homeana, NMZB-UM 33496, Ghana
Chersina angulata, NMZB 6462, Port Elizabeth, Eastern Cape Province, South Africa
Stigmochelys pardalis babcocki, NMZB 7170, Bulawayo, Zimbabwe
Psammobates geometricus, NMZB 6565, Elandsberg Nature Reserve, Voëlsvlei, Western Cape Province, South Africa
Psammobates oculiferus, NMZB-UM 12755, 250 km S of Mamono, Botswana
Psammobates tentorius, NMZB 7070, Karoo National Park, Eastern Cape Province, South Africa
Homopus boulengeri, NMZB 7178, Sutherland, Western Cape Province, South Africa
Homopus femoralis, NMZB 6651, Molteno, Eastern Cape Province, South Africa
Testudo horsfieldi, NMZB 7764, 'southern U.S.S.R.'
Malacochersus tornieri, NMZB-UM 33658, Dodoma, Tanzania

A fresh look at chemical fossil extraction

Ceri McCrae [1,2*] **& Stephany Potze**[2]

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

[2]*Human Origins and Past Environments (HOPE), Transvaal Museum, Northern Flagship Institution, Pretoria, South Africa*

In this age of microtechnology, now more than ever before, detail is indispensable. In the past, the damage to fossils during retrieval, preparation and storage was an accepted downfall of the scientific process. With the increasing use of advanced techniques, which rely on high-resolution applications such as scanning electron microscopes and microtomography, there is a definite need to improve on the actual fossil extraction methods currently used. The aim of this work is to achieve an ideal method of extraction where the fossil is retrieved in its entirety without adding or taking away any evidence whatsoever.

Chemical preparation of vertebrate fossils has been used since the late 19th century, and as early as 1908 was described by Bather (Lindsay 1987; Rixon 1976). The process involves the immersion of calcareous fossil-bearing rocks into aqueous solutions of organic acids (Rutzky *et al.* 2005). Even when only a small percentage of the matrix is calcium carbonate, the acidic action will break down the structure and therefore the cohesion of the rock (Toombs & Rixon 1959). In recent years, chemical preparation and in particular, acid preparation has received bad press. This is mainly due to the inferior methods and materials used in the past, resulting in damaged fossils. It also poses a health and safety risk to the preparator and requires stringent protective measures, such as stable temperatures, masks, gloves and good ventilation. This said, acid preparation remains the only reliable method of retrieving certain fossils, including microfossils or really delicate specimens, from a calcareous matrix (Rixon 1976). Chemicals are able to access areas that mechanical tools can never reach and differentiation between matrix and fossil is more subtle and accurate (Lindsay 1987). Acid preparation has the advantage of gradually revealing fossils hidden below the matrix surface. This eliminates any assumption on the part of the preparator (Cooper & Whittington 1965).

In this ongoing study, experiments are being conducted using new and old techniques in order to improve on the speed and efficiency of fossil extraction from different matrices without sacrificing the quality of the finished product, ideally an undamaged fossil. The aim is to develop a more controlled and empirical method of chemical preparation. It is extremely important that the various steps and observations along the way are fastidiously recorded (Shelton & Chaney 2005). Records of materials and methods were often not kept in the past and this poses problems for modern conservation and curation (Lindsay 1987).

All Plio-Pleistocene-aged material from the Cradle of Humankind World Heritage site prepared at the Transvaal Museum is chemically retrieved. Acetic acid ($C_2H_4O_2$) is used, as it dissolves limestone and other rocks that contain carbonates (Stringer *et al.* 1985), but bones and teeth, mostly composed of calcium phosphate are resistant to it (Lindsay 1987; Rixon 1976). Blocks of breccia are photographed and thoroughly investigated with the weights, densities and colours recorded. A sample of the matrix is ideally removed before acid treatment and retained for future study (Rutzky *et al.* 2005). A thin coat of consolidant, usually Paraloid B-72 (an ethyl methacrylate copolymer, known as Acryloid in the United States) is painted onto any exposed bone. The consolidant not only protects the bone from the acid, but also reinforces it for future storage in a collection. Paraloid is a thermoplastic resin, soluble in acetone, but resistant to water and acids. It is non-yellowing, has a low-gloss and is extremely flexible (Hamilton 2007). Once applied, the consolidant must be allowed to dry thoroughly for at least 24 hours to prevent the acid from lifting the protective coating and attacking the bone. The blocks are immersed in diluted acetic acid ($C_2H_4O_2$). It is prudent to start at a low concentration of about 6% until the reactivity of the subject matter is determined. It is very important to ensure complete immersion in the liquid, as exposure of any part of the blocks to air will result in calcium acetate salts forming in the bone, causing cracking (Rixon 1949; Stringer *et al.* 1985). This is extremely destructive to the specimens and many fossils prepared in the past are now showing signs of calcium acetate damage. The blocks are usually left immersed in the solution for 24 hours, after which they are removed and the liquid is strained off using a fine mesh. The block and any sediment related to it is then neutralized by flushing with running H_2O for twice to three times longer than it was subjected to acid treatment (Rixon 1949). After the allotted time, the liquid is strained off and all sediment is gathered and labelled for sorting. The blocks are dried thoroughly and any newly exposed bone is painted with consolidant. The process is then repeated and the strength of the acid (up to about 8%) is adjusted accordingly until the entire block has been broken down into sediment. It would appear that the corrosive action actually accelerates briefly after each introduction of H_2O. This needs to be kept in mind when devising a suitable preparation plan. It is worth considering whether the fossil would be better suited to stronger concentrations and fewer immersions as opposed to multiple immersions into weaker solutions.

Various experimental techniques are being investigated. The entire process may be sped up by the gentle heating of an acid; in fact, even natural sunlight proves to be an effective catalyst. Electrochemical dissolving has proved to speed up the process considerably. This technique involves passing a current through a decalcifying electrolyte, causing the movement and separation of ions to electrodes of different polarity. Electrolysis of this kind has allowed for preparation time to be shortened drastically and the strengths of the acid concentration to be dropped significantly (Kulich 1991). Localizing the corrosive action on unwanted sediment is often preferable to stressing

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[*]Author for correspondence. E-mail: rudget@mweb.co.za

sensitive specimens by repeated immersion in chemicals. This may be achieved by constraining the chemical within a carrying agent, such as a water-based lubricant, in order to focus on particular areas that need preparation, while avoiding unnecessary contact with the fossil.

Different chemicals are currently being experimented with. The acids used in this study are: acetic acid ($C_2H_4O_2$), formic acid (CH_2O_2), nitric acid (HNO_3), sulphuric acid (H_2SO_4), phosphoric acid (H_3PO_4) and hydrochloric acid (HCl in H_2O). Bases include hydrogen peroxide (H_2O_2) and sodium hydroxide (NaOH). The most compatible consolidant for each corrosive chemical is sought out through a process of systematic elimination. Samples from various fossiliferous deposits from South Africa, ranging from the Permo-Triassic (Lower Beaufort) to Plio-Pleistocene (Cradle of Humankind) are subjected to varying strengths of different chemicals and closely monitored. This investigation aims to determine the correct chemical for the job at hand.

Great care needs to be taken when working with corrosive agents. Compatibility of different chemicals needs to be thoroughly investigated before new substances are introduced into the laboratory (Rixon 1976).

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PAPERS

Gondwanan Middle Triassic cynodonts from Namibia

F. Abdala[1*] & R.M.H. Smith[2]

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

[2]*Department of Karoo Palaeontology, Iziko South African Museum, P.O. Box 61, Cape Town, 8000 South Africa*

**E-mail: abdalaf@geosciences.wits.ac.za*

Recent fossil findings exposed an amazingly abundant record of mammal-like cynodonts in the Namibian Upper Omingonde Formation. A re-evaluation of these fossils has revealed a much greater diversity for this group in the Namibian Middle Triassic than was previously known. Besides fossils of *Cynognathus, Diademodon* and *Trirachodon,* the new findings include the presence of *Luangwa, Aleodon* and *Chiniquodon.* The traversodontid *Luangwa* is represented in the Omingonde fauna by at least four skulls and associated postcranial remains. An isolated skull attributed to *Aleodon* has alveoli for three upper incisors, lingually expanded postcanines and an elongated palate, typical of this cynodont. *Chiniquodon* is represented by a skull with articulated lower jaw and unprepared postcranial remains. The particular combination of features that characterize this taxon include sectorial postcanines having a backward recurved main cusp, long secondary palate, extremely elongated pterygoid processes and the zygoma with a suborbital angulation between the maxilla and jugal. The newly enhanced record of Namibian cynodonts positions the assemblage as one of the most diverse cynodont faunas from Gondwanaland, and as the primary connection between Middle Triassic faunas from Antarctica, South Africa, Tanzania, Zambia, Argentina and Brazil. Prior to this record, the range of *Aleodon* was restricted to the Manda Formation in Tanzania, while *Luangwa* was known from the Ntawere Formation in Zambia, and more recently also documented from the Brazilian Santa Maria Formation. *Chiniquodon* has been described from the Middle Triassic Santa Maria Formation of Brazil, and the Middle and Upper Triassic Chañares and Ischigualasto Formations from Argentina. The record of *Chiniquodon* in Omingonde represents the third strand of evidence of faunal commonality among cynodonts from South America and Africa. The other two taxa common to these continents, *Cynognathus* and *Luangwa,* are moreover also represented in the Namibian fauna. More significantly, the Namibian record of *Chiniquodon* is a remarkable biostratigraphic enigma inasmuch as this carnivorous cynodont, previously known only from South America, represents the first Ladinian-Carnian aged taxon discovered from Middle Triassic faunas of continental Africa. The presence of *Chiniquodon* in the Omingonde Formation suggests a younger age for the Namibian fauna, which can thus extend to the earliest Ladinian. The possible Ladinian age for this fauna is of great consequence as terrestrial ecosystems with vertebrate fossils of this period are poorly known in Gondwana sequences. In fact, the record of Middle Triassic vertebrates in continental south-central Africa is generally considered to be restricted to the Anisian.

The Late Triassic Molteno as World Heritage

J.M. Anderson

South African National Biodiversity Institute, Private Bag X101, Pretoria, 0001 South Africa

E-mail: anderson@sanbi.org

South Africa is remarkably richly endowed with palaeontological superlative – from the earliest bacteria to early man – that put South Africa clearly on the global map. The case for the Late Triassic Molteno Fm., within this context of overabundance, being put forward for World Heritage status is made. In the history of terrestrial life on Earth since the colonization of the continents by vascular plants around 430 million years ago in the Silurian, the Molteno stands out in sharp focus.

If the Cape Floristic Region is seen as the biodiversity centre of the flowering plants (angiosperms) at their heyday, so the Molteno Fm. represents the known biodiversity hotspot of the cone-bearing plants (gymnosperms) at their heyday. And in the overall history of terrestrial life, the gymnosperms stand out much more significantly than do the angiosperms: they dominated global vegetation for close on 200 million years (Early Permian to Middle Cretaceous) while the latter, derived from them, have dominated for only half that time (Mid-Cretaceous to the present). Seen from a different perspective, that of overall biodiversity at all ranks, species to classes, the gymnosperms appear also to have attained a far greater range of basic morphology than did the angiosperms. Even in their relict extant 'old age', the gymnosperms are recognized as falling into four classes, the conifers, cycads, ginkgos and gnetaleans; while 225 million years back in their Late Triassic heyday, they possibly spread across as many as 10 classes (the collections from 100 sites around the outcrop of the Molteno demonstrate this diversity far more comprehensively than elsewhere globally). The wonderfully rich angiosperms of our time, from grasses to baobabs, nearing a quarter million species worldwide, are recognized in contrast as falling within a single class.

The Molteno, then, as currently understood, represents the continental biodiversity hotspot through geological time. It was essentially in the prolific ecosystems best known in the Molteno – at the peak of the Triassic Explosion of life following the end-Permian Extinction – that both the dinosaurs and the mammals evolved. It was at this time also that the familiar spectrum of insect orders of today came into being, and that the spectacular diversity of beetles first appears. The origin of the flowering plants is very likely rooted at this time. The Molteno is the clearest window we have onto the dawn of the extant world.

Looking towards the next generation of palaeontologists in South Africa, the Molteno offers tremendous opportunity. With an outcrop extending *c.* 400 km north–south and 200 km east–west as a distorted rectangle around the outskirts of Lesotho, the potential for further collecting is almost limitless. Already our collection of some 30 000 slabs from 100 'localities' (close on half also include insects) is the most extensive (taphocoenoses) and intensive (specimens) that we are aware of from any formation internationally. The scope for ecological studies, for statistics relating to biodiversity, for comparative morphology, for palynology, for palaeoentomology is open-ended.

With the Department of Science and Technology, through their African Origins Platforms, looking to the future, seeking ways of promoting our science holistically and placing it even more firmly on the global canvas, the Molteno has much to offer. With UN Global Heritage recognition it would draw ample funding and offer countless opportunities to many.

An integrative approach to distinguishing the dicynodont species *Oudenodon bainii* and *Tropidostoma microtrema*

K.D. Angielczyk[1*] **& J. Botha**[2]

[1]*Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol BS8 1RJ, U.K.*

[2]*Karoo Palaeontology, National Museum, P.O. Box 266, Bloemfontein, 9300 South Africa*

**E-mail: k.angielczyk@bristol.ac.uk*

The dicynodonts *Oudenodon bainii* and *Tropidostoma microtrema* are remarkably similar in most aspects of their cranial and postcranial morphology. The most obvious distinguishing feature is the presence of tusks and postcanine teeth in *T. microtrema* and their absence in *O. bainii.* However, some specimens of *T. microtrema* lack tusks or postcanine teeth, and others display intermediate conditions such as possessing an erupted tusk on only one side of the skull. This variability raises the question of whether *O. bainii* and *T. microtrema* truly are distinct species, or simply endpoints on a morphological continuum. Resolution of this uncertainty is necessary because both species play important roles in Upper Permian terrestrial biostratigraphy. Here we address the issue using several types of data.

Our results show that variability in most discrete characters of the skull preclude them from being completely diagnostic of either species. However, both a geometric morphometric analysis of snout shape and a traditional morphometric analysis of skull dimensions can reliably differentiate tuskless specimens from those with tusks and/or postcanine teeth. The histology of several *T. microtrema* limb bones was also examined. The primary bone tissue consists of moderately vascularized fibro-lamellar bone, which becomes parallel-fibred with annuli and/or LAGs towards the periphery. A free medullary cavity is usually absent or if present, is very small. These bone tissue characteristics are notably similar to those of *O. bainii.*

Stratigraphic range data and patterns of phylogenetic relationship suggest that the two morphotypes are best regarded as distinct species, not sexual dimorphs or other variants. Because *O. bainii* specimens have been collected at *Tropidostoma* Assemblage Zone localities in the Karoo Basin of South Africa, the first appearance of *O. bainiii* can no longer be used to define the base of the *Cistecephalus* Assemblage Zone and *Oudenodon*-based correlations with other basins should be made with caution.

Large mammal mass death accumulation in the Holocene of South Africa

L.R. Backwell[1*]**, C.M. Steininger**[1]**, J. Brink**[2]**,**
J. Neveling[3] **& L. Pereira**[1]

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

[2]*National Museum, P.O. Box 266, Bloemfontein, 9300 South Africa*

[3]*Council for Geoscience, Pretoria*

**E-mail: lucinda.backwell@wits.ac.za*

Heelbo 1 is a palaeontological and archaeological site on the farm Spion Kop, near the town of Senekal in the eastern Free State. The grass-covered landscape is characterized by scenic flat-toped mountains of Karoo Supergroup rocks, with small alluvial fans draping many of the hill foot slopes and grading downslope into the floodplains of local rivulets. These fans are in turn dissected by large 'dongas' (gullies), revealing successions of silt-rich and gravelly palaeosols which represent repeated cycles of donga erosion and fill.

A remarkably dense and well-preserved fossil bone bed, extending over an area 35 × 13 m^2, has been discovered within one of the ancient donga floors. The bone accumulation is overlain by about 1.5 m of sediment, but is exposed in the wall of a donga near the foot of a fan. Preliminary investigations show that most of the remains belong to the black wildebeest (*Connochaetes gnou*). Several examples of articulated vertebral series, as well as bones showing little damage caused by sub-aerial weathering, indicate rapid burial before decomposition of the soft tissue. There appears to be no distinct orientation in the long bones, which together with a paucity of transport-induced abrasion of the bones, suggests deposition under relatively low-energy conditions, with little or no secondary movement by water once decomposed. While the exposed fossils do not appear to record percussion- or cut-marks, the occurrence of Later Stone Age tools at and around the site bear testament to human activity in the area, and the possibility that people were the accumulators of the bones. Different scenarios are explored to explain the mode of death and accumulation of the fossil deposit.

Comments on the Late Permian cynodonts (Synapsida, Therapsida) from South Africa

B. Battail

Muséum National d'Histoire Naturelle, Département Histoire de la Terre;
USM 0203–UMR 5143 du CNRS; Paléobiodiversité et Paléoenvironnements;
CP 38, F-75231 Paris cedex 05, France

E-mail: bbattail@mnhn.fr

During the two first thirds of the twentieth century, a number of genera and species of Late Permian cynodonts were described in South Africa. Most of them were attributed to the family Procynosuchidae Broom, 1948, whereas a few tiny forms were grouped by Haughton & Brink (1954) in the family Silphedestidae. Later, it became obvious that the number of real taxa had been overestimated. Indeed, earlier authors had sometimes created new taxa on the basis of inadequate, fragmentary material; post-mortem distortion had not always been taken into consideration; little attention had been paid to the fact that specimens of various sizes could have represented ontogenetic stages of only one species (see Anderson 1968). Then, to the time of 'splitters' succeeded the time of 'lumpers', which brought a welcome clarification to the classification of early cynodonts. It may however be asked whether the lumping process did not go sometimes too far. Two examples are given below.

The procynosuchids of south africa. According to Hopson & Kitching (1972), all the procynosuchids from South Africa belong to the species *Procynosuchus delaharpeae.* However, if we compare the complete skull of an adult specimen of *P. delaharpeae* and the skull of the type specimen of *Procynosuchus rubidgei,* it appears that both skulls have snouts of the same length, whereas the skull of *P. rubidgei* is much shorter and much narrower than that of *P. delaharpeae.* In my opinion, the differences in skull proportions are too big to fall within the range of individual variation, and the two species should be retained as valid (Battail 1991).

The 'silphedestids'. A few tiny Late Permian cynodonts were in the past placed in the now forgotten family Silphedestidae, created by Haughton & Brink in 1954. All these small forms are considered by Hopson & Kitching (1972) as juvenile specimens of *P. delaharpeae.* A careful examination of the 'silphedestids' reveals, however, many differences between them and *Procynosuchus,* especially in the tooth structure. At present, as the available material is rare and poorly preserved, it would perhaps not be wise to revive the family Silphedestidae. Doubts can be raised, however, regarding the attribution of the 'silphedestid' specimens to the procynosuchids.

Conclusions. Early cynodonts from the Upper Permian of South Africa were, in my opinion, more diversified than currently thought. A better fossil record, especially of small forms, could perhaps strengthen this hypothesis.

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Early Triassic vertebrate recovery following the end-Permian extinction event in South Africa

J. Botha[1*], R.M.H. Smith[2] & S.P. Modesto[3]
[1]*Karoo Palaeontology Department, National Museum, P.O. Box 266, Bloemfontein, 9300 South Africa*
[2]*Iziko South African Museum, P.O. Box 61, Cape Town, 8000 South Africa*
[3]*Cape Breton University, Sydney, Nova Scotia, B1P 6L2, Canada*
**E-mail: jbotha@nasmus.co.za*

The end-Permian extinction is widely accepted to be the most devastating mass extinction event in Earth's history (Erwin 1994). Until recently, most research on this extinction event has focused on the marine record because few fully preserved terrestrial Permo-Triassic boundary sequences were recognized. The main Karoo Basin of South Africa is now known to preserve several non-marine Permo-Triassic boundary sequences, which have become the focus of intensive research into the nature of the extinction and its possible causes (e.g. Ward *et al.* 2000; Smith & Ward 2001; Retallack *et al.* 2003; Smith & Botha 2005; Botha & Smith, in press). Detailed logging of multiple sections through the boundary sequence at several Karoo Basin sites reveals an extinction level of 54% of latest Permian vertebrate species, followed by the onset of a relatively rapid recovery, within an estimated 40–50 thousand years (based on the calculation of floodplain aggradation rates and compaction ratios), which included the origination of at least 12 new vertebrate species during the earliest Triassic. The Early Triassic recovery fauna comprises eosuchians, small temnospondyls, small procolophonoids, medium-sized dicynodonts, small therocephalians and non-mammalian cynodonts. The facies interpretation and taphonomic data allow us to propose that pronounced climatic warming and increased seasonality and storminess at the onset of an unreliable, monsoonal rainfall regime contributed to the mass extinction of terrestrial vertebrates in southern Gondwana.

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New developments in a search for fossils of ancestral animals in Neoproterozoic limestones of Namibia

C.K. Brain[1*], A.R. Prave[2], K-H. Hoffmann[3], A.E. Fallick[4] & A.J. Botha[5]
[1]*Transvaal Museum, Northern Flagship Institution, P.O. Box 413, Pretoria, 0001 South Africa*
[2]*School of Geography and Geosciences, University of St Andrews, Fife KY16 9AL, Scotland*
[3]*Geological Survey, Ministry of Mines and Energy, Private Bag 13297, Windhoek, Namibia*
[4]*Scottish Universities Environmental Research Centre, Rankine Avenue, East Kilbride, Glasgow G75 OQF, Scotland*
[5]*Laboratory for Microscopy and Microanalysis, University of Pretoria, Pretoria, 0002 South Africa*
**E-mail: brainnew@iafrica.com*

In recent years, one of us (C.K.B.) has been involved in a search for micro-invertebrate fossils in Namibian Neoproterozoic limestones, initially in the Nama Group, but more recently in the Otavi Group further to the north. Many samples of limestone from the Otavi-Tsumeb-Grootfontein area were examined in thin-section and as acetic acid-treated residues, but recrystallization of these limestones from the folded Otavi Mountainland appeared to mitigate against the finding of fossils of well-preserved soft-bodied organisms there. But, to the north, on the flat calcrete-covered plain of the Etosha basin, several limestone hills make their appearance, well away from the metamorphic folded belt. When C.K.B. examined residues of some of these carbonates, he found numerous sponge-like objects that proved to have been phosphatized (Brain *et al.* 2001). Detailed geological mapping of these outcrops had not been done, but it was clearly important to establish just where in the Group's stratigraphy the sequence was positioned. The outcrops were therefore examined in detail in the field by K-H.H., A.R.P. and C.K.B. and samples were taken at close intervals for carbon isotope analysis and interpretation by A.E.F. and A.R.P. When a preliminary description of these sponge-like fossils was circulated for comment by specialists in the field, a number of pertinent issues were raised that needed to be considered when interpreting microfossils of such antiquity. These issues have now been addressed and a formal description of *Otavia antiqua* will be submitted for publication soon.

In the interim, the stratigraphic range of *Otavia* has been extended from a variety of new localities, such that it now spans the entire interval between the first of the 'Snowball Earth' glacials, the Sturtian Chuos diamictite at 720 million years, to the Marinoan Ghaub one at 635 million. C.K.B. has also recently recognized similar fossils from a limestone in the Mara Formation of the Nama Group in southern Namibia, considerably more recent than those in the Otavi Group. And now, more unexpected and exciting than ever, he has, in May 2006, found *Otavia* fossils in a limestone of the Ombambo Subgroup of the Otavi Group, considerably older than the Sturtian glacial and perhaps 750 million years in age. Thus we now have evidence that the calcareous sponge lineage is far older than had been thought, although molecular evidence predicted that this would be the case. The detective story continues!

We wish to thank Conrad Brain for drawing our attention to this particular Ombambo limestone outcrop as a likely source of microfossils similar to those in Etosha.

Brain, C.K., Hoffmann, K-H., Prave, A.R., Fallick, A.E., Coetzee J. & Botha, A.J. 2001. *Palaeontologia africana* **37**: 1–12.

Vicariance in coastal large ungulate populations during the Middle and Late Pleistocene in southern Africa

J.S. Brink

Florisbad Quaternary Research, National Museum, P.O. Box 266, Bloemfontein, 9300 South Africa

E-mail: jbrink@nasmus.co.za

In southern Africa there is a clear distinction between coastal and inland environments. The interior of southern Africa includes the Nama Karoo and Grassland Biomes. From a large ungulate point of view these biomes can be seen as one biogeographic entity in that they share an open habitat structure, which is reflected in the distribution patterns of ungulates such as grazing bovids and plains zebra. This faunal composition is not found in the coastal environments beyond the Cape Fold Mountains, because of the lack of suitable open habitat. The Cape costal areas are generally inhabited by closed habitat forms and not by plains ungulates. However, a surprising aspect of the Middle and Late Pleistocene large ungulate faunas from the Cape coastal zone is the periodic presence of a faunal component that resembles the interior faunas of today. This can be explained by open plains habitat becoming available during glacials, when lowered sea levels exposed the continental margin to produce habitat suitable for plains-living ungulates. In this study the appearance of biogeographic uniqueness in glacial populations of black wildebeest from the Cape coastal zone is demonstrated. In black wildebeest (*Connochaetes gnou*), as in the case of springbok (*Antidorcas marsupialis*), there appears to have been a decrease in body size compared to contemporary inland populations. This reflects genetic drift due to the reproductive isolation of populations on the eustatically exposed continental margin to the south of the Cape Fold Mountains. These populations, the descendants, or daughter populations, of ancestors from the interior became extinct in the Cape coastal zone when sea levels returned to their present levels after the Last Glacial. The exception to this extinction event is the bontebok (*Damaliscus pygargus pygargus*), a vicariant form of the blesbok, which survived as a glacial relict in the southern Cape.

Palaeobiological implications of the bone microstructure of early mammals

A. Chinsamy[1*] & J.H. Hurum[2]

[1]*Zoology Department, University Cape Town, Private Bag, Rondebosch, 7700 South Africa*

[2]*Paleontologisk Museum, Universitetet i Oslo, Sars gate 1, N-0562 Oslo, Norway*

**E-mail: achinsam@botzoo.uct.ac.za*

Here we report on the first histological studies of early mammals. We examined the bone microstructure of *Morganucodon* from the Jurassic Pant Fissures of Wales, and multituberculates and eutherians, from the Late Cretaceous of the Gobi Desert. Our studies have provided significant insight into the biology and growth patterns of these five early mammals. We show that the two eutherian taxa (*Zalambdalestes* and *Barunlestes*) grew relatively slowly with periodic pauses in growth indicated by the presence of rest lines, while the multituberculates (*Kryptobaatar* and *Nemegtbaatar*) and *Morganucodon* had a faster rate of bone formation that suggests an overall rapid growth rate that slowed down later in ontogeny. The bone microstructure of these early mammals is also compared with that of non-mammalian cynodonts and traversodontids, extant monotremes, and placentals. Our findings suggest differences in the growth rate between the multituberculates and the Mesozoic eutherians, and moreover, both groups appear to have slower growth rates compared with modern monotremes and placentals.

An osteo-histological assessment of *Pterodaustro guiñazui*

A. Chinsamy[1]*, L. Cordorniú[2] & L. Chiappe[3]

[1]*Zoology Department, University of Cape Town, Private Bag, Rondebosch, 7701 South Africa*

[2]*Becario CONICET, Department de Geología, Universidad Nacional de San Luis, Chacabuco y Pedernera, CP 5700, San Luis, Argentina*

[3]*Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA 90007, USA*

**E-mail: achinsam@botzoo.uct.ac.za*

Pterodaustro guiñazui is a medium-sized, filter-feeding pterodactyloid recovered from the Lower Cretaceous laminated shales of the Lagarcito Formation of Central Argentina (Sierra de Las Quijadas, San Luis Province). It is represented by hundreds of individuals – wing spans ranging from 300 mm to 2.5 m. This unique ontogenetic sample of pterosaurs has permitted deductions regarding allometric changes during postnatal development and has made significant contribution to our understanding of the palaeobiology of *Pterodaustro.* Here, we report on the preliminary results of our bone microstructure studies of *Pterodaustro.* Our sample included material to assess histological variability in single skeletons, as well as histological variation within the taxon. We also studied growth series of specific skeletal elements of different sized individuals to assess changes in bone microstructure during ontogeny. Our preliminary results highlight the contribution of bone microstructure in interpreting the biology and growth of this ctenochasmatid pterodactyloid.

A 'nycteroleter' parareptile in the Permian of South Africa

J.C. Cisneros[1]* & L.A. Tsuji[2]

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

[2]*Humboldt-Universität, Museum für Naturkunde, 10099, Berlin, Germany*

**E-mail: cisneros.jc@gmail.com*

The fossil was found on the farm Blaaukranz, Prince Albert District, Eastern Cape Province, in the lower *Tapinocephalus* Assemblage Zone (Permian: Guadalupian) (Gow & Rubidge 1997). It consists of a relatively small partial postcranium, including an almost complete vertebral column, partial pelvic girdle and right hind limb. The specimen has parareptilian features and it has been regarded as the earliest global record of a procolophonoid (Gow & Rubidge 1997). The previous oldest record of a procolophonoid was represented by *Owenetta rubidgei,* from the *Cistecephalus* Assemblage Zone (Permian: Lopingian). A reappraisal of this specimen, however, indicates that it is probably not a procolophonoid. The ventral surfaces of the thoracic pleurocentra are deeply concave and lack the laterally 'pinched' anteroposterior ridge that is characteristic of the Procolophonoidea. The specimen is also considerably larger than *Owenetta* or any Permian to lowermost Triassic procolophonoid.

Nevertheless, the anatomy of this fossil is entirely compatible with the group of parareptiles known as 'nycteroleters'. Nycteroleters are small- to medium-sized parareptiles, being notable for displaying a suite of characters that combine procolophonoid and pareiasaurid features. They are recorded in the Upper Kazanian and Early Tatarian (Permian: Guadalupian) of the Russian Cis-Urals (Ivachnenko *et al.* 1997). Apart from *Macroleter poezicus* (Tsuji, in press), the group is poorly known and its members have not been recently reviewed, nor have they been the subject of phylogenetic studies. Most nycteroleters are smaller than the Karoo specimen, but the genus *Macroleter* is equivalent in size. *Macroleter* is known from several articulated skeletons from the Mezen Fauna in the Cis-Urals. The vertebrae of *Macroleter* are in fact indistinguishable from that of the Karoo specimen, except for the absence of intercentra in the latter. This feature, however, is likely an artifact of taphonomy. Despite of the similarities with the genus *Macroleter,* we refrain from identifying our specimen to the genus level at this time, owing to the incompleteness of our material.

The presence of a taxon closely related to *Macroleter* in the lower *Tapinocephalus* Assemblage Zone is stratigraphically consistent with the age of the Mezen fauna of Russia, where *Macroleter* is found. *Macroleter* has been recently reported for the Chickasha Formation in the U.S.A. (Reisz & Laurin 2001), and it was employed by these authors to claim a Guadalupian age for that formation. The South African nycteroleter expands the geographic range of these parareptiles to Gondwana, a fact not surprising when considering that the closely related procolophonoids and pareiasaurids also possess trans-Pangaean distributions.

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Searching for signal in the early actinopterygian record

M.I. Coates

Organismal Biology & Anatomy, University of Chicago, 1027 East 57th Street, Chicago Il 60637, U.S.A.

E-mail: mcoates@uchicago.edu

The Actinopterygii (ray-finned fishes) is the largest and most diverse group of vertebrates, but little is agreed about the timing and branching pattern of its early evolution. Recent estimates based on mitochondrial genomic data suggest that the major actinopterygian clades are much older than previous age estimates indicate, based on available fossil data. This presentation will report the results of a multi-authored project (Hurley *et al.*, in press), combining morphological (Recent and fossil) with nuclear genetic data, to re-assess the time-scale of actinopterygian phylogeny.

Analyses of all data demonstrate that the age of the Neopteryii radiation, including teleosts, *Lepisosteus,* and

Amia, has been underestimated by at least 40 myr. The previous incongruity between molecular and morphological date-estimates was largely the result of missing and misinterpreted fossil data. Morphologically advanced stem-group neopterygians are present by the latest Lower Carboniferous, and the earliest crown-group example dates from the Early Permian.

These results imply that the early radiation of ray-finned fishes is under-determined, that groups associated with Mesozoic faunas have Palaeozoic roots, and that Upper Carboniferous and Permian collections of actinopterygians need to be re-examined for overlooked examples of early neopterygians. Finally, the results of this project allow reconciliation between Palaeozoic date estimates for the actinopterygian whole genome duplication event, and the hypothesis that this round of gene-duplication was specific to teleosts. However, there is no clear evidence that this event is tied to extinction event survivorship, or sudden episodes of morphological innovation.

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Stable isotopes and palaeodiet: beyond the confines of C_3/C_4 barriers

D. Codron

Florisbad Quaternary Research, P.O. Box 266, Bloemfontein, 9300 South Africa

E-mail: daryl@nasmus.co.za

Ever since the discovery that the $^{13}C/^{12}C$ ratio of C_3 and C_4 photosynthesizing plants are consistently distinct, and that this distinction persists in the body tissues of animals feeding on these plants, stable carbon isotope ecology has been increasingly applied to study the diets of modern and fossil fauna. Linear mixing models allow researchers to quantify dietary inputs of C_3 (browse) and C_4 (grass) biomass in savanna herbivores from carbon isotope data. However, linear models cannot resolve diet beyond C_3/C_4 consumption, because resolution of more than two food sources from carbon isotope data alone yields more mathematical unknowns than equations. Dual-isotope mixing models based on combined evidence from more than one element, e.g. $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios, can be used to resolve multiple source inputs into diet, but these have seldom been applied to mammal diet studies because mammalian $^{15}N/^{14}N$ ratios are influenced by numerous non-dietary parameters such as climate, protein uptake, ecophysiological adaptation, and water and nutritional stress. Thus, isotope-based diet studies have been limited largely to environments in which C_4 grasses predominate.

Here, I employ a novel approach using a multiple regression model to identify and control for non-dietary sources of variation on ^{15}N-abundances in faeces of 19 ungulate species. Results are based on vegetation and faeces collected over three years across multiple spatial and seasonal scales from the Kruger National Park. I demonstrate that, after controlling for the effects of protein uptake, ecophysiology, and climate, $^{15}N/^{14}N$ and $^{13}C/^{12}C$ data from herbivore faeces lie within the distribution of available food sources when plotted as a mixing polygon in isotope space. I use a dual-isotope multiple-source mixing model (Isosource; Phillips and Gregg 2003) to resolve dietary inputs of multiple C_3 (foliage, fruit, reeds and sedges) and C_4 (NAD/PCK and NADP grass sub-types) food groups. Results show high consistency with expectations based on data derived from field observations. In addition, I demonstrate similar reliability for reconstruction of complex diets in mammalian carnivores. I propose that similar approaches can be applied to body tissues to resolve diet in palaeoecological settings, for specimens with intact biological proteins (up to ~10 000 years). Future studies of proxies less susceptible to diagenetic alteration, such as $^{18}O/^{16}O$ data, may also allow for improved dietary reconstructions of diet in deep time, even in pre-Miocene palaeoenvironments predating the origins of C_4 photosynthesis.

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The Devonian, Famennian, Witpoort Formation (Witteberg group) fauna of Grahamstown

R. Gess

Bernard Price Institute for Palaeontology, School for Geosciences, Johannesburg; c/o P.O. Box 40, Bathurst, 6166 South Africa

E-mail: robg@imaginet.co.za

During the Devonian, plants evolved from small simple forms to a wide range of taxa, many the size of trees. With the exception of the angiosperms, all major divisions of the plant kingdom had evolved by the end of the period. Fish reached their broadest ordinal diversity during the Devonian as many ancient orders co-existed with emergent new ones.

At the Late Devonian Frasnian-Famennian boundary plants experienced a major extinction event, possibly precipitated by the movement of Gondwana into the Antarctic region – its consequent glaciation lowering global temperatures and sea levels. Alternately, lowered global temperatures may have resulted from reduced atmospheric CO_2 levels, resulting from the rapid spread of *Archaeopteris* forests during the Frasnian. This would have increased levels of fixed C entering drainage systems, perhaps accounting for the common precipitation of C-rich anaerobic sediments during the Famennian. A number of minor extinction events during the Famennian, culminated in a major extinction of marine organisms at the end. This resulted from widespread marine regression, or perhaps was triggered by the rapid spread of seed-bearing plants into relatively dry habitats.

The Bokkeveld Group contains a well-studied record of coastal marine invertebrate communities, as well as a small number of Early and Middle Devonian fish. Until recently, however, the Late Devonian rocks of the lower Witteberg Group had yielded very little record of life. Apart from the presence of '*Spirophyton*' trace fossils, and *Leptophloem australe* lycopod stem impressions, a few taxa had been erected on the basis of sparse plant fragments from a black shale of the (Upper Devonian, Famennian) Witpoort Formation at Howiesons Poort near Grahamstown. The exposure of rich fossil-bearing Witpoort Formation black shale during roadworks at Waterloo Farm south of Grahamstown in 1985, however, opened a southern African window into the latest Devonian. The shale is interpreted as having been deposited as anaerobic mud in a palaeolagoon, on the protected side of a series of barrier islands and beaches cut by tidal inlets.

In addition to plant material similar to that from Howiesons Poort, but generally more complete, the new site provided a wealth of formally unrecorded algal and plant taxa, as well as fish and arthropod remains. A large sample of this material was collected during an excavation carried out at the locality between 1993 and 1995. Based on this material a number of phaeophyte and charophyte taxa, as well as a new species of progymnosperm, were formally diagnosed, and a large diversity of plant and algal material was recorded. Three species of placoderm fish were described, the antiarch *Bothriolepis africana*, in addition to two arthrodire placoderm species, *Groenlandaspis riniensis* and *Africanaspis doryssa.* A chondrichthyan specimen was described as *Plesioselachus macracanthus.* A large number of other fish fragments were tentatively identified as gyracanthid acanthodian spines, small actinistian body impressions, elements of a large rhipidistian and a dipnoan, possible actinopterygian scales, isolated ptyctodontid placoderm plates and a range of problematic fragments. Remains of an unidentified eurypterid were also noted. These faunal elements could not be described due to the incomplete nature of the specimens available. Continued road works at Waterloo Farm have, however, allowed much new material to be collected. A large sample of shale has also been set aside for ongoing investigation. New material includes more complete specimens of recorded taxa, as well as remains of formally unrepresented species, including, Agnatha, Placodermi, Acanthodii, Chondrichthyes, Actinopterygii, and Arthropoda. Description of the new material will give unprecedented opportunities for biogeographic and biostratigraphic analyses, the Waterloo farm locality being the only one known in western Gondwana with a well represented fauna and flora from this important time period.

Two dicynodont postcranial morphotypes from the *Cynognathus* Assemblage Zone (subzone B) of South Africa and their taxonomic implications

R. Govender

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

E-mail: romala@discoverymail.co.za

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 how this affected Triassic dicynodont taxonomy and phylogeny. There has been little work on the postcranial anatomy of *K. simocephalus,* which remains poorly understood. A detailed descriptive analysis of the postcranial anatomy of *K. simocephalus* has lead to the identification of diagnostic characters of the postcranial skeleton. During the course of the analysis of the postcranial anatomy of *K. simocephalus* it was noted that material previously assigned to this taxon was significantly different from that recognized as *K. simocephalus.* Unfortunately, this material consists only of postcranial material and it is therefore referred to as Morphotype B rather than a new species of *Kannemeyeria* or as a new taxon from the *Cynognathus* Assemblage Zone (subzone B). A phylogenetic analysis was performed which included *K. simocephalus* and Morphotype B, and used cranial and postcranial characters. The preliminary phylogenetic results show that there are possibly two taxa of medium to large dicynodonts in the *Cynognathus* Assemblage Zone (subzone B); one a kannemeyeriid and the second a stahleckeriid. It has also become evident that more attention needs to be paid to the study of the postcranial anatomy of Triassic dicynodonts, especially those from Africa and Asia.

Why are species not all asexual? A simulation approach to an old problem in population biology.

E.H. Harley

Department of Clinical Laboratory Sciences, University of Cape Town, Private Bag, Rondebosch, 7701 South Africa

E-mail: harley@chempath.uct.ac.za

The two-fold advantage in growth rate of genetically similar populations of asexual and sexual populations should result in the sexual population rapidly going extinct if the two populations coexist sympatrically at a constant carrying capacity for the species, yet this seldom seems to occur in practice.

Populations of asexual and sexual individuals of defined genetic composition were generated in a computer program (ASPIC – Asexual and Sexual Populations In Competition). Mutations at diploid loci were generated at a defined rate. Other variables included population sizes, values of selection and dominance coefficients, and percentage of mutations that were advantageous. The two groups were allowed to evolve separately for a variable number of generations before being mixed in a single competing population, when one or other population would invariably become extinct. Neutral loci were an optional inclusion to monitor genetic diversity. The probability of an individual being able to breed was made a function of the average fitness across all loci under selection. By performing multiple reiterations, accurate measures of extinction rates could be recorded under each set of conditions.

Results showed that the number of generations before mixing, mutation rate, percentage of advantageous mutations, value of selection coefficient, and value of dominance coefficient (expressivity) all affected the probability of one or other group going extinct. The key finding was that the sexual population would succeed only when the accumulation of mutations during separate evolution caused the ratio of sexual to asexual fitness levels to exceed 2, and has the general implication that provided the two groups are not constrained geographically, or that niches are available which delay mixing, then an emergent asexual population, with its faster declining fitness, will not drive its sexual competitors to extinction.

New insights into therocephalian phylogeny (Amniota: Therapsida): a comparison of stratigraphy-free and stratocladistic methods

A.K. Huttenlocker[1*], J. Marcot[2] & D. Fox[2]

[1] *Department of Biology, California State University, San Bernardino, 5500 University Parkway, San Bernardino, CA 92407, U.S.A.*

[2] *Department of Geology and Geophysics, University of Minnesota, 310 Pillsbury Drive SE, Minneapolis, MN 55455-0129, U.S.A.*

**E-mail: huttenla@csusb.edu*

Therocephalians constitute a diverse group of 'mammal-like' therapsids whose evolutionary radiation paralleled that of their sister taxon (cynodonts) in many respects. Within the Therocephalia, at least six major clades are currently recognized: Lycosuchidae, Scylacosauridae, Akidnognathidae (=Euchambersiidae), Hofmeyriidae, Whaitsiidae, and Baurioidea. Past systematic investigations have highlighted temporal trends in therocephalian evolution, emphasizing character evolution in the dentition and especially the secondary palate, yet high levels of homoplasy and inadequate descriptions in the literature have raised doubt over their higher-level relationships. Since previous systematic studies have failed to produce robust cladistic hypotheses, these investigations have lacked a well resolved phylogenetic context.

The phylogenetic relationships of therocephalian therapsids were studied based on a preliminary re-examination of poorly described holotypes and new specimens and utilizing multiple methods of computer-assisted phylogenetic analysis. Two key methods, traditional morphology-based cladistics and stratocladistics, were employed and the robustness of the phylogenetic hypotheses was tested against the stratigraphic record. The resulting tree topologies generally agreed on the monophyly and relative positions of the well-known clades, differing only in their placement of Akidnognathidae. Cladistic results placed Akidnognathidae at the base of Eutherocephalia, while stratocladistic results placed the group as the sister taxon to Hofmeyriidae + Whaitsiidae, supporting a monophyletic 'Whaitsioidea.' Results of the stratigraphy-free cladistic analysis showed relatively low statistical support due to high levels of homoplasy in Therocephalia. Furthermore, the stratocladistic trees appeared to be only slightly less optimal than cladistic trees with respect to morphology, yet are considerably more optimal with respect to the stratigraphic data. The consensus tree topology derived from the stratocladistic analysis is favoured because (1) the method can recruit operational taxonomic units (OTUs) that lack conspicuous autapomorphies as potential ancestors (whether direct or indirect); (2) the results generally show a higher level of stratigraphic congruence with less stratigraphic debt (whether or not the divergence models demonstrate budding cladogenesis or bifurcation); and (3) as a consequence, the method further minimizes the required duration of ghost lineages to explain divergence times between closely related OTUs in possible instances of budding cladogenesis (since the divergence time for the descendant taxon need not be equal to the earliest stratigraphic appearance of the ancestral taxon). A systematic re-evaluation of basal akidnognathids, hofmeyriids, and enigmatic Eastern European whaitsiids is suggested in order to further test and refine the phylogenetic hypotheses offered here.

Cranial mechanics of Dicynodontia using Finite Element Analysis and quantitative histology

S.C. Jasinoski[1*], E. Rayfield[2] & A. Chinsamy[3]

[1] *Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, U.K.*

[2] *Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, U.K.*

[3] *Department of Zoology, University of Cape Town, Private Bag, Rondebosch, 7700 South Africa*

**E-mail: s.jasinoski@bristol.ac.uk*

Dicynodonts were a diverse group of herbivorous non-mammalian therapsids known predominantly from the Permo–Triassic of South Africa and Russia. Unlike most dicynodont genera, *Lystrosaurus* crossed the Permo-Triassic extinction boundary, possibly due to its ability to exploit more resistant vegetation (King & Jenkins 1997). Although dicynodonts had a highly derived masticatory apparatus that allowed propaliny, it has been hypothesized that *Lystrosaurus* utilized more orthal jaw movements to crush tough vegetation. Several cranial specializations of *Lystrosaurus*, such as a patent premaxilla-nasal suture and a posteriorly deepened skull, may have increased the efficiency of its masticatory system relative to purely Permian dicynodonts such as *Oudenodon.*

This study quantitatively examines the biomechanical significance of cranial form of *Lystrosaurus* and *Oudenodon,* a generalized dicynodont, using Finite Element Analysis (FEA) and bone histology. FEA is a computational analysis that assesses the mechanical behavior of complex structures, thus it can be used to test whether the skull of *Lystrosaurus* was capable of withstanding high cranial stresses associated with the mastication of tougher vegetation. The concomitant histological analysis involved thin-sectioning of cranial bone at homologous points. Several features that may correlate with function will be quantified including: 1) density, size, and shape of secondary osteons; 2) orientation of channels in the bone; and 3) thickness of cortical bone.

In order to accurately model the distribution and magnitude of masticatory stresses in *Oudenodon* and *Lystrosaurus,* a three-dimensional skull model was created from CT data. Two bite directions were modelled: 1) a vertical and dorsally directed bite at the premaxilla-maxilla sutural junction to simulate the beak bite and 2) a horizontal and anteriorly directed bite at the palatine to represent shredding during propaliny. An average bite force was calculated by integrating adductor and temporal fossa dimensions and previous jaw muscle reconstructions. For the orthal biting model, the preliminary FEA indicates that overall higher peak compressive stresses accumulate in the *Oudenodon* skull, suggesting that the *Lystrosaurus* skull could withstand higher compressive stresses; whereas the horizontal biting model suggests the opposite. Tensile stresses in *Oudenodon* and *Lystrosaurus* accumulated in the pterygoid-palatal region in both the orthal and horizontal biting models.

The preliminary FEA suggests that the *Lystrosaurus* skull could withstand higher stresses during a vertical bite, thus supporting the hypothesis that it was capable of a more powerful vertical bite necessary for feeding on resistant vegetation. Results of the histological analysis will be compared with the biomechanical results of FEA, thereby validating the results of this computational analysis.

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A double tusked dicynodont and its biostratigraphic significance

Z.A. Jinnah[1]* & B.S. Rubidge[2]

[1]*School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa*

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

**E-mail: jinnahz@science.pg.wits.ac.za*

As part of an ongoing project to determine the stratigraphic ranges of fossil taxa in the lowermost Beaufort Group in South Africa, the well-preserved skull and lower jaw of a small dicynodont with postcanine teeth was collected from the Abrahamskraal Formation north of Prince Albert Road. The specimen was found 1062 m above the Ecca-Beaufort contact and 498 m above the first maroon mudrocks of the Beaufort group.

The presence of large, laterally flared pterygoid processes, postcanine teeth that lie lateral to the lower jaw and laterally located post-temporal fossae allow the specimen to be identified as the most primitive dicynodont known. A remarkable feature is the presence of a double canine on the left side of the skull. While replacement canine teeth are well documented for theriodonts, a double canine on one side of the skull has been recorded in only three dicynodont specimens, despite the fact that dicynodonts comprise by far the largest proportion of therapsids which are known from the Beaufort Group. Apart from the specimen of reported here, the other two dicynodont specimens are and a specimen with affinity to . Explanations offered for the double tusked condition include tooth replacement, pathology and intraspecific variation. Examination of specimens of and suggest that the roots of their tusks are open-ended, and therefore, tusks presumably grew throughout the animals' lives. This suggests that the double tusk condition is pathological rather than representing canine replacement.

The distribution of is restricted to the southwestern part of the basin between the towns of Rietbron and Laingsburg, and so far all specimens have been found below the lowest maroon mudrocks of the Beaufort Group. This specimen is thus the first from above the lowest maroon mudrocks and occurs higher in the stratigraphy than any other yet collected. Although the position of the lowest maroon mudrocks varies from place to place in the basin, they are possibly significant as indicators of environmental change, such as increasing subaerial exposure of sediments. The occurrence of Assemblage Zone fossils higher in the stratigraphic succession in the area around Prince Albert Road may have implications for Karoo basin development models.

A palaeobiological hypothesis for the origin of the Therapsida

T. Kemp

Oxford University Museum of Natural History and St John's College, Oxford, U.K.

E-mail: tom.kemp@oum.ox.ac.uk

The replacement of the basal synapsid pelycosaurs by the more 'mammal-like' therapsids in the Permian was an important event in the history of tetrapods because it involved changes in many characters, and effectively initiated the eventual transition to the mammals. It is also an example of taxon-replacement in the fossil record that is potentially amenable to explanation, based on a combination of analysis of the biological significance of the inferred character changes with the stratigraphic, palaeogeographic, and palaeoecological circumstances of the time. An hypothesis is presented in which the origin of the therapsids resulted from a correlated progression of character evolution leading to higher levels of metabolic activity and homeostatic regulation of the body. It was a response to the availability of a seasonally arid, savanna-like biome. The subsequent explosive radiation of therapsids was associated with the ecological opportunity for habitat expansion made possible by the Mid-Permian development of geographical continuity between that biome and temperate biomes. The final extinction of the few pelycosaurs that lingered into the mid-Permian was probably a case of incumbent replacement by the new therapsid lineages.

Distribution of Tubulidentata species and their relationships with early hominids

T. Lehmann

Transvaal Museum, Palaeontology Section, P.O. Box 413, Pretoria, 0001 South Africa

E-mail: tlehmann@nfi.org.za

Currently, a single extant species represents the order Tubulidentata: *Orycteropus afer,* the aardvark. This mammal is very important in African ecology as many animals use the aardvark's deserted burrows. The occurrence of certain species even depends on the presence of the aardvark. They are also closely associated with modern humans in Africa. All over the continent, tribes are known to hunt the animal, consider it as a divinity, represent it in their art, use parts of its body as charms, or follow it when foraging termites. Plio-Pleistocene hominids also added termites to their diet. The study of the distribution of fossil aardvarks with respect to early hominids is thus of great interest.

The extant aardvark is restricted to sub-Saharan Africa but the fossil record extends this distribution. The oldest unquestionable Tubulidentata come from the early Miocene of Kenya.

Slightly younger specimens have also been found in Namibia. By the late Miocene, Tubulidentata are found in central, eastern and southern Africa. Moreover, within the last seven million years in Africa, the co-occurrence of aardvarks and early hominids at many important sites (for example at Aramis, Koobi-Fora, Laetoli, Lukeino, Makapansgat, Olduvai, Swartkrans, and Toros-Menalla in Chad) is striking.

According to the fossil record, the first aardvarks reached Eurasia during the early middle Miocene. From the late Miocene to the early Pliocene, their European distribution spans Pakistan, Iran, Turkey, Greece, Italy, and France. The distribution of Tubulidentata has been restricted to Africa since the Plio-Pleistocene. Noticeably, within the same period, *H. erectus* dispersed out of Africa in regions that were more temperate and seasonal than eastern and southern Africa. At Swartkrans, Olduvai and East Turkana, *H. erectus* have been found in association with fossil aardvarks. Obviously, the dispersal pattern of those early hominids and the aardvarks deviated during this crucial period. It is important to try to understand the reasons for this divergence, as they might be linked to local environmental changes that did not affect both taxa to the same extent.

The Ecca–Beaufort contact in the Eastern Cape Province – reappraisal of litho- and biostratigraphy

R.M. Mason, B.S. Rubidge* & P.J. Hancox

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

**E-mail: bruce.rubidge@wits.ac.za*

In contrast to the situation in the southern and western parts of the Karoo Basin, relatively little lithostratigraphic and biostratigraphic research has been performed on the Ecca–Beaufort contact in the south-eastern Karoo Basin. Thus the Ecca–Beaufort contact in this area has remained problematic. The Ecca–Beaufort contact in the southern and western Karoo Basin occurs between the Koonap/Abrahamskraal Formation (lower Beaufort) and the Waterford Formation (upper Ecca) (Johnson 1976; Rubidge 1988). The Koonap/Abrahamskraal Formation comprises fluvial facies and represents deposition in a subaerial lower delta plain environment. The Waterford Formation represents deposition in a subaqueous delta front environment and contains fives unique facies (Facies A–E) (Rubidge 1988). Beneath the Waterford Formation lies the Fort Brown Formation that was deposited in a prodeltaic environment. Currently the Waterford formation is considered to be absent in the southeastern Karoo Basin and the Ecca–Beaufort contact in this area is mapped between the Koonap (subaerial fluvial) and Fort Brown (prodelta) Formation, an interpretation that is problematic.

Fieldwork conducted over the past three years has shown that the five distinct lithofacies of the Waterford Formation do indeed occur in the southeastern Karoo Basin, albeit that this Formation is substantially thinner (65–202 m) than in the areas further west. The Ecca-Beaufort contact in this area thus occurs between the Koonap and Waterford formations and stratigraphically conforms to the situation in the rest of the southern Karoo Basin. The presence of dinocephalians and *Eunotosaurus* in the middle Koonap Formation indicates that the *Tapinocephalus* Assemblage Zone is present. This biostratigraphic interpretation supports the diachronous nature of the Ecca-Beaufort contact as previous workers have suggested (Welman *et al.* 2001).

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The palaeoecological and evolutionary implications of the micromammals from Langebaanweg (Mio-Pliocene, South Africa)

T. Matthews

Iziko South African Museum, P.O. Box 61, Cape Town, 8000 South Africa

E-mail: tmatthews@iziko.org.za

The Mio-Pliocene site of Langebaanweg (LBW) represents one of the largest collections of Mio-Pliocene fossils in Africa, and contains an extremely rich and diverse range of over 230 vertebrate and invertebrate taxa. LBW is unique not only because of the richness of the fossil deposits, but because it is the only site in the Western Cape Province representing the Mio-Pliocene, a slice of time when modern micromammal genera were emerging. LBW is therefore a crucial site for our understanding of the evolution and dispersion of modern rodent taxa from southern Africa. Fossil micromammal (murid, chrysochlorid, macroscelid and soricid) accumulations are frequently used in palaeoclimatic and palaeoecological research as micromammals are effective environmental indicators – they do not migrate long distances, they have small home ranges, and in many cases, they have precise ecological requirements. Micromammals were recovered from the two main fossil-bearing members of the Varswater Formation, that is the Langeberg Quartzose Sand Member (LQSM), and the Muishondfontein Pelletal Phosphate Member (MPPM).

The relationship between the LQSM and MPPM is complex and not very clearly understood, but the LQSM generally underlies the MPPM, and is thought to be the older member. Several of the large ungulate species in the MPPM show enamel hyperplasia on molars, and it has been postulated that the environment was becoming drier, and rainfall more unpredictable, at the time that the MPPM sediments were deposited. With this in view, the palaeoecological implications of the micromammal populations of the LQSM and MPPM are discussed. The micromammal population at LBW is placed within the context of other southern and East African fossil sites.

A new genus of the cockroach family Umenocoleidea from Cretaceous deposits at Orapa, Botswana

I.J. McKay
Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag X3, WITS, 2050 South Africa
E-mail: mckayi@geosciences.wits.ac.za

The Cretaceous kimberlite deposits from Orapa, Botswana have revealed a diverse assemblage of fossil plants and insects. Many of the insects show a similarity to modern forms. However, the deposit also includes extinct Cretaceous forms. One of these is the archaic cockroach family Umenocoleidea, a group of cockroaches distinguished from modern forms by a pair of sclerotized tegmina and a short ovipositor. The umenocolids are known from the Early Cretaceous of Siberia, China, Brazil and Lebanon, as well as the Late Cretaceous of New Jersey. The Orapa forms, which probably represent two species, are unique, not only amongst umenocolids, but also in the insect world because they have tiny reduced tegmina with a similar pitted pattern to that of a golf ball. The only other insects with similarly reduced and pitted tegmina are the earwigs (Dermaptera) and staphylinid beetles (Coleoptera). The presence of the Umenocoleidea from Orapa confirms the Cretaceous age of the deposits and suggests that many more intriguing archaic forms remain to be discovered in the collections.

Palaeontology and evolutionary thought in South African schools: providing a fresh context to promote palaeontology and launch a new network of museums – the Kitching Fossil Gallery, the Wits Origins Centre and the Kitching Fossil Exploration Centre

I.J. McKay
Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag X3, Wits 2050, South Africa.
E-mail: mckayi@geosciences.wits.ac.za

Although South Africa's school curriculum has been changing since 1998, the first matriculants that are wholly steeped in the new system will only graduate in 2008. Senior school teachers are, therefore, presently facing the serious challenge of preparing their students for an unknown examination, with some completely new subject and skills areas. New subject areas in the Grade 12 Biology curriculum include 'fundamental aspects of fossil studies', 'cradle of mankind – South Africa', and 'popular theories of mass-extinction'. In addition, teachers are also expected to cover the basics of evolutionary theory with their students.

These developments suggest that there is a strong new role for palaeontological museums to support life science teachers as they grapple with the new topics in the curriculum. Museums provide a venue that schools can visit to see real fossils and allow teachers and learners access to the actual evidence for evolution, including 'extinction', 'macro evolution', 'missing links' and 'living fossils'.

This revival of interest in palaeontology will also provide renewed demand for palaeontology museums. This is good news for established museums and suggests a role for new initiatives. Two interconnected initiatives are described here. The first is the Kitching Fossil Exploration Centre (KFEC), an initiative of the Albany Museum, Bernard Price Institute of Palaeontology, the Owl House Foundation, the Department of Science and Technology and a Private Donor. Essentially, the KFEC, located at Nieu Bethesda, consists of a small exhibition centre and fossil trail in the Gats River bed. The exhibition, which utilises specially adapted displays from a number of institutions, draws attention to the incredible diversity of fossils in the area, the nearby Permo-Triassic extinction boundary, and James Kitching who grew up in Nieu Bethesda. Five guides from Nieu Bethesda have been trained and are available seven days a week to take tours.

The second initiative is the Origins Centre at the University of the Witwatersrand. Phase one of this project is devoted to Rock Art and was opened at the beginning of this year. Phase 2 will be devoted to palaeontology and should achieve fruition in two years' time. However, the education outreach programmes of the rock art museum and the School of Geosciences are already merging to make maximum use of the Wits university facilities.

It is hoped these initiatives, which draw on the resources of the public, private and tertiary education sectors, will make a significant and sustainable impact on Palaeontology Outreach in South Africa.

Taphonomy of the fauna from the Plover's Lake cave flowstone bounded unit

Tebogo Mothupi & Lucinda Backwell
Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag X3, WITS, 2050 South Africa
**E-mail: tebogomothupi@yahoo.co.uk*

Recent excavations at Plover's Lake cave, a site located in the Cradle of Humankind World Heritage area, South Africa, have yielded rich archaeological and palaeontological assemblages from a flowstone-bounded stratigraphic horizon dated by Uranium series and Electron Spin Resonance to between 62 000 and 88 000 years ago. This cave represents one of the few inland Middle Stone Age (MSA) sites in Sub-Saharan Africa, and the studied horizon contains human remains bearing possible cut- and impact-like marks, suggesting that peri- or postmortem treatment of the human body took place at the site. Analysis of the associated fauna, numbering 874 pieces, was conducted to identify the agent of accumulation and substantiate arguments in favour of cannibalism. This was done by comparing and quantifying the modifications recorded on the human and non-human fossils. Microscopic examination of the fauna from this layer revealed no diagnostic cut marks, relatively few traces made by carnivores in the form of tooth scores and pits, and an abundance of marks made by rodents. Some of these marks bear features identifying porcupines as the agent of modification and probably accumulation, while others are attributed to smaller unidentified rodents. A number of tiny star-like traces were noted, reminiscent of those observed on the Plio-Pleistocene-aged fauna from Laetoli, interpreted by different authors as insect damage, caused by ant and termite gnawing. In sum our results show little, if any, involvement of humans in the modification of the faunal remains from the flowstone bounded unit, thus providing no evidence for an interpretation of the modifications recorded on the human remains as the result of cannibalism. It is widely accepted that such an interpretation requires identifying the same treatment of human and non-human remains from the same deposit.

Sedimentological perspectives on a unique Upper Elliot fossil locality in the northeastern Free State

J. Neveling[1*], P.J. Hancox[2], A.M. Yates[3] & M.F. Bonnan[4]

[1]*Council for Geoscience, Pretoria, South Africa*
[2]*CCIC South Africa, Postnet Suite 81, Private Bag X9, Melville, 2109 South Africa*
[3]*Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag X3, WITS, 2050 South Africa*
[4]*Department of Biological Sciences, Western Illinois University, Macomb, U.S.A.*
**E-mail: jneveling@geoscience.org.za*

For a long time the vertebrate fossil fauna of the Late Triassic to Early Jurassic Elliot Formation has received comparatively little research attention in Karoo palaeontological studies. This has resulted in an unsatisfactory knowledge of the taxonomic composition of this important interval spanning the Triassic-Jurassic boundary. The two biozones currently recognized within the Elliot Formation, the '*Euskelosaurus*' Range Zone (equated with the lower Elliot Formation) and *Massospondylus* Range Zone (equated with the upper Elliot Formation), are characterized by relatively depauperate vertebrate faunas, generally represented by isolated fossils, with rare complete or semi-complete skeletal remains.

Given this situation, research conducted on the farm Spioen Kop (Senekal district, northeastern Free State) over the last three years represents a very important contribution to this palaeontological dataset. At this locality the entire Elliot Formation is exposed on the slopes of a series of low hills, and over the last decade numerous fossils have been discovered from these rocks. Several field crews have visited this locality during the study period to excavate dinosaur fossils, with the primary focus on two partially complete skeletons from the upper Elliot Formation (or *Massospondylus* Range Zone). Early results indicate that these specimens are significant not only for representing as yet undescribed dinosaur taxa, but also for the semi-complete nature of the skeletons and excellent surface preservation exhibited by individual bones.

In order to ascertain the local palaeo-environment of the fossil-bearing rocks, we undertook a detailed sedimentological and taphonomic investigation of the site. Fossil material from upper Elliot Formation is largely confined to the red siltstones of the Elliot Formation, but detailed facies analysis has shown that they are often found at the base of muddy channel fills. Both arenaceous and argillaceous channels deposits are more common in the study area than expected, raising the possibility that the locality may have served as a channel locus area. At this stage research is continuing to determine whether the presence of well-preserved fossils should be attributed to collecting and preservational agents only, or whether unusual local palaeo-environmental conditions also played a role.

Analysis and application of Beaufort Group data

M. Nicolas

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag 3, WITS, Johannesburg, 2050 South Africa
E-mail: nicolasm@science.pg.wits.ac.za

For more than a century large collections of fossils have been built up at various museums in South Africa. With the cooperation of all the South African museums that house collections of Karoo fossils, a single standardized database has been put together for the fossils collected from the Beaufort Group.

The incorporation of the datasets from the various museums required rigorous standardization, quality testing and manipulation. In particular, locality information had to be entered onto the database so that it would be useful for qualitative evaluation. This unique dataset now, for the first time, provides a record of fossil vertebrate continental biodiversity from the Middle Permian to Middle Triassic, and provides accurate numbers of specimens of the various taxa that have been collected.

The methodology used to set up this database will be presented and analysed, and preliminary findings on Permian-Triassic biodiversity and palaeontological patterns will be addressed.

Preliminary report on restoring identity to mummified human remains from South Africa: uncovering hidden information

L.M. Pereira

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa
E-mail: pereiralm@science.pg.wits.ac.za

The majority of ancient human remains reported in the literature are skeletonized, leaving only the bone available for observation. Mummified remains in southern Africa are rare and potentially contain a wealth of information on such diverse topics as sex, stature, genetic affiliation, palaeo-diet, mobility patterns, pathology, ancient disease, cultural practices and processes of decomposition.

In the 1930's the remains of a single mummified individual were donated to the Transvaal Museum and subsequently relocated to the National Cultural History Museum (NCHM) in Pretoria. In the past, the remains were displayed with cultural artefacts; however, their association as well as provenance data were not clearly recorded in the early museum catalogues.

Multi-disciplinary techniques and collaborative work using for example, anthropometrics, entomology, geology, botany, ethnography, stable light isotopes, genealogy and DNA, are being applied in the study in order to recover the context and cultural affinity of the remains, as well pathology, disease and reasons for preservation. The likely area of origin of the remains has been established as spanning from the Rustenburg area north of Pretoria to the Bronkhorstspruit area east of Pretoria. The remains are of those of a woman in her early twenties from the Iron Age. Results of the research to date are presented.

Current research into uranium–lead dating of Sterkfontein Cave, South Africa

R. Pickering[1]*, J. Kramers[1], T. Partridge[2] & T. Venneman[3]

[1]*Institute for Geological Sciences, University of Bern, Erlachstrasse 9A, CH-3012, Bern, Switzerland*

[2]*Institute for Human Evolution, University of the Witwatersrand, Johannesburg, South Africa*

[3]*Institute of Mineralogy and Geochemistry, University of Lausanne, Switzerland*

**E-mail: robyn.pickering@geo.unibe.ch*

The absolute dating of the South African hominid-bearing caves is an outstanding issue in palaeoanthropology. Without an extensive and precise chronostratigraphic framework, the South African hominid-bearing deposits can only be compared in broad terms to the deposits found elsewhere in Africa. Recent advances in the understanding of global climate shifts during the last ~5 Ma and how these changes are reflected in the climate of Africa, have revealed that climate may have played an important role in the emergence and evolution of hominids. Quite how and why changing climates affect landscape and organism evolution is an ongoing debate, one in which a secure chronology is essential. Recent advances in isotopic dating techniques have provided new opportunities to date the South African caves by cosmogenic isotopes of ^{10}Be-^{16}Al on quartz in breccias (Partridge *et al.* 2003) and the radiogenic decay of U to Pb in speleothem layers (Walker 2005).

U-Pb dating is not a simple task; problems with contamination of common lead persist and ages have to be calculated using isochrons, increasing the number of measurements needed to produce an age. We have adapted the method used in the pioneering work of Walker (2005). Without modelled or measured initial 234/238 ratios only maxium ages can be obtained. We model initial conditions, i.e. excess initial 234U and depleted 230Th. Samples are pre-screened using β-scanner imaging to identify U-rich layers. Initial MC-ICP-MS results indicate that relatively U-rich layers can exist near the base of flowstones, with U concentrations of between 0.1 and 2.4 ppm. Strong inital (234U/238U) disequilibrium is found for samples younger than 2.5 Ma. Both high U and large initial 234U excess may result from slow weathering of bedrock, without leaching, in the arid phase preceding conditions conducive to flowstone formation. [Pb] ranges between 20–200 ppb and is highly heterogeneous. Small scale (~cm spaced) sampling of U-rich speleothem layers provides a range of U-Pb ratios, and isochron ages can be calculated.

A number of problems remain: discrepancies between ages obtained by different dating methods, poor stratigraphic control of the breccias at Sterkfontein and estimates of initial 234U/238U values for samples >3 Ma. Efforts to constrain the latter using O and C isotopes as proxies are under way.

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New Cretaceous and Palaeogene vertebrates from the East African Rift, Tanzania: stratigraphic, tectonic and palaeobiogeographic implications

E.M. Roberts[1]*, P.M. O'Connor[2], N.J. Stevens[2] & M.D. Gottfried[3]

[1]*School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa*

[2]*Department of Biomedical Sciences, Ohio University, Athens, Ohio, U.S.A.*

[3]*Department of Geological Sciences, Michigan State University, East Lansing Michigan, U.S.A.*

**E-mail: robertse@geosciences.wits.ac.za*

The Rukwa Rift is located in southwestern Tanzania and forms part of the western branch of the East African Rift System. Late Neogene tectonics and sedimentation are superimposed on a complicated sequence of earlier rift-filling events, ranging from Carboniferous–Palaeogene in age, associated with repeated tectonic reactivation of Precambrian basement lineaments.

Based on reports of fossiliferous strata in the southwestern Tanzania and the extreme paucity of fossiliferous Cretaceous and Paleogene strata in sub-Saharan Africa, a research project was initiated in 2002 to explore the palaeontology and stratigraphy the Red Sandstone Group in the Rukwa Rift Basin. Four field seasons of work have resulted in the discovery of diverse new vertebrate faunas of both Cretaceous and Paleogene ages. Over 40 new vertebrate fossil localities have been discovered, with specimens ranging from heavily abraded, isolated elements to exquisite, nearly complete articulated skeletons. Cretaceous vertebrate remains include osteoglossomorph and ceratodontid fish, turtles, crocodyliforms, mammals, and at least four taxa of dinosaurs, including theropods and lithostrotian sauropods. Palaeogene vertebrate discoveries include phiomorph rodents, elephant shrews, anthropoid primates, birds, fish, and crocodyliforms. A range of other non-vertebrate fossils have also been recovered from these Cretaceous and Palaeogene sequences, including plant macrofossils, pollen, gastropods, bivalves, and crustaceans.

Stratigraphic and sedimentological investigations, conducted in tandem with palaenotological investigations, have helped to resolve the much disputed age of the Red Sandstone Group. This work demonstrates a more complex tectonic and depositional history for East Africa than has previously been recognized. Based on detailed mapping and stratigraphy, the Red Sandstone Group has been subdivided into three new informal members: Unit I (Cretaceous), Unit II (Oligocene), and Unit III (late Miocene–Pliocene?). Conventional and unconventional methods have been utilized to determine the age of each of these temporally distinct units, including: biostratigraphy, radiometric dating, detrital zircon geochronology, and heavy mineral provenance. Tied to improved stratigraphic control, these new fossil discoveries hold promise for testing and refining a myriad of phylogenetic and palaeobiogeographic hypotheses relating to the origin and diversification of Southern hemisphere vertebrate groups.

Only Albany dinocephalian reveals new toothy information

B.S. Rubidge[1]* & W.J. De Klerk[2]

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

2Albany Museum, Somerset Street, Grahamstown, 6139 South Africa

**E-mail: bruce.rubidge@wits.ac.za*

Dinocephalians are a diverse group of basal therapsids known primarily from Middle Permian rocks of South Africa and Russia (Chudinov 1983, Boonstra 1969), although new finds have been reported from Zimbabwe (Lepper *et al.* 2000), Brazil (Langer 2000) and China (Li *et al.* 1996). They were the first large tetrapods to live on land and a wide diversity of taxa were present right from their earliest appearance. Despite their early success, however, they soon became extinct (Boonstra 1971), probably by the end of the Middle Permian. Of the five main groups of dinocephalians, the anteosaurids, titanosuchids and tapinocephalids are most abundantly represented in South Africa.

This paper reports the discovery of the only dinocephalian from the Albany area, and is also most easterly record of a dinocephalian in South Africa. The presence of heels on the incisors, reduced canine, and all teeth interdigitating, identifies the specimen as a tapinocephalid dinocephalian, despite the fact that it lacks great pachyostotic thickening of the skull roof which is a characteristic of all tapinocephalids (Rubidge 1991). The presence of intermeshing incisors distinguishes dinocephalians from other therapsids and was a mechanism of dental occlusion which was not utilized by other therapsids. In all South African dinocephalians the teeth are poorly known, especially in tapinocephalids where the teeth tended to fall out of the alveoli before fossilization (Boonstra 1962). The new specimen is the first tapinocephalid dinocephalian which has all its teeth well preserved so that it is possible now, for the first time, to provide an accurate dental formula for a tapinocephalid and to study dental occlusal patterns.

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Quest for African dinosaurs

S.D. Sampson

Utah Museum of Natural History and Department of Geology and Geophysics, University of Utah, Salt Lake City, Utah, 84112 U.S.A.

E-mail: ssampson@umnh.utah.edu

Despite the vast area encompassed by Africa, greatly exceeding that of any other southern continent, we still know relatively little about the Mesozoic world of African dinosaurs. Nevertheless, the past two decades have witnessed a plethora of dinosaur discoveries in such countries as South Africa, Kenya, Tanzania, Niger, Morocco, and Egypt, as well as the nearby island of Madagascar. These finds, when combined with work on other southern landmasses—including South America, India, and Antarctica—have begun to fill major gaps in our knowledge, relating to such topics as diversity, phylogeny, biogeography, and terrestrial ecosystems. Of particular interest, has been the integration of dinosaur biogeography and Gondwanan fragmentation, with great potential for reciprocal illumination. Most notable and surprising has been recognition of several derived clades of Late Cretaceous dinosaurs and other terrestrial vertebrates in both South America and Indo-Madagascar, suggesting a degree of cosmopolitanism that was previously unsuspected. These findings, combined with new geophysical data, have resulted in the formulation of a pair of rival hypotheses. The 'pan-Gondwana' hypothesis postulates that the observed biogeographic patterns are the result of origination and dispersal of these clades throughout Gondwana prior to its fragmentation into isolated landmasses. By contrast, the 'Africa-first' model posits that Africa broke away and persisted as an island continent for millions of years during the Cretaceous while faunal exchange was occurring between and among other southern landmasses. Although imbalanced sampling across Gondwanan landmasses currently prevents rigorous testing of these ideas, observed patterns are arguably most consistent with the Africa-first model.

Reconstructing palaeoclimates: an exploratory study using the technique of xylem analysis

E. Scholtz

P.O. Box 6301, Grahamstown, 6140 South Africa

E-mail: antononmountain@hotmail.com

A digitizer/computer-based approach to the quantitative analysis of areas of wood sectioned in the transverse plane is applied in the analysis of nine charcoal assemblages from Boomplaas Cave, Congo Valley, southern Cape. Values for a range of wood anatomical variables are used to reconstruct eight climatic periods. The data are examined as (1) the mean values for wood anatomical variables for each assemblage; (2) the mean values for wood anatomical variables for individual morphological types per assemblage; (3) the distribution of dimensions in the trachea system for selected taxa; (4) the distribution of dimensions in the trachea system of a constructed 'typical' area of xylem tissue for each assemblage.

The results indicate that: from *c.* 60 000 to 11 000 BP the climate was generally harsh, cold and dry; for a period around 32 000 BP, winter rainfall probably prevailed while around 22 000 BP summer rainfall is indicated; a major change toward more mesic conditions occurred between 11 000 and 14 000 B.P.; the climate was optimum, mesic and equable, for a period during the end Pleistocene, *c.* 14 000 to 12 000 BP, and that subsequently, temperatures were higher and xeric conditions were experienced during the mid-Holocene, 1000 to 5000 BP; there is again evidence for summer rainfall during the late Holocene.

The xylem analytical approach is briefly contrasted with the established discipline of dendroclimatology in order to highlight the limitations and potential of the former.

Drought conditions in the South African Karoo Basin at the Permo-Triassic Boundary

R.M.H. Smith[1*] & P.D. Ward[2]

[1]*Iziko South African Museum, P.O. Box 61, Cape Town, 8000 South Africa*

[2]*Department of Earth and Space Sciences, University of Washington, Seattle, WA 9815, U.S.A.*

E-mail: rsmith@iziko.org.za

Isotope and palaeomagnetic stratigraphy have been used to position Permo-Triassic boundary (PTB) in the main Karoo Basin of South Africa and correlate the study sections with terrestrial PTB sequences in other parts of the world (Ward *et al.* 2005). The Karoo PTB coincides with a major extinction episode recorded in the fossil record of the *Glossopteris* flora (Retallack *et al.* 2004) and the therapsid-dominated tetrapod fauna (Smith and Ward 2001). This study uses field observations of the sedimentary facies, and taphonomy of *in situ* fossils of two well-exposed PTB sequences in the southern Karoo Basin to provide evidence of environmental aridification that may have brought about the breakdown of the Late Permian terrestrial ecosystems in southern Gondwana.

*Pattern of tetrapod extinction.*The End-Permian extinction in the central Karoo basin lasted some 100 000 years (Smith and Ward 2001) during which time there was a gradual extinction of small herbivorous dicynodonts and their gorgonopsian predators before the main pulse of extinction that involved medium and large herbivores and carnivores. This pattern suggests that the smaller ground foraging animals, feeding on the undergrowth of ferns and clubmosses, disappeared before larger browsing fauna feeding on *Glossopteris* shrubs and trees. This is in keeping with the interpreted onset of drought conditions. The fact that the medium- and large-sized *Lystrosaurus* arrived in the basin and seemingly flourished as the *Dicynodon* fauna began to fade, indicates that it was somehow pre-adapted to survive the worsening drought conditions. The characteristic spade-shaped maxilla with shock-resistant sutures was most likely the key to the survival of *Lystrosaurus* (Botha and Smith, submitted). It had the ability to continue grazing throughout the drought, probably on the tough equisetalian 'reeds' that remained growing in the moist areas around ponds and along the increasingly ephemeral floodplain channels. It appears that *Dicynodon* and associated herbivores were unable to digest the fibrous stems and leaf whorls of the horsetails efficiently enough to ensure their survival.

Karoo PTB palaeoenvironments. The Karoo PTB facies sequence is interpreted as a relatively rapid change in fluvial landscape from an alluvial plain traversed by a few large highly meandering rivers with expansive lowland floodplains (*massive dark grey mudrock*) through a transitional stage when the rivers straightened and widened and branched into a distributary channel network that scoured the now abandoned floodplains (*massive maroon siltstone*). As the sediment load increased these channels continued to widen and formed in-channel bars that eventually separated the flow into a braidplain of interconnected sand-dominated ephemeral channels (*conglomeratic sandstone*). During deposition of the massive maroon siltstone facies there was an apparently synchronous depositional event that coincided with the extinction of *Dicynodon* – the last of the Permian dicynodonts to disappear from the Karoo basin. This resulted in the accumulation of up to five metres of red laminated mudrocks (*maroon laminites*) that show evidence of shallow standing water with periodic sub-aerial exposure and desiccation. This is interpreted as an interval when soil formation almost ceased over large parts of the Karoo floodplains. Periodic flooding deposited sand/mud couplets that show little post depositional colonization by either animal or plant life except for a calliannassid-like burrowing arthropod.

Evidence for drought. The calcic palaeosols reflect not only a change in rainfall regime but also an increase in mean annual temperature in the early Triassic resulting in widespread reddening of the floodplain mudrocks. The conclusion drawn from sedimentological and taphonomic evidence of waterhole bone accumulations is that for a period following the disappearance of *Dicynodon*, the central Karoo basin was subject to an increasingly more unreliable and stormy rainfall regime combined with an increase in mean annual temperature which effectively allowed only drought-tolerant flora, and their dependent fauna, to survive into the Early Triassic.

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Palaeoenvironments and indenter mechanics of an Early Jurassic tracksite in southern Lesotho

R.M.H. Smith[1*], C.A. Marsicano[2] & C.A. Sidor[3]

[1]*Department of Karoo Palaeontology, Iziko South African Museum, P.O. Box 61, Cape Town, 8000 South Africa*

[2]*Departamento de Cs. Geolögicas, Universidad de Buenos Aires, C1428 DHE, Buenos Aires, Argentina*

[3]*Burke Museum and Department of Biology, University of Washington, Seattle, WA, 98195, U.S.A.*

**E-mail: rsmith@iziko.org.za*

In Moyeni, southern Lesotho, abundant ornithopod, theropod and sauropod tracks are preserved on a sandstone surface 15 m above the base of the Upper Elliot Formation, a contact that is widely cited as the Triassic/Jurassic boundary. This study is a re-investigation of the site with particular emphasis on the environmental setting of the tracksite and the sequence of colonization during emergence and desiccation of the surface. A new 'cheirotheriod' trackway at the site questions the use of this ichnotaxon as a Triassic indicator.

The tracks are preserved on several convex scroll bar surfaces, showing evidence of shallow falling water levels, emergence and early stages of desiccation. The surfaces dip approximately 20 degrees toward the inferred palaeochannel. Numerous rib-and-furrow palaeocurrent readings indicate they were formed on the inner bank of a channel meander.

The majority of the vertebrate tracks were made higher on the bar, into a firmer substrate covered in adhesion warts. Smaller tridactyl trackways are mostly confined to the bar top and clearly run up and down the long axis parallel to the inferred strandline. Larger three- and five-toed trackways follow the same trend, but lower down on the bar surface and, judging from toe scrapes, were probably made beneath shallow, gently flowing water.

Regularly spaced skip marks associated with large tridactyl bipedal trackways have been interpreted as tail drag marks. However, detailed analysis of the cross-cutting relationships with the prints and the direction of movement of the indenter both appear contrary to conventional tail drag dynamics.

Scratches and pits: the usefulness of dental microwear for interpreting palaeo-diets

C. Steininger

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

E-mail: steinic@science.pg.wits.ac.za

Palaeoenvironmental reconstruction has increasingly gained support in the past two decades. Morphology, behaviour and the migration of mammals including hominids is directly linked to the environment which they inhabit.

The time between 2.5 and 1.5 Ma is of particular interest as species of *Paranthropus* and *Homo* coexisted. Over time *Paranthropus* became extinct while *Homo* thrived and dispersed into other regions of Africa and out of Africa. What was the environment like for these major evolutionary transformations to have taken place? Was our adaptation to a cooler and more seasonal environment the key to the survival of our genus *Homo* and to the detriment of *Paranthropus*?

To better answer these questions about the habitat occupied by hominins, we look towards a particular group of mammals – the Artiodactyla. They are often used as palaeoenvironmental indicators because of their abundance in most fossil assemblages, and importantly, because they can easily be separated into general dietary categories that reflect habitat preferences.

Study of dental microwear represents one of the most effective techniques from which to infer palaeo-diets. Microwear is the result of abrasion and attrition during the process of mastication, providing a record of what the animal ate during its life. Different types of foods have different material properties and shapes, and will require different strategies of mastication. A grazer must process grass using a lateral cyclical motion. The combination of this movement and the phytoliths found in grass results in abrasion across the occlusal surface of the tooth. Under a high magnification microscope, the abrasions appear as linear scratches. Conversely, browers that prefer leaves, seeds, nuts or fruit use vertical pressure for breaking these brittle food items. An animal that is a predominate browser will have a higher percentage of pits on the occlusal tooth surface than one which grazes.

Dental microwear thus reflects dietary preference directly, and this in turn can be used to interpret palaeoenvironments. One of the strengths of microwear study that is not offered by other techniques is that it can reveal dietary patterns such as seasonal variation and uses of fall-back foods when the animal is under dietary stress due to environmental change or competition for resources.

Microwear analysis on its own is effective in determining dietary preferences, and is therefore useful as a proxy for broad-brush palaeoenvironmental reconstruction, but in combination with other techniques such as stable isotope analysis and ecomorphological studies, it promises a much more comprehensive and reliable interpretation of past environments.

A new dinosaur fauna from the Early Jurassic of South Africa

A. Yates[1*], M. Bonnan[2], J. Neveling[3] & J. Hancox[1]

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

[2]*Western Illinois University, Macomb, Illinois. U.S.A.*

[3]*Council for Geoscience, Pretoria*

**E-mail: adam_m_yates@yahoo.co.za*

The upper Elliot Formation (UEF) of South Africa has a well-known fauna, dominated by a single species of basal sauropodomorph dinosaur *Massospondylus carinatus.* Sedimentological evidence suggests that the environment of deposition was a semiarid to arid floodplain with sediment supplied by small, ephemeral streams with intermittent flashy discharge. Calacareous pedogenic horizons are common, as are pedogenic nodule conglomerates in channel lags. A distinctive, reworked palaeosol, called the *Tritylodon* acme zone, is widespread near the base of this unit. The section of the upper Elliot formation at Spioenkop (Heelbo Farms), Rosendal District, northern Freestate is sedimentologically atypical. Palaeosols are only represented at the base of the UEF and the bulk of the unit is formed by stacked channel sands, some laid down in large, possibly permanent, streams. The *Tritylodon* acme zone is not present. Several bonebeds are present in the UEF at Spioenkop. Our team has systematically excavated two of these bonebeds over three field seasons between 2004 and 2006. These have revealed that the fauna is also atypical. *Massospondylus,* which is so common elsewhere, is apparently absent. Instead there is a diverse sauropodomorph fauna consisting of three new species: a basal sauropodomorph similar to *Thecodontosaurus;* a riojasaurid; and a basal sauropod more derived than *Antetonitrus ingenipes.* The basal sauropodomorph can be distinguished from other UEF sauropodomorph taxa by its plesiomorphic dentary, which lacks a ventrally curved rostral tip and any trace of a buccal emargination. Its teeth are also plesiomorphic in having a smooth enamel surface and extensively denticulated carinae on the mesial and distal margins. The riojasaurid is an unusual, strongly autapomorphic taxon that can be diagnosed by: a highly pitted and foraminate band around the dentigerous margins of the maxilla and dentary; low, triangular cervical neural spines; and stout pedal elements including phalanges that are wider than long in all cases. The third taxon can be referred to Sauropoda on the basis of: the lingual concavities of the tooth crowns; extensively rugose enamel surfaces of the tooth crowns; dorsal neural spines that are much higher than long; hyposphenal ridges in the caudal vertebrae; and transversely compressed and laterally canted pedal unguals. It can be diagnosed by the autapomorphic anteroventral inclination of the anterior face of the cervical centra. The quarry that produced the sauropod bones was rich in small, irregular rounded bones that are interpreted as osteoderms. This would be the first record of ossified armour in a non-titanosaurian sauropod. Other elements of the fauna include an *Allosaurus*-sized theropod, known only from teeth. The only typical UEF faunal elements found at Spioenkop are the small carnivores *Protosuchus haughtoni* and *Coelophysis rhodesiensis.* The unusual fauna, with its diverse fauna of large herbivores, is interpreted as inhabiting a well-vegetated microenvironment on the upper Elliot floodplain. Given the absence of the typical palaeosols and the dominance of channel sands we suggest that this microenvironment was a riparian gallery forest alongside one of the larger, more permanent streams crossing the floodplain.

POSTERS

The taphonomy of an Early Jurassic dinosaur bone-bed in the northern Free State

M. Blackbeard* & A. Yates

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

**E-mail: blackbeard.m@gmail.com*

The taphonomy of a bone-bed in the upper Elliot Formation (Early Jurassic) on the farm Spioenkop (Rosendal District, Free State) is described and discussed. The bone bed was excavated, gridded and mapped by a team from the Bernard Price Institute during the 2006 field season. All bones were numbered and collected. Well over 95% of the bones in this bed can be attributed to a new taxon of large (juvenile femur length = 700 mm) basal sauropodomorph. The minimum number of individuals of the sauropodomorph is two (based on ribs). The only other taxa present are two theropods, one very large and represented by isolated tooth crowns, the other is small (femur length = 146 mm long) and is represented by a femur and a sacrum. The latter can be referred to *Coelophysis rhodesiensis,* which is known from other sites in the upper Elliot Formation.

The bones are buried in an upwardly-fining lens of sand and are of limited lateral extent (6 m in outcrop). This package is interpreted as the fill of a small-scale channel on the floodplain. The bones are densely packed with 160 bones having been recovered from an area of less than 5 m^2. The bones are often found lying on top of one another, but with no sign of articulation, or association. The lack of articulation indicates some degree of transport by water and this is supported by a preferred orientation of the long bones (strike: 301–121°, dip: 007°S). Nevertheless, transport of the bones is likely to have been minimal, as the bones (including several delicate skull bones) have pristine surfaces that show no sign of abrasion due to extended water transport. The pristine bone surfaces (on both upper and lower surfaces), also indicate that exposure at the surface was limited. Nevertheless there is some evidence of *in situ* modification before final burial. A few fully buried bones were cleanly broken and ended abruptly, despite not having been exposed to recent erosion. The dorsal process of a maxilla was found to have been folded through 150° from its original vertical position. The base of the process shows that the bone deformed plastically up to 90°, after which brittle failure occurred. No other bones show such signs of deformation, indicating that the force involved was highly localized and happened while the bone was fresh enough to bend. We believe the cause of this damage was trampling by another dinosaur, possibly the large theropod. Another source of evidence that a theropod visited the site before final burial, is a possible coprolite buried amongst the bones. The coprolite is a flattened, irregular mass of bone chips dispersed through a hematitic groundmass, surrounded by small, closely spaced stringers of hematite and bone chips spread over an area with an approximate diameter of 30 cm. The flattened irregular shape is also thought to be the result of trampling.

The sauropodomorph bones show several signs of belonging to juveniles, including the striated texture of many bone surfaces and the lack of sutural closure between the braincase elements, as well as the neural arches and their centra. The agent that killed the juvenile sauropodomorphs remains unknown.

Ichnological Problematica from the Lower Jurassic Clarens Formation, southern Africa

E.M. Bordy

Department of Geology, Rhodes University, Grahamstown, 6140 South Africa

E-mail: e.bordy@ru.ac.za

The ichnological record of the Lower Jurassic Clarens Formation in southern Africa contains a number of unique trace fossils unlike any other known modern or ancient biostructures. Here some enigmatic horizontal, regularly-oriented biogenic sedimentary structures (Fig. 1) are described that occur in association with features that were previously interpreted as Early Jurassic termite nests. These spectacular, but rather puzzling trace fossils are exposed in enormous profusion as straight, ~0.5 cm cylinders in parallel alignment to one another and to ancient horizontal bedding planes. The structures, which occur in both epirelief and full relief, and which show no evidence of overlapping or crosscutting, are filled with material identical to the rest of the host rock: a compositionally and texturally uniform, very fine to fine-grained, massive quartzarenite. In cross-sections, each structure is defined by a subtle, ~0.1 mm thin, concentric gap.

Spatiotemporal distribution patterns of the oriented structures and associated back-filled trace fossils, as well as other sedimentological and palaeontological lines of evidence, collectively imply recurrence of favourable ecological parameters (e.g. increased moisture content of the substrate) related to periodic climate fluctuations in the Early Jurassic of Gondwana. The limited stratigraphic resolution of the Clarens Formation hampers correlation of the study sites, and thus the question as to whether or not the preserved biotic communities were secluded in time and space, flourishing only in certain favourable landscape mosaics of the more arid Clarens palaeoclimate, remains open for future research.

Without comparable modern biogenic structures of similar dimensions and spatial arrangement, the evidence for organic origin of these enigmatic structures remains equivocal. Furthermore, the function these structures served is also rather perplexing. Hopefully, this morphological description and hypothesis put forward regarding their origin will stimulate further investigations, leading to the recognition of similar ancient and modern structures, and eventually revealing their true genesis.

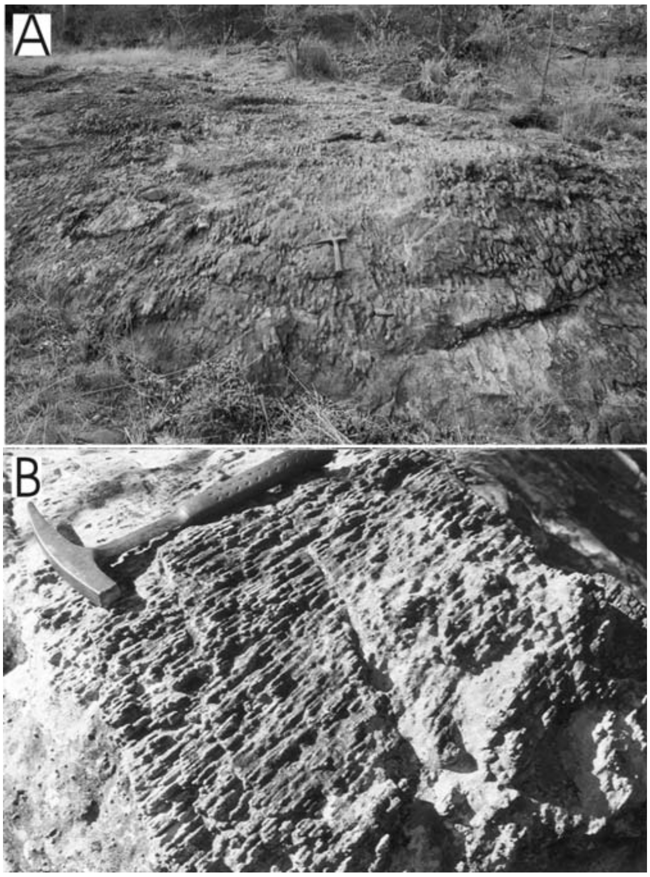

Figure 1. Field occurrences of the enigmatic horizontal, regularly-oriented structures form the Lower Jurassic Clarens Formation of southern Africa (30 cm long hammer for scale). The structures often occur in great profusion, *en masse* on weathered, horizontal surfaces up to 100 m^2 (**A**) as well as in localized, smaller (eroded) patches (**B**). Note that these unbranched, smooth, straight, cylindrical structures of ~0.5 cm diameter show no evidence of overlapping or crosscutting.

Analysis of microfauna-bearing breccia from Kromdraai-A in the Cradle of Humankind World Heritage Site

C. McCrae[1,2]

[1]*Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag 3, WITS, Johannesburg, 2050 South Africa*
[2]*Transvaal Museum, Human Origins and Past Environments Programme (HOPE), P.O. Box 413, Pretoria 0001, South Africa*
E-mail: rudget@mweb.co.za

Kromdraai-A is situated 1.75 km east of Sterkfontein in the Cradle of Humankind World Heritage Site. It is rich in mammalian microfauna, largely deposited by owls (Brain 1981). Calcified breccia from the Kromdraai-A dump, as well as stratigraphically constrained, *in situ* samples, were chemically analysed using X-Ray Fluorescence. Correlation of the samples was attempted, with the aim of determining the original host matrix, and hence stratigraphic location, of each dump-site sample.

There appear to be two specific types of breccia present at the site, representing two separate periods, or modes of deposition. The distinction between the two breccias is based on differences in colour, faunal density, faunal preservation and chemistry.

Detailed analysis of the breccia, before and after preparation in dilute acetic acid, serves to address the question as to whether it is possible to reassign context to ex-situ breccia, as well as whether bone density is correlated with chemical differences that relate to environmental factors. It is clear that two different sets of conditions prevailed during deposition. Taxonomic investigation is underway to further clarify these conditions.

The latest dirt on acid preparation

C. McCrae[1,2*] **& S. Potze**[2]

[1]*Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag 3, WITS, Johannesburg, 2050 South Africa*
[2]*Transvaal Museum, Human Origins and Past Environments Programme (HOPE), P.O. Box 413, Pretoria, 0001 South Africa*
**E-mail: rudget@mweb.co.za*

Acid preparation remains the only reliable means of preparing certain fossils, such as microfaunal specimens, which are too delicate to undergo mechanical preparation. In fact, the Transvaal Museum and Hope experimental laboratory prepares all Plio-Pleistocene material in this manner. Advances in materials and techniques have minimized the influence of the chemicals upon the faunal remains. Consequently, this means of preparation deserves renewed investigation. The quest for new methods that will not compromise the fossils' integrity has led to an experimental approach in order to test new techniques in dealing with traditionally problematic tasks, including bulk and localized preparation.

Cranial bone (Sts 5 (i)) adhering to calcified matrix associated with 'Mrs Ples'

S. Potze

Transvaal Museum, Human Origins and Past Environments Programme (HOPE), P.O. Box 413, Pretoria, 0001 South Africa
E-mail: potze@nfi.co.za

When Robert Broom prepared Sts 5 ('Mrs Ples') mechanically with hammer and chisel in 1947, after discovery of the fossil at Sterkfontein on 18 April of that year, he removed six blocks of breccia, each of which had a thin veneer of bone representing the outermost layers of the cranium of this specimen of *Australopithecus africanus.* One of these pieces has been catalogued as Sts 5 (i). This block of breccia is being carefully prepared with the intention of exposing potential evidence of temporal lines and other external features on the cranium. The surface of 'Mrs Ples' as prepared by Broom does not represent the outer table of cranial bone. This accounts for the fact that temporal lines have not been recognized previously. Current work in preparation expects to address this problem. The identification of temporal bones is relevant to issues relating to the developmental age of Sts 5, believed to have been adolescent at the time of death, 2.1 million years ago.

Palaeontology in the Digital Age: the future of electronic publication

Rose Prevec[1]*, Ian Miller[2] & Jennifer Pattison Rumford[3]

[1]*Geology Department, Rhodes University, P.O. Box 94, Grahamstown, 6140 South Africa*

[2]*Denver Museum of Nature and Science, 2001 Colorado Blvd., Denver, CO 80205-5798, U.S.A*

[3]*Ocean Drilling Program, 1000 Discovery Drive, College Station, Texas 77845-9547, U.S.A.*

**E-mail: rose.adendorff@ru.ac.za*

Palaeontologia Electronica (PE) is an open access publication, primarily sponsored by the Palaeontological Association, Society for Vertebrate Paleontology and the Paleontological Society. Not only is it free to authors and subscribers, it is a journal to be taken seriously. PE is now ISI listed, and is also fully compliant with both the International Code for Zoological Nomenclature (ICZN) and the International Code for Botanical Nomenclature (ICBN). This has opened the door for the electronic publication of all types of palaeontological papers, and will allow palaeontologists to fully embrace the age of burgeoning digital scientific communication.

At the forefront of electronic publication of palaeontological articles, PE has had to overcome many challenges in its pioneering nine-year history. Not the least of these, has been achieving compliance with the ICZN and ICBN. Both codes express a reluctance to entrust posterity to digital media, and insist that certain minimum requirements be met for the valid electronic publication of new names and nomenclatural modifications, including deposition of web, CD-Rom and paper versions of each PE issue at a specified number of archive libraries.

The concerns regarding electronic publication of botanical and zoological taxonomy no doubt stem from a mistrust of digital media as a long-term storage option. Such concerns are not entirely unfounded, with issues such as rapidly changing software, hardware and data-storage technology, and the limited lifespan of data storage media, providing ample reason for concern. However, systems are currently being developed to combat these problems. Library administrators are deeply invested in their role as custodians of world knowledge in the digital age, and many are taking a proactive stance toward finding effective long-term methods of electronic data storage and preservation. For instance, one of the most successful and widely supported initiatives is the LOCKSS (Lots of Copies Keeps Stuff Safe) Program, developed by Stanford University Libraries. LOCKSS provides a means for libraries to collect, protect and provide access to web-based journals. Long-term preservation of archived data on hard disk is effected though a self-regulating, cooperative, peer-to-peer process of damage detection and repair across a global network of computers.

Despite lingering fears surrounding the permanence of digital information, the benefits of on-line publication overwhelmingly outweigh the potential hazards. Open access journals such as PE provide a venue for taxonomic work that is cost-free, rapidly published, universally distributed, and where unlimited pages, illustrations and colour images are available to describe a new species accurately. Open-access publication takes us one step closer to creating a synergistic community of palaeontologists able to freely exchange ideas, without discriminating against those unable to afford costly subscriptions or access limited distribution documents.

The freedom provided to palaeobotanists and botanists alike by an electronic journal format is limited only by the imaginations of the author and editor, and the available technology. A publication need not only contain text and photographs, but video clips, interactive images, and 3D models—all in full colour. We are already fully immersed within a new culture of digital freedom, and we should be prepared to exploit it to the full.

A non-size-dependent metrical and non-metrical study of the pelvic complexes of *Australopithecus africanus* and *Australopithecus afarensis*

M. Tawane

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

E-mail: tawanem@yahoo.com

There is ongoing debate amongst palaeoanthropologists regarding the limb and body proportions of two of the best represented early hominin species, *Australopithecus africanus* and *Australopithecus afarensis.* The greatest area of difference is argued to be in joint areas associated with habitual bipedalism, namely the knee, pelvis and lumbar sacral complex. This research compares the pelvic complexes of the two fossil hominin species to establish the extent of variation, independent of size. Original fossil specimens Stw 431 and Sts 14, as well as a high-quality cast of AL 288, will be used. Modern human pelvic complexes will be used as a control for sex. It is hypothesized that no significant difference exists between the morphology of these two pelvic complexes.

This study should shed light on the debate concerning differences and similarities in early hominin pelvic complexes and add to the debate of the mode and tempo of the bipedal evolution of early hominins, their body proportions and phylogeny.

Breaking down barriers: the use of Venn diagrams to illustrate that *Australopithecus, Paranthropus* and *Homo* are not necessarily three discrete taxa

F.J. Thackeray
Transvaal Museum, Human Origins and Past Environments Programme (HOPE), P.O. Box 413, Pretoria, 0001 South Africa
E-mail: mrsples@global.co.za

African hominins dated between 1.5 and 2.5 mya are significant in relation to questions concerning the origin and diversification of species within the genus *Homo,* relative to penecontemporaneous species attributed to the genera *Australopithecus* and *Paranthropus.* It is generally considered that hominin species within the past 2.5 mya can be assigned to one or other discrete genus. However, boundaries between genera are not necessarily clearly expressed. Venn diagrams are used here as an example whereby relationships between African hominin species can be re-assessed, without assuming distinct boundaries between genera.

For example, a hominin temporal bone from Chemeron in the Baringo area, catalogued as KNM-BC 1, has previously been claimed to be the earliest representative of the genus *Homo* in Africa, dated *c.* 2.4 mya. Pairwise comparisons between KNM-BC 1 and temporal bones of other African hominins, using geometric morphometric (Procrustes) analyses, indicate that the Chemeron specimen displays a striking morphological similarity with specimen TM 1517, the type specimen of *Paranthropus robustus* from Kromdraai in South Africa. In fact the degree of similarity reflects a high probability of conspecificity, using extant hominoids as a frame of reference. The minimum date for the TM 1517 cranium, based on faunal associations and magnetostrigraphy, is 1.95 mya (Thackeray *et al.* 2002). KNM-BC 1 is also morphologically similar to AL 444-2, a Pliocene hominin attributed to *Australopithecus afarensis* from Ethiopia. In terms of a Venn diagram, the Chemeron fossil is placed at the intersection of three sets A, P and H, respectively representing *Australopithecus, Paranthropus* and *Homo.*

Excavations at Kromdraai A and B

J.F. Thackeray*, F. Senegas, D. Gommery, J. de Braga, S. Potze, C. McCrae & V. Balter
Transvaal Museum, Human Origins and Past Environments Programme (HOPE), P.O. Box 413, Pretoria, 0001 South Africa
**E-mail: mrsples@global.co.za*

Excavations have been undertaken at Kromdraai since 1938, beginning with the discovery of the type specimen of *Paranthropus robustus* (TM 1517) described by Robert Broom. Since then, excavations have been undertaken at Kromdraai under the direction of Bob Brain, Elizabeth Vrba and Francis Thackeray of the Transvaal Museum. We present a summary of results obtained from recent research and fieldwork. Of particular interest is the discovery of a hominid humerus shaft, which probably originated from the same individual as specimen TM 1517 (the type of *P. robustus*). A minimum date of 1.95 million years has been obtained for TM 1517, based on palaeomagnetic and biostratigraphic data. It is evident that hominids were probably scavenging for bones from carcasses of animals such as wildebeest, which were preyed upon by predators such as *Dinofelis.* Kromdraai A was probably a *Dinofelis* lair. However, Kromdraai A was also visited at least temporarily by hominids, as indicated by the presence of stone artefacts. X-ray diffraction analyses have indicated traces of bone apatite on stone artefacts (polyhedral cores), suggesting that hominids may have been occasionally breaking long-bones of ungulates for marrow.

Hybridization and osteology: the case of bontebok and blesbok

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

Damaliscus pygargus is one of three species found within this genus of Alcelaphinae. It has two subspecies: *Damaliscus pygargus pygargus* and *Damaliscus pygargus phillipsi,* which show hybridization since the introduction of the former in the Free State during the 1960s. The aim of the study is to investigate discrimination of the two subspecies by means of an osteological approach using specimens from the National Museum, Bloemfontein, and the Iziko South African Museum, Cape Town. It is hypothesized that bone measurement will serve to differentiate between the subspecies, which are adapted to different environments, and thus experience different stresses. This research project can be envisaged as a proxy for studying speciation events in southern African bovid populations, and will contribute to our knowledge of bovid evolution as it represents the first exploration of this methodology on *Damaliscus* subspecies.

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Bernard Price Institute for Palaeontological Research
University of the Witwatersrand
Private Bag 3
WITS 2050
South Africa
Telephone: [+27-11] 717-6694
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ROMER, A.S. 1966. *Vertebrate Palaeontology* (3rd edn). Chicago, University of Chicago Press.
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