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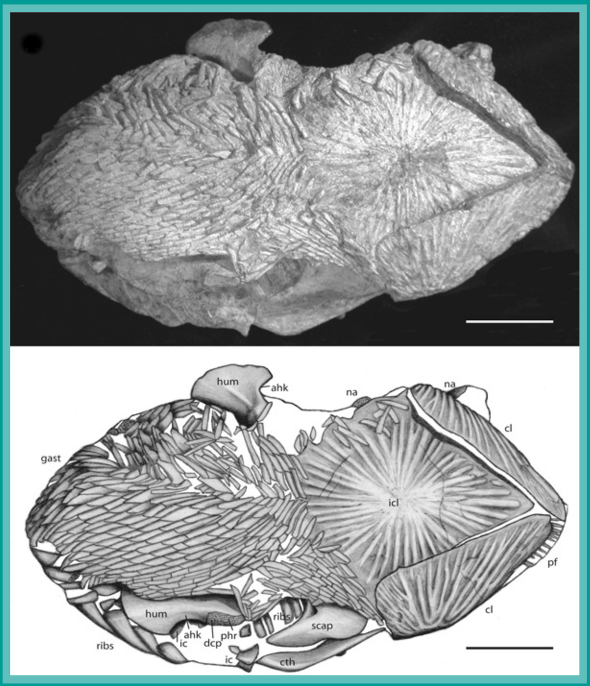

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Immaturity *vs* paedomorphism: a rhinesuchid stereospondyl postcranium from the Upper Permian of South Africa

Kat Pawley* & Anne Warren
Department of Zoology, La Trobe University, Melbourne, Victoria, 3086, Australia

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The postcranial skeleton of a medium-sized rhinesuchid from the Late Permian *Dicynodon* Assemblage Zone of South Africa is described. The well-preserved, articulated specimen consists of a partial skull, vertebral column and ribs, pectoral girdle, proximal limb elements, and ventral scales. Interesting features rarely preserved in stereospondyls include the extensive ventral scales and the pectinate anterior border of the interclavicle. SAM-PK-K10021 is of an average size for a rhinesuchid, but possesses a poorly ossified postcranial skeleton in comparison to larger rhinesuchid specimens. The scapulocoracoid lacks an ossified coracoid plate, the humerus lacks a supinator process, and the femur lacks a well-developed internal trochanter and adductor blade. Despite its relatively large size, SAM-PK-K10021 is an immature stage of a large rhinesuchid, thus contributing to our knowledge of the changes to the postcranial skeleton that occur during ontogeny. The assessment of heterochronic processes, especially paedomorphism, in the postcranial skeleton of temnospondyls, and the implications for cladistic analysis, are discussed.

Keywords: Rhinesuchidae, postcranial skeleton, stereospondyl, temnospondyl, ontogeny, heterochrony.

INTRODUCTION

The Rhinesuchidae are a little-studied group of large, semi-aquatic stereospondyls, with a temporal range from the Late Permian to the Early Triassic. They are one of the most basal taxa in the diverse, mainly Mesozoic, group of temnospondyls known as the Stereospondyli (Yates & Warren 2000, Fig. 1). The postcranial skeleton of most of the derived stereospondyls is considered to be paedomorphic (*sensu* McNamara 1986), and adapted to an aquatic existence, as evidenced by the reduced, imperfectly ossified postcranial skeleton commonly seen in these taxa (Watson 1919). In distinct contrast, what is known of the postcranial skeleton of some basal stereospondyls is well-ossified and presumably capable of extended terrestrial locomotion (Panchen 1959; Pawley & Warren 2005; Yates 1999). While the postcranial skeleton of some of the more derived stereospondyls is well described, the description of the most basal stereospondyls is insufficient for comprehensive comparison and determination of the character polarities of many postcranial characteristics.

While many specimens of rhinesuchids have been collected (Kitching 1978), few of these have associated postcranial skeletons. Those that do are: *Uranocentrodon senekalensis* (Haughton 1915; Van Hoepen 1915); *Broomistega putterilli* BP/1/3241 (Shishkin & Rubidge 2000); an unnamed rhinesuchid, field no. M460, consisting of a skull and articulated anterior pectoral girdle; and SAM-PK-K10021. *Uranocentrodon* and M460 have large skulls, the skull fragment of SAM-PK-K10021 is of medium size, while the specimens of *Broomistega* are small and considered by Shishkin & Rubidge (2000) to be paedomorphic compared to other rhinesuchids. To date, the only rhinesuchid postcranial skeleton described is that of the two-metre-long *Uranocentrodon* (Haughton 1915; Van Hoepen 1915), prepared from the dorsal side, however neither of the descriptions of this material provides sufficient detail for cladistic analysis.

All known rhinesuchid specimens are of Gondwanan origin, with the majority found in the Karoo Basin in South Africa, where they are an uncommon component of the fauna (Kitching 1978; Shishkin & Rubidge 2000). Most specimens have been found in Late Permian deposits, but they also represent one of the few higher level taxa to survive the end-Permian mass extinction, with one genus, *Broomistega,* found in the Early Triassic (Shishkin & Rubidge 2000). *Uranocentrodon* has previously been considered to have come from the Early Triassic *Lystrosaurus* Assemblage Zone (Kitching 1978; Groenewald & Kitching 1995), but is now firmly placed in the Late Perm-

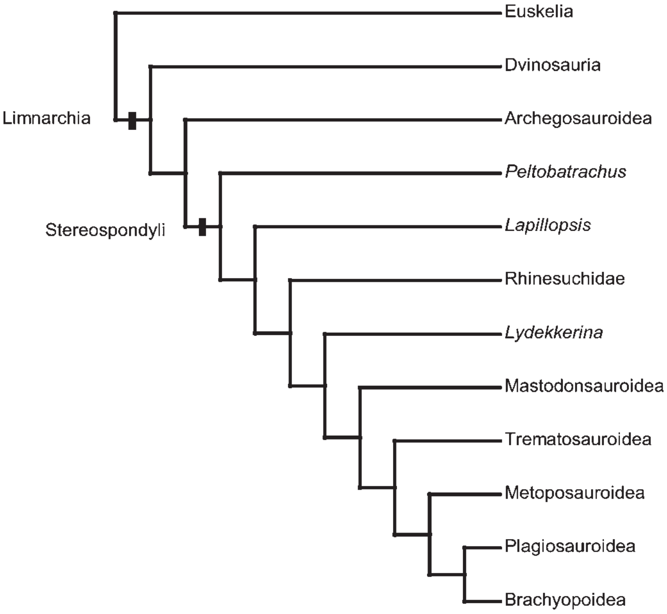

Figure 1. Cladogram depicting relationships of major taxa within the Temnospondyli (after Yates & Warren 2000; Damiani 2001).

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*Author for correspondence. E-mail: kpawley@latrobe.edu.au ian *Dicynodon* Assemblage Zone (Latimer *et al.* 2002).

The only large-scale, computer-based analysis of 'higher' temnospondyl relationships is that of Yates & Warren (2000), who placed the Rhinesuchidae among the most basal stereospondyls. Damiani (2001) removed the Lydekkerinidae from the Mastodonsauroidea and placed them between the Rhinesuchidae and the Mastodonsauroidea, which was supported by Pawley & Warren (2005). Some of the basal taxa are terrestrially adapted, with well-ossified limbs and skulls that lack lateral line canals. These include *Peltobatrachus pustulatus* (Panchen 1959), *Lapillopsis nana* (Warren & Hutchinson 1990a; Yates 1999), and *Lydekkerina huxleyi* (Shishkin *et al.* 1996; Pawley & Warren 2005).

The more derived Stereospondyli are all adapted for an aquatic existence, with deep lateral line canals on the skull roof and small, feeble, weakly ossified limbs with reduced processes for muscle attachment. The postcranial skeletons of these stereospondyls is paedomorphic because their prolonged growth phase results in attainment of a large size while retaining an essentially immature morphology (McNamara 1986). These stereospondyls commonly reach 2–3 m in length, with the largest known being *Mastodonsaurus giganteus* at 6 m (Schoch 1999). However, despite the apparently immature nature of the postcranial skeleton of many stereospondyls, there is little data available on ontogenetic stages, apart from those of *Benthosuchus sushkini* (Bystrow & Efremov 1940), *Mastodonsaurus giganteus* (Schoch 1999) and *Gerrothorax pustuloglomeratus* (Hellrung 2003).

Specimen SAM-PK-K10021, a newly discovered specimen of a medium-sized rhinesuchid with postcranial elements preserved, is interesting for several reasons. It is a basal stereospondyl, the ventral surface is exposed unlike other rhinesuchid specimens, and because it is an immature growth stage of a rhinesuchid. It is also one of the latest known rhinesuchids, collected from the Tatarian age deposits just below the Permo-Triassic boundary on Lucerne 70 farm, at Lootsberg Pass near Graaff Reinet, South Africa (Roger Smith, pers. comm.). This locality is noted for the overlap of two stratigraphic marker taxa, the Late Permian *Dicynodon* overlapping in occurrence for a depth of approximately 25 m with the Early Triassic *Lystrosaurus* (Smith & Ward 2001). The Permo-Triassic boundary is not clearly defined in these regions, but has been placed at the uppermost limit of the *Dicynodon* Assemblage Zone (Smith 1995; Smith & Ward 2001; Retallack *et al.* 2003). Collected from a fluvial deposit within the overlap zone, SAM-PK-K10021 is the latest known Permian rhinesuchid.

The purpose of this study is to further knowledge of the basal stereospondyl postcranial skeleton as part of work in progress on the temnospondyl postcranial skeleton. In particular, examination of the postcranial skeleton of the Rhinesuchidae is important for providing more information on the morphological variation that occurs amongst the basal members of the Stereospondyli. After preparation, it became apparent that the degree of ossification of the postcranial skeleton of SAM-PK-K10021 was not as extensive as anticipated. Growth stages of post-larval to adult sizes in stereospondyls are uncommon, and, as a medium-sized rhinesuchid, SAM-PK-K10021 provides information on the changes in the postcranial skeleton during these ontogenetic stages.

MATERIALS AND METHODS

Material. SAM-PK-K10021 housed in the South African Museum, Cape Town, consists of a partial skull, vertebral column and ribs, pectoral girdle, proximal limb elements and ventral scales of a rhinesuchid, preserved in a grey mudstone block from the Late Permian (Tatarian), *Dicynodon* Assemblage Zone, Lucerne 70 farm near Graaff-Reinet, South Africa.

Comparative material. M460, a skull and articulated anterior part of the pectoral girdle, *Cistecephalus* Assemblage Zone, Beaufort West. *Uranocentrodon senekalensis* NMQR1438; TM75, 77 79, 85, 103, 208 and 4703, complete skeletons, *Dicynodon* Assemblage Zone, Senekal. *Broomistega putterilli* BP/1/3241, skull and anterior skeleton, *Lystrosaurus* Assemblage Zone, Oliviershoek.

Methods. Staff at the South African Museum initially prepared SAM-PK-K10021, while the senior author, using an Aro airscribe, undertook further preparation. Small cracks were repaired with cyanoacrylate (Paleobond). Terminology in descriptions follows Romer (1922), Bystrow & Efremov (1940) and Coates (1996), unless otherwise noted.

DESCRIPTION

The dorsal surface of SAM-PK-K10021 (Fig. 2) consists of the posterior right side of a skull and mandible, some disarticulated neural arches and intercentra, articulated ribs, scattered ventral scales, a ventrally exposed femur, the dorsal processes of both clavicles, and both humeri. The ventral surface (Fig. 3) consists of an articulated interclavicle, clavicles, humeri, partly articulated ribs, ventral scales, and disarticulated intercentra.

Skull

Only the right posterior portion of the skull is preserved. This consists of parts of the parasphenoid, right pterygoid, right occipital region, squamosal, and quadratojugal. While the posterior portion of the mandible is present, the ventral surface remains buried in matrix. This specimen has been identified as a rhinesuchid because of a particular combination of cranial and mandibular features as follows: the otic flange of the pterygoid is deep, a falciform crest of the squamosal overhangs the otic notch, the postglenoid area on the mandible is absent, the ornament of the skull roof and mandible is coarsely ridged rather than finely reticulate or pustulate, there is a single occipital condyle, 'pockets' are present on the ventral surface of the parasphenoid, and the parasphenoid has a long suture with the pterygoid (not visible in figures) (Damiani 2001).

Assignation of SAM-PK-K10021 to a rhinesuchid genus was not undertaken because it does not have sufficient cranial material for specific taxonomic assessment. The Rhinesuchidae in general are in need of revision (Kitching 1978; Damiani & Rubidge 2003), so it was considered that assignation of SAM-PK-K10021 to a genus was unwise until such revision is undertaken.

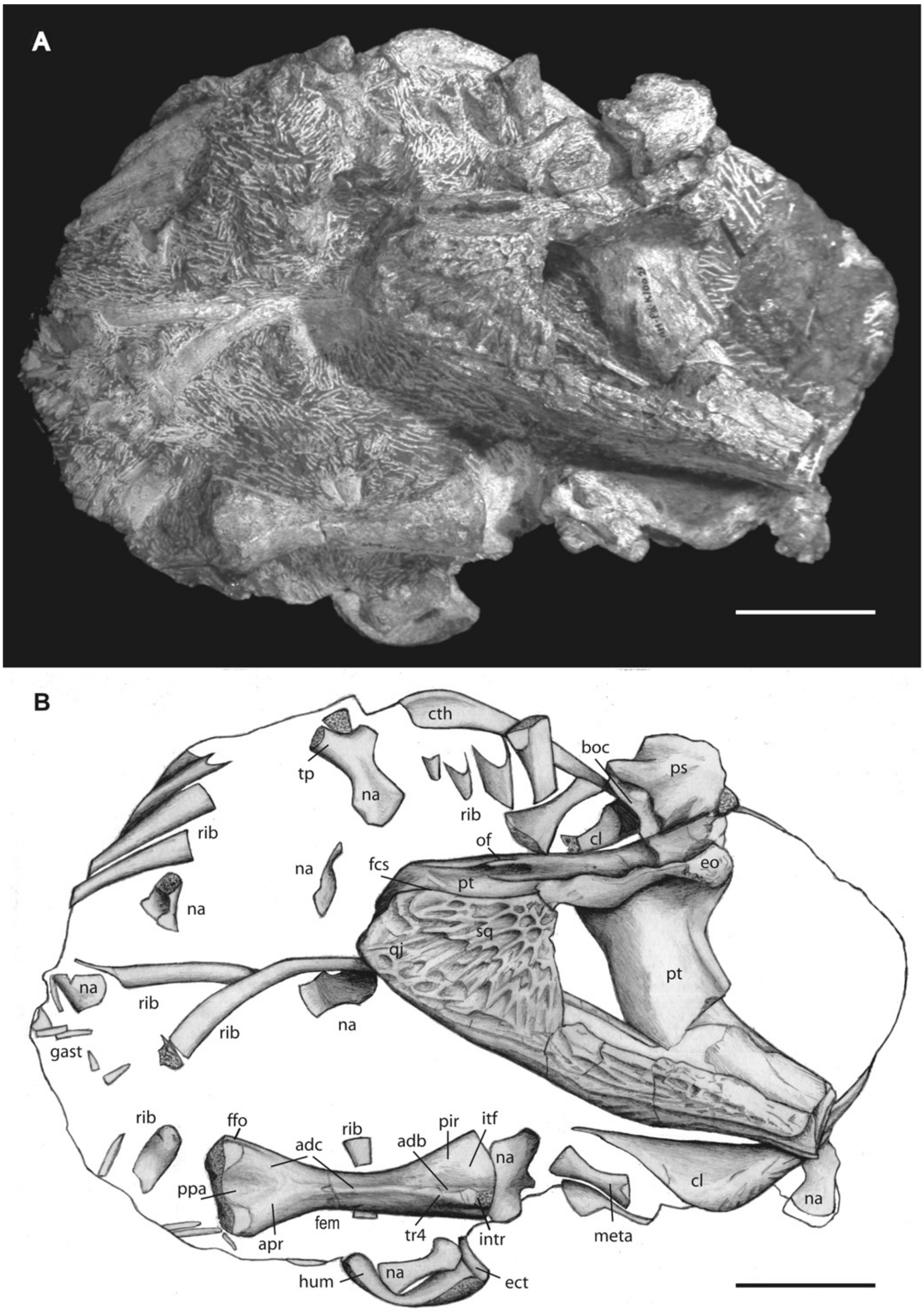

Figure 2. **A, B**. Dorsal view of SAM-PK-K10021. Scale bars = 50 mm.

Postcranial skeleton

The partly disarticulated dorsal surface of the specimen consists of the femur lying next to the skull, surrounded by scattered neural arches and ventral scales. On the ventral surface, the pectoral girdle and ventral scales are articulated and well preserved. Pelvic and distal limb elements are absent.

Many of the disarticulated vertebral elements of SAM-PK-K10021 are scattered throughout the block of matrix. The vertebrae are typically neorhachitomous (Romer 1947), in that the intercentrum is the dominant vertebral element. No pleurocentra, sacral vertebrae, or haemal arches were found.

Neural arch (Fig. 2). The neural spines are posteriorly offset and subrectangular in lateral view, with the height of the spines approximately equal in length to the distance between the well-developed pre- and postzygapophyses. Stout transverse processes terminate in anteroventral to posterodorsally inclined diapophyses. A supraneural canal does not penetrate the neural arch.

Intercentrum (Fig. 3). Thin, crescentic intercentra are associated with the ribs. Most intercentra have only the smooth, unornamented periosteal ventral surface exposed. In anterior or posterior view, the intercentra form a half circle, whose walls are uniformly thick.

Ribs (Figs 2, 3). Most of the ribs are only partially exposed. The visible ribs are long and thin, oval in cross-section, distally expanded and gently ventrally curved. None of

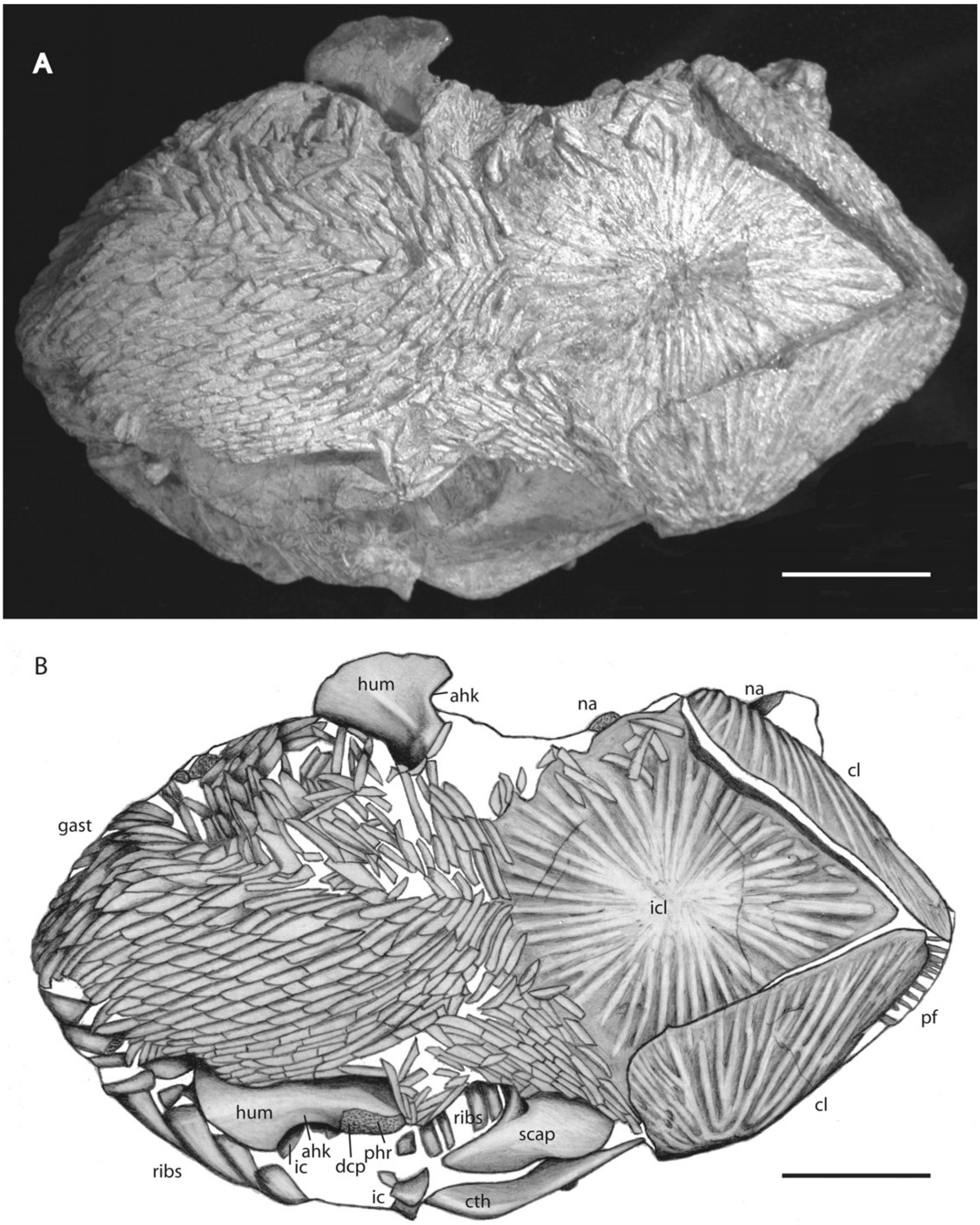

Figure 3. Ventral view of SAM-PK-K10021. Scale bars = 50 mm.

the exposed ribs bears an uncinate process; however, the thoracic ribs that are most likely to bear uncinate processes (Moulton 1974; Schoch 1999) are not exposed.

Interclavicle (Fig. 3). The coarsely ornamented main body of the interclavicle is of the flattened rhomboidal shape typical of stereospondyls, and lacks an elongate parasternal process. In outline, it is symmetrical about the centre of ossification, which is level with the posterior border of the clavicular facets, with the anterior half similar in size to the posterior half. The clavicular facets join anteriorly, so that the articulated clavicles meet and cover the anterior margin of the interclavicle. Posteroventrally, the border of the interclavicle is flat rather than recessed to fit the ventral scales; the ornament fades out where the ventral scales overlap. Where the edges of the interclavicle are exposed, they gradually become thinner until they taper out, so that no delimiting edge is discernible. A small portion of the anterior border extends beyond the front of the left clavicle as a thin and delicate pectinate fringe.

Clavicle (Figs 2, 3, 4A). Both articulated clavicles have the medial edges displaced slightly ventrally. Each clavicle has a coarsely ornamented, anteroposteriorly expanded ventral blade, with reticulate ornament near the origin of the dorsal clavicular process and grooved ornament radiating from here towards the anterior and medial margins. Like the edges of the interclavicle, the ornament terminates a short distance from the border of the medial margins of the clavicles, which continues medially, tapering into a thin almost imperceptible film of bone. The ornament

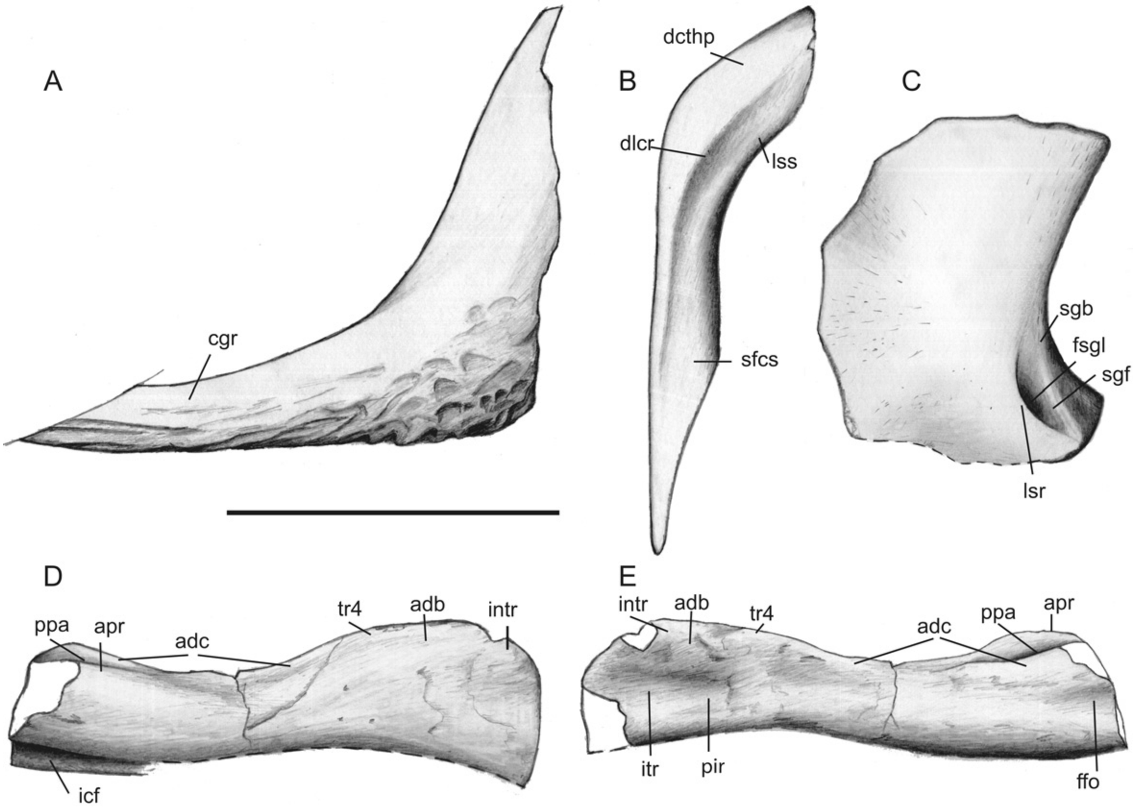

Figure 4. **A**, lateral view of left clavicle; **B**, lateral view of left cleithrum; **C**, lateral view of left scapulocoracoid; **D**, medial view of right femur; **E**, lateral view of right femur. Scale bar = 50 mm.

at the base of the dorsal clavicular process is flush with the dorsal clavicular process rather than raised. A narrow unornamented clavicular groove runs along the anterolateral edge of the blade, terminating at the base of the dorsal clavicular process. The robust dorsal clavicular process arises from the posterolateral corner of the ventral blade. Dorsally it is gently recurved near the tip, anteriorly it lacks a flange, but an extensive, posteriorly convex posterior lamina is present.

Cleithrum (Figs 3, 4B). The articulated left cleithrum is a stoutly constructed, robust element that expands slightly over the dorsal surface of the scapulocoracoid. A gentle posterior curve marks the anterior edge of the dorsal cleithral process, which lacks a cleithral crest; while the ventrolateral surface bears a shallow suprascapular lamina. In lateral view, a shallow ridge, the dorsolateral cleithral ridge (new term) rises from the dorsolateral surface of the dorsal clavicular process, it passes ventrally across the junction of the dorsal cleithral process and cleithral shaft to the anterior edge of the shaft. While the anterior edge of the cleithral shaft is smoothly rounded, the flattened scapular flange of the cleithral shaft (new term) forms the posterolateral border.

Scapulocoracoid (Figs 3, 4C). The poorly ossified, articulated left scapulocoracoid lacks both the dorsal scapular blade and the coracoid portion. The dorsally rounded scapular portion has shallow depressions along the anterodorsal border and ventral surface. A shallow, flattened, lateral supraglenoid ridge (new term) continues the posterior border of the scapular blade. The supraglenoid foramen is anteroventrally directed, so that in lateral view it is aligned with the posterior border of the scapular blade, while in posterior view it is located slightly lateral to the middle of the supraglenoid buttress. While the unfinished ventral edge of the supraglenoid buttress is apparent, the presence or absence of a coracoid plate is difficult to confirm, as the interclavicle and ventral scales cover much of the area ventral to the scapular blade.

Humerus (Fig. 3). Both articulated humeri are of the standard waisted temnospondyl form, with the proximal and distal ends set at right angles to each other. Each humerus displays a low degree of ossification and lacks prominent processes for muscle attachment. On the anterior surface, the proximal humeral ridge (new term) is unossified between the glenoid articulation surface and the deltopectoral crest. The latissimus dorsi process is not apparent, the ectepicondyle reduced, the distal border of the entepicondyle is rounded, and there is no evidence of a capitulum for articulation with the radius. A sharp-edged anterior humeral keel curves smoothly from the distal side of the deltopectoral crest down the anterior margin, with no evidence of a supinator process.

Metapodial (Fig. 2). A single disarticulated metapodial found near the clavicle is of the typical temnospondyl elongated hourglass shape. While the proximal end is steeply angled, it is impossible to determine its position within either the manus or pes.

Femur (Figs 2, 3, 4D,E). The disarticulated slender right femur has a long narrow shaft, with incompletely ossified ends. On the ventral surface, a shallow intertrochanteric fossa is present on the proximal head. The deep adductor blade anterior to the intertrochanteric fossa bears a flattened internal trochanter, barely differentiated from the articulation surface at its proximal end. Distal to the internal trochanter on the adductor blade is the weakly defined bulge of the fourth trochanter. An ill-defined posterior intertrochanteric ridge bounds the posterior edge of the intertrochanteric fossa; it joins the adductor blade at its junction with the adductor crest. This is distinguished from the adductor blade by a slight change in angle, and rapidly decreases in height as it passes down the midline of the femur. As the adductor crest reaches the proximal side of the shallow popliteal area, it becomes low and ill defined; it bifurcates at this point into the again poorly defined anterior popliteal ridge (new term). Hidden in ventral view, the shallow fibula fossa is located on the distal posterior surface of the femur. The intercondylar fossa on the dorsal side of the femur is hidden underneath it, what can be observed is deep, and smoothly rounded on both dorsal edges.

Ventral scales (Fig. 3). Ventral scales (dermal ossicles) cover the ventral surface of the specimen posterior to the interclavicle. On the left side of the specimen they are articulated, but are partly disarticulated and scattered on the right. All ventral scales are spindle-shaped, with a ridge in the centre of the element, similar to those described in *Uranocentrodon senekalensis* (Findlay 1968). The main body of the ventral scales forms an inverted chevron with the two arms of the V meeting in the midline, beginning at the posterior border of the interclavicle. There are a maximum of ten ventral scales preserved in each row. Additional ventral scales cover the flanks anterior to the humerus. The rows of these ventral scales parallel the posterior border of the interclavicle and clavicles, meeting the main body of the ventral scales at the level of the proximal insertion of the humerus. Unfortunately, the posterior and lateral borders of the ventral scale field are not preserved. The medial ends of the ventral scales expand slightly where they overlap along the midline, although there are no distinct median ventral scales. Dorsal scales are not preserved in this specimen.

DISCUSSION

It is not the intention of this work to compare exhaustively the postcranial skeleton of SAM-PK-K10021 with that of other temnospondyls, as this study contributes to work in progress on the temnospondyl postcranial skeleton. Hence, only basic comparisons will be presented here, and comparative taxa confined to those considered to be sister taxa to the Rhinesuchidae, that is, the Stereospondylomorpha, which includes the Archegosauroidea and Stereospondyli (*sensu* Yates & Warren 2000).

Features of SAM-PK-K10021 that are uncommon in stereospondyls

The pectinate border of the interclavicle is a common feature amongst temnospondyls and basal tetrapods, but its preservation is rare among stereospondyls, because it is thin, fragile, easily broken and readily destroyed in disarticulated specimens. However, it is commonly preserved amongst the sister taxa to the Stereospondyli, the Archegosauroidea, notably *Archegosaurus decheni* (Meyer 1857), *Cheliderpeton latirostre* (Boy 1993), and *Sclerocephalus* spp. (Broili 1926; Boy 1988; Werneburg 1992). The thin edges of the interclavicle and medial edges of the clavicles are also usually broken off in disarticulated specimens and the preservation of SAM-PK-K10021 is useful in demonstrating their true extent.

Preservation of ventral scales is uncommon among stereospondyls, having been described so far only in the rhinesuchid *Uranocentrodon senekalensis* (Haughton 1915; Van Hoepen 1915; Findlay 1968), *Laidleria gracilis* (Kitching 1957; Warren 1998) and *Gerrothorax* spp. (Nilsson 1946; Hellrung 2003). The arrangement in SAM-PK-K10021, whereby the anterolaterally directed rows of ventral scales meet the posterolaterally directed rows at the level of the humerus, is similar to that of other temnospondyls and basal tetrapods. The ventral scales are similar in shape and arrangement to those described by Findlay (1968) in *Uranocentrodon senekalensis.* One of the specimens of *Uranocentrodon* (TM75) has the pectoral girdle prepared from the dorsal surface, showing a comparable arrangement of ventral scales around the pectoral girdle. Findlay did not comment on the arrangement of the ventral scales but described in detail how the inverted chevron shape on the thorax would reduce friction from belly drag during locomotion.

Among the Stereospondylomorpha, similar ventral scales are common in the Archegosauroidea, particularly *Archegosaurus decheni* (Meyer 1857), *Cheliderpeton vranyi* (Werneburg & Steyer 2002), *Sclerocephalus* spp. (Broili 1926; Boy 1988; Lohmann & Sachs 2001), and *Platyoposaurus stuckenbergi* (Konzhukova 1955). The apparent absence of dorsal scales or osteoderms in SAM-PK-K10021 may be an artefact of preservation, as the dorsal surface of the specimen is not particularly well preserved.

Plesiomorphic characteristics of the postcranial skeleton of SAM-PK-K10021

In comparison with other stereospondyls, even as an immature specimen, SAM-PK-K10021 displays some of the plesiomorphic postcranial skeleton characters found in *Uranocentrodon senekalensis* and *Lydekkerina huxleyi* (Pawley & Warren 2005) and not seen in more derived stereospondyl taxa. Unlike the intercentra of many stereospondyls (Warren & Snell 1991), the intercentra are not thick in cross-section, although this may also be due to the immature condition of SAM-PK-K10021. The enclosed supraglenoid foramen is present on the scapula even though the coracoid is not present, indicating that the ventrally open supraglenoid foramen found in more derived taxa within the Stereospondyli is a derived characteristic rather than an indication of immaturity, or a retention of a juvenile character into adulthood. The lack of an anterior flange on the dorsal process of the clavicle is also a plesiomorphic trait among stereospondyls.

Morphological comparison of SAM-PK-K10021 within the Rhinesuchidae

In contrast to the interpretation of its skeleton as immature, the poorly ossified postcranial skeleton of SAM-PK-K10021 invites the proposal that SAM-PK-K10021 represents a more derived type of rhinesuchid, closer to the typical paedomorphic stereospondyls as understood by Watson (1919). It could be argued that there are two types of rhinesuchid postcranial skeleton, dividing the Rhinesuchidae into two phylogenetic groups, one retaining the primitive fully ossified condition and one developing the poorly ossified postcranial skeleton. The idea that the Rhinesuchidae may be composed of two taxonomic groups was put forward by Romer (1947), who considered that the Rhinesuchidae were more primitive than the Uranocentrodonidae because they retained the exposure of the opisthotic in the paraoccipital bar. More recently, Shishkin & Rubidge (2000) concluded that this morphological interpretation was incorrect, and division of the Rhinesuchidae was not justifiable on the basis of cranial characteristics. However, if two separate taxonomic groups were present, one would be represented by postcranial material of the well-ossified and large M460 (*Cistecephalus* Assemblage Zone, (Johann Neveling, pers. comm.) and *Uranocentrodon* (*Dicynodon* Assemblage Zone, Latimer *et al.*(2002), both found lower stratigraphically than the other group, which is represented by the small to medium, poorly ossified and stratigraphically higher SAM-PK-K10021 (uppermost *Dicynodon* Assemblage Zone, Roger Smith, pers. comm.) and *Broomistega* which is from the Early Triassic *Lystrosaurus* Assemblage Zone (Shishkin & Rubidge 2000), just above the level of SAM-PK-K10021. This could imply that the Rhinesuchidae were evolving reduced postcranial skeletons over time, following the trend shown by later stereospondyls. However, the correlation between size and degree of ossification in the specimens does not support this hypothesis.

Comparison of the postcranial skeleton of SAM-PK-K10021 with that of other rhinesuchids is necessarily limited because most specimens do not have associated postcranial material. Of those that do, the large specimens of *Uranocentrodon senekalensis* (NMQR1438, and TM75) and M460 are the best preserved and prepared. Although many rhinesuchid skulls of medium size are known, SAM-PK-K10021 is the only specimen of medium size with an associated postcranial skeleton. A single small rhinesuchid, the Triassic *Broomistega putterilli* BP/1/3241 (Shishkin & Rubidge 2000), has associated postcranial material although these remain undescribed.

Surprisingly, SAM-PK-K10021 has a poorly ossified postcranial skeleton, more like that of some of the later stereospondyls and *Broomistega,* making an interesting contrast to the robust and well-ossified postcranial skeleton of *Uranocentrodon* and M460. This suggests that it is an immature growth stage. However the assessment of the state of maturity of SAM-PK-K10021 can only be achieved by comparison with a growth series. While postcranial skeletons of the early larval stages of some temnospondyls have been identified (e.g. Schoch 1992; Schoch 2003), the ontogenetic changes that occur in the postcranial skeleton between the larval and the mature condition in rhinesuchids, and indeed in most stereospondyls, are almost unknown.

The evidence that SAM-PK-K10021 is an immature growth stage of a larger rhinesuchid is by necessity based on comparisons with the ontogenetic changes in the postcranial skeleton observed in closely related but more derived taxa. A partial growth series of small to large and presumably adult specimens is known for the mastodonsaurids *Benthosuchus sushkini* (Bystrow & Efremov 1940) and *Mastodonsaurus giganteus* (Schoch 1999). A large number of specimens of *Lydekkerina huxleyi* are known (Kitching 1978), but the postcranial skeleton is known only in the largest specimens. In *Mastodonsaurus,* a correlation exists between size and degree of ossification; only the largest specimens become comparatively well ossified (Schoch 1999). While an increase in ossification correlates with size in *Benthosuchus,* none of the specimens shows the same degree of ossification as the largest *Mastodonsaurus.* In *Lydekkerina* (Pawley & Warren 2005) the postcranial skeleton is comparable in its degree of ossification to that of *Uranocentrodon,* although it is much smaller. There is no doubt that the specimens of *Lydekkerina* studied are mature, as nearly 200 specimens of varying sizes have been collected (Kitching 1978) and the skulls of specimens described were of a large size. The similarity of the postcranial skeleton of *Lydekkerina* to that of *Uranocentrodon* indicates that they both differ from SAM-PK-K10021 in exactly the same features. A study of the postcranial skeleton of smaller-sized specimens of *Lydekkerina* would be useful in determining the immature condition of the postcranial skeleton in that taxon for comparative purposes, but unfortunately none of the smaller skulls collected has associated postcranial material.

Comparison of the individual postcranial elements of SAM-PK-K10021 with those of the stereospondyls listed above highlights various similarities and differences. The scapulocoracoid of SAM-PK-K10021 (Figs 3, 4C) is again comparable with that of the medium-sized specimens of *Mastodonsaurus* (Schoch 1999). The coracoid plate of *Mastodonsaurus* is separate from the scapular blade until late in ontogeny, when it fuses to form a scapulocoracoid similar to that of *Uranocentrodon* and *Lydekkerina.* In other mastodonsaurids such as *Benthosuchus* and *Eryosuchus* (*Parotosaurus*) *pronus* (Howie 1970), the coracoid is unknown and presumably remains unossified even in the largest specimens. The scapula also becomes much better ossified with ontogeny in the archegosaur *Sclerocephalus hauseri* (Meckert 1993), with the coracoid ossified only in the largest specimens. While a ventrally open supraglenoid foramen is found in most of the more derived stereospondyls (Warren & Snell 1991), SAM-PK-K10021 retains the plesiomorphic, ventrally enclosed supraglenoid foramen seen in *Uranocentrodon* and *Lydekkerina.*

The humerus of SAM-PK-K10021 (Fig. 3) is comparable in morphology with that of medium-sized specimens of *Mastodonsaurus* and *Benthosuchus,* where the proximal humeral ridge is unossified, the supinator process absent and the entepicondyle distally rounded rather than square. In the larger specimens of *Uranocentrodon, Mastodonsaurus,* and *Benthosuchus,* and in *Lydekkerina,* the proximal humeral ridge becomes ossified between the proximal articulation surface and the deltopectoral crest, a well-developed supinator process is present and the distal edge of the entepicondyle becomes squared off.

The morphology of the femur in SAM-PK-K10021 (Figs 2, 4D,E), with its slender outline, reduced adductor crest, and ill-defined fourth and internal trochanters, is consistent with that of immature specimens of *Mastodonsaurus* and *Benthosuchus.* In immature specimens of *Benthosuchus* the internal trochanter lacks a distinct process so that it is not distinct from the proximal articulation surface, similar to that of SAM-PK-K10021. In mature mastodonsaurids, and in *Uranocentrodon* and *Lydekkerina,* the adductor crest is deep and the trochanters well defined, with the internal trochanter terminating distal to the proximal articulation surface. The internal trochanter in SAM-PK-K10021 is broken, but there is no evidence for the large ventromedial expansion seen in *Uranocentrodon* and *Lydekkerina.*

In summary, the postcranial skeleton of SAM-PK-K10021 displays ontogenetic characteristics consistent with that of the medium-sized specimens of *Mastodonsaurus* and *Benthosuchus,* whereas the postcranial skeletons of *Uranocentrodon* and M460 are most similar to the largest specimens of *Mastodonsaurus.* The undescribed postcranial skeleton of *Broomistega* BP/1/3241 is most consistent with the smallest specimens of *Mastodonsaurus* and *Benthosuchus.* SAM-PK-K10021 most likely represents the immature condition for the rhinesuchid postcranial skeleton, with *Uranocentrodon* representing the mature morphology and *Broomistega* BP/1/3241 the most immature.

Certain features of the postcranial skeleton are only seen in the largest and most mature specimens and these are all absent in SAM-PK-K10021. The largest specimens possess a fully ossified scapulocoracoid, a humerus with an ossified proximal humeral ridge and supinator process, a femur with a robust internal trochanter distinct from the proximal head, and a deep adductor crest. The presence of these features of the postcranial skeleton in any stereospondyl indicates that the specimen is likely to be of a late ontogenetic stage. It is possible that specimens lacking these features may be immature even if they are of a substantial size.

These results also indicate that the specimen of *Broomistega putterilli* BP/1/3241 discussed in this study may be immature. *Broomistega* BP/1/3241 is one of three specimens considered by Shishkin & Rubidge (2000) to be paedomorphic adults. *Broomistega* BP/1/3241, with a midline skull length of 75 mm is substantially smaller than the largest *Broomistega* specimen, TM 184, with an estimated midline skull length of 110 mm. It is reasonable to assume that specimen BP/1/3241 represents an immature individual rather than a paedomorphic adult.

Assessment of the paedomorphic condition of the postcranial skeleton in temnospondyls

Temnospondyls, including stereospondyls, display indeterminate growth in that, after an initial rapid growth phase, they continue to increase in size during their lifespan (Steyer *et al.* 2004). The postcranial skeleton of many large stereospondyls is paedomorphic through the process of neoteny; the postcranial skeleton remains immature for an extended period, finally reaching the most ossified condition in the largest specimens. Thus, the postcranial skeleton of these taxa progresses through ontogenetic stages throughout the life of the animal, supported by the evidence presented above.

Studies of heterochronic processes within temnospondyls (McNamara 1988; Schoch 1995) have focused exclusively on cranial characteristics, with the exception of McKinney & McNamara (1991), who discussed some postcranial heterochronies of taxa they erroneously placed within the Temnospondyli.

Traditionally, heterochronic processes are determined within a group of organisms relative to the ancestral condition. Current conflicting phylogenies of temnospondyl taxa (Yates & Warren 2000; Ruta *et al.* 2003a; Ruta *et al.* 2003b) make determination of the ancestor–descent relationships within temnospondyl taxa uncertain, and therefore it is difficult to determine the most plesiomorphic temnospondyls. Outgroup comparison is possible but fraught with the same phylogenetic instability. Analysis of heterochronic processes among temnospondyls is limited because few taxa have growth series. This means it is currently impossible to determine the ontogenetic age of most temnospondyl taxa for comparison with that of more plesiomorphic or derived taxa. It is simpler and more feasible to look for the most advanced ontogenetic stages for comparison with apparently less well-developed taxa.

Well-ossified taxa are the most likely to display the greatest fulfilment of ontogenetic potential. Members of the Euskelia such as *Eryops megacephalus* (Cope 1888; Case 1911; Romer 1922; Miner 1925; Moulton 1974) and *Acheloma cumminsi* (*Trematops milleri*) (Williston 1909; Olson 1941; Schaeffer 1941) are temnospondyls that possess postcranial skeletons with the highest degree of ossification. Their limb bones have convex ends with relatively small amounts of cartilage between the joints, as well as fully ossified carpals and tarsals. These taxa can provide a benchmark for the fully ossified condition of the postcranial skeleton within temnospondyls. It is possible to interpret this high degree of ossification as peramorphic (extension of the growth phase to include more stages than that of the ancestor, resulting in a derived morphology (*sensu* McNamara 1986). Ongoing research indicates that other unrelated taxa such as diadectomorphs share many derived similarities of their postcranial skeletons with temnospondyls, and achieve similar high degrees of ossification. Either the Euskelia and diadectomorphs have independently evolved similar peramorphic changes to the postcranial skeleton or, more parsimoniously, they both display the fully or near fully ossified condition, which implies that they share a common ancestor above the level of stem tetrapods, including the Anthracosauria (*sensu* Panchen 1970), as suggested by Pawley & Warren (2001). This interpretation contradicts current understanding of basal tetrapod relationships (Ruta *et al.* 2003a).

If members of the Euskelia (e.g. *Eryops megacephalus* and *Acheloma cumminsi*) represent the fully ossified and most ontogenetically developed condition then, by comparison, most temnospondyls are paedomorphic. Study of a growth series of a taxon that develops a highly ossified postcranial skeleton, such as *Eryops megacephalus* would resolve this issue. A partial growth series of the humerus was briefly described by Bakker (1982). The smallest humerus in this series lacks the ossified proximal humeral ridge, enlarged supinator process, convex radial condyle, and squared off entepicondyle seen in the larger specimens. The smallest humerus displays features consistent with those of later ontogenetic stages of other temnospondyls which remain poorly ossified throughout their growth series. This small amount of evidence supports the hypothesis that the majority of temnospondyls are paedomorphic. Further evidence is needed to clarify the issue.

Paedomorphosis and implications for cladistics

Some cranial characters previously used for classification purposes have been shown to change with ontogeny in *Watsonisuchus aliciae* (Warren & Hutchinson 1990b; Warren & Schroeder 1995). Steyer (2000) demonstrated that using ontogenetically variable characters for phylogenetic analysis can have marked effects on the resulting cladogram topologies, and cautioned their use in taxonomy. As characters of the postcranial skeleton are starting to be used in analysis of temnospondyl relationships (Yates & Warren 2000; Ruta *et al.* 2003a; Ruta *et al.* 2003b), it is important that the characters chosen are not simply separating immature specimens from more mature specimens.

The paedomorphic status of many temnospondyls means that some character states that develop with ontogeny may not be present in specimens of a taxon due to the immature morphology of even the largest and presumably most mature specimens available. This presents problems for cladistic analysis. An example of a character used in phylogenetic analysis of temnospondyls (e.g. Yates & Warren 2000; Ruta *et al.* 2003a) is the absence (plesiomorphic state) or presence (derived state) of a supinator process of the humerus. These analyses considered that the sporadic distribution of the derived state was due to homoplasy. The evidence presented in this study instead indicates that it may be more parsimonious to suggest that the emergence of the derived state, shown above to be present only in the largest specimens of some taxa, is a fulfilment of ontogenetic potential rather than convergent evolution. Careful analysis of growth series is necessary to determine other characters affected by ontogeny. A further implication is that some postcranial character states may be universally present within the Temnospondyli, but unexpressed in the majority of taxa due to their immature morphology.

CONCLUSIONS

The postcranial skeleton of SAM-PK-K10021 represents an immature ontogenetic stage of a taxon that retains a paedomorphic postcranial morphology throughout its life. As a rhinesuchid, SAM-PK-K10021 contributes to our knowledge of ontogenetic changes of the postcranial skeleton among temnospondyls. Determination of the paedomorphic status of the postcranial skeleton among temnospondyls is most feasible through comparison with well-ossified taxa. The use for cladistic purposes of characters affected by ontogeny is cautioned.

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ABBREVATIONS

Institutional

BP:	Bernard Price Institute, Johannesburg, South Africa;
M:	Field abbreviation of the Council of Geosciences, Pretoria, South Africa;
NMQR:	National Museum at Bloemfontein, Bloemfontein South Africa;
SAM:	South African Museum, Cape Town, South Africa;
TM:	Transvaal Museum, Pretoria, South Africa.

Anatomical

adb	adductor blade
adc	adductor crest
ahk	anterior humeral keel
apr	anterior popliteal ridge
boc	basioccipital
cgr	clavicular groove
cl	clavicle
cth	cleithrum
dcthp	dorsal cleithral process
dlcr	dorsolateral cleithral ridge
dcp	deltopectoral crest
ect	ectepicondyle
eo	exoccipital
fcs	falciform crest of squamosal
fem	femur
ffo	fibula fossa
fsgl	supraglenoid foramen
gast	gastralia
hum	humerus
ic	intercentrum
icf	intercondylar fossa
icl	interclavicle
itf	intertrochanteric fossa
intr	internal trochanter
lsr	lateral supraglenoid ridge
lss	suprascapular lamina
meta	metapodial
na	neural arch
of	otic flange
pf	pectinate fringe
pir	posterior intertrochanteric ridge
phal	phalange
phr	proximal humeral ridge
ppa	popliteal area
ps	parasphenoid
pt	pterygoid
qj	quadratojugal
scap	scapula
sfcs	scapular flange of cleithral shaft
sgb	supraglenoid buttress
sgf	supraglenoid fossa
sq	squamosal
tp	transverse process
tr4	fourth trochanter
vs	ventral scales

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A traversodontid cynodont of African affinity in the South American Triassic

F. Abdala[1*] **& A.M. Sa-Teixeira**[2]

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

[2]*Rua São Luis 600, 90.620-170, Porto Alegre, RS, Brazil*

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The Traversodontidae represent one of the most diverse and abundant families of non-mammaliaform cynodonts, particularly in Gondwanan faunas of Middle to Late Triassic age. Although a great diversity of traversodontids is known for South American (approximately nine species) and African (six to seven species) Triassic faunas, the record of the group in these continents does not show similarities beyond the family level. Here we describe a new traversodontid, *Luangwa sudamericana,* from the Santa Maria Formation of southern Brazil, which is most similar to the Anisian traversodontids *Luangwa drysdalli* from the upper portion of the Ntawere Formation in Zambia, and *Scalenodon angustifrons* from the Manda Formation in Tanzania. Features in common with these African taxa are oval-outlined upper postcanines presenting an anterior labial cingulum. The new species is similar to *L. drysdalli* in a number of features, including the presence of a posterior cingulum in the upper postcanines, anterior cingulum in front of the transverse crest in the lower postcanines, short snout, enormous orbits and short temporal region. Differences with *L. drysdalli* are the less developed posterior cingulum behind the upper transverse crest that does not extend along the entire posterior border of the tooth, and the presence of a well-defined posterior accessory cusp on the sectorial crest of the upper postcanines. The comparison of the quadrate, preserved *in situ* in the squamosal notch of the new taxon, and that from other traversodontids, suggests that the quadratojugal is involved in the formation of the lateral condyle of the traversodontid suspensorium. *Luangwa* represents the first genus of traversodontid, and the second of non-mammaliaform cynodont shared by South American and African faunas. A significant biochronological implication of this finding is that part of the Santa Maria Formation may now be considered Anisian in age, and thus older than generally recognized for the unit.

Keywords: Traversodontidae, Middle Triassic, Brazil, Zambia, Cynodontia, *Luangwa.*

INTRODUCTION

The southern Brazilian Santa Maria Formation is well known for its record of an important continental Triassic vertebrate fauna. Pioneering studies in this unit were performed by Friedrich von Huene, a German palaeontologist who in 1928 conducted a six-month field trip to various localities in the Rio Grande do Sul State, southern Brazil. Huene discovered and published many species of tetrapods, including *Gomphodontosuchus brasiliensis*, the first traversodontid cynodont ever described (Huene 1928; Hopson 1985). He later identified other species of the Traversodontidae in his seminal work on the Brazilian Triassic reptile fauna (Huene 1936). Barberena (1974, 1981a,b) reinterpreted some of the traversodontid materials previously studied by Huene (1936) and, based on new discoveries, described new species of this group (Barberena 1981a).

Many traversodontid species have been described from Triassic faunas from Brazil and Argentina (Bonaparte 1982; Abdala *et al.* 2002) and genera such as *Massetognathus* (Romer 1967; Barberena 1981a; Abdala & Giannini 2000) and *Exaeretodon* (Bonaparte 1962; Abdala *et al.* 2002) were recognized from Ladinian and Carnian faunas of both countries. This family is also well diversified in Triassic deposits of Africa (including Madagascar), where it is represented by six to seven species (Crompton 1955; Brink 1963; Kemp 1980; Gow & Hancox 1993; Flynn *et al.* 2000). Despite this relatively high diversity of the group in South America and Africa, the faunas of these continents do not show similarities beyond the family level, with the carnivorous *Cynognathus* being the only genus evidencing faunal commonality between these continents. This taxon has been recorded in the fauna biostratigraphically known as the *Cynognathus* Assemblage Zone, from strata of the Burgersdorp Formation, Karoo Basin, South Africa (Kitching 1995; Hancox 2000), and in the Puesto Viejo Formation, Argentina (Bonaparte 1969; Abdala 1996).

In this report, we describe *Luangwa sudamericana* sp. nov. from the Santa Maria Formation of southern Brazil. One of the specimens included in the new species (UFRGS 267PV) was previously described as *Luangwa* sp. by Teixeira (1995). The new species is most similar to *Luangwa drysdalli* from the upper beds of the Ntawere Formation, Zambia, and to *Scalenodon angustifrons* from the Manda Formation, Tanzania, in eastern central Africa (Crompton 1955, 1972; Brink 1963; Kemp 1980), and thus demonstrate traversodontids of African affinity in the South American Middle Triassic. This finding also has important chronological implications, because both the Manda Formation and the upper portion of the Ntawere Formation are considered Anisian in age (Cox 1991; Battail 1993), and, as a consequence, some of the outcrops of the Santa Maria Formation in southern Brazil could be older than the Ladinian age usually recognized for its oldest fauna.

Institutional abbreviations. BP: Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; MCP: Museo de Ciências e

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

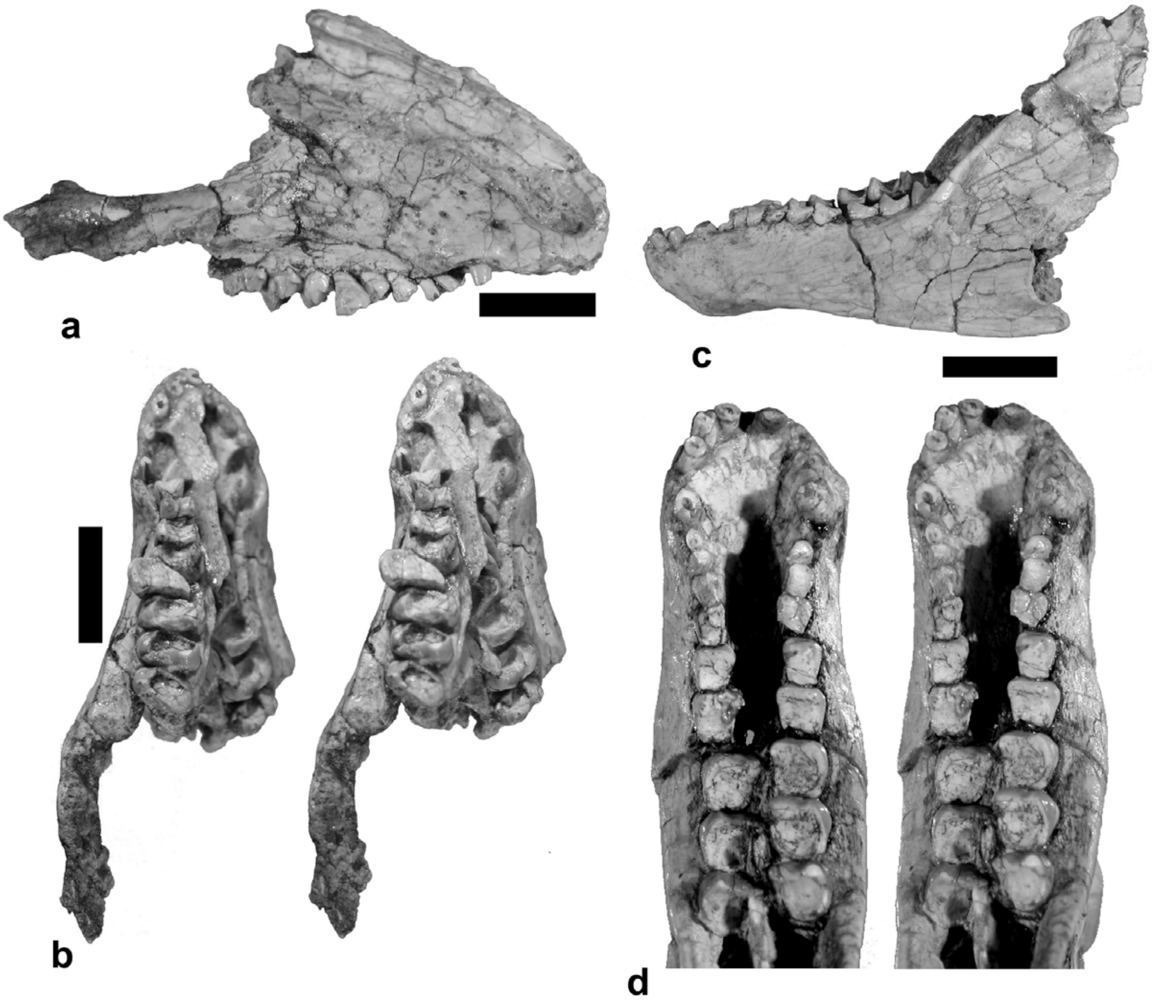

Figure 1. *Luangwa sudamericana,* holotype (MCP 3167PV); **a**, lateral view of snout; **b**, stereopair of upper dental series; **c**, lateral view of mandible; **d**, stereopair of lower dental series. Scale bars = 20 mm.

Tecnología, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachussets; NMQR: National Museum, Bloemfontein; OUMNH: Oxford University Museum of Natural History; SAM: South African Museum, Cape Town; UFRGS: Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Porto Alegre; UMZC, University Museum of Zoology, Cambridge.

SYSTEMATIC PALAEONTOLOGY

Therapsida Broom 1905
Eucynodontia Kemp 1982
Traversodontidae von Huene 1936
Luangwa Brink 1963

***Luangwa sudamericana* sp. nov.**, Figs 1–5

Etymology. Sudamericana refers to the first record for South America of a genus of Traversodontidae previously known only in east Africa.

Holotype. MCP 3167PV, a well-preserved partial skull and mandible. The skull includes the rostrum and rim of the right orbit, with complete dentition, and an isolated portion of the basicranium, and the most posterior portion of the zygoma, including the quadrate *in situ* (Figs 1, 4 & 5).

Referred material. UFRGS 267PV, a well-preserved partial skull and a fragment of the left lower jaw with three postcanines (Figs 2 & 3).

Horizon and locality. Santa Maria Formation, Middle to Upper Triassic. Specimen MCP 3167PV is from an unknown locality; specimen UFRGS 267PV comes from an unknown outcrop located on the border between the districts of Candelaria and Vera Cruz, Rio Grande do Sul State, Brazil. Many outcrops are present in this area, and recent field trips to the various outcrops yielded only fragmentary remains. Thus, the exact locality remains uncertain.

Comparative material. BP/1/3731, skull with articulated mandible and some postcranial bones, probably of the manus, attached to the snout; holotype of *Luangwa drysdalli* (Brink 1963; Fig. 6); BP/1/3733, poorly preserved anterior portion of the skull with dentition. Specimen smaller than the type, most likely a juvenile of the same species; OUMNH TSK121, partial skull with mandible (Fig. 7) and postcranial elements assigned to *Luangwa drysdalli* by Kemp (1980). These specimens come from outcrops of the upper beds of the Ntawere Formation in the Luangwa Valley, Zambia (Drysdall & Kitching 1963; Kemp 1975).

UMZC T.907, partial skull with lower jaw, holotype of *Scalenodon angustifrons* (Parrington 1946; Crompton 1955;

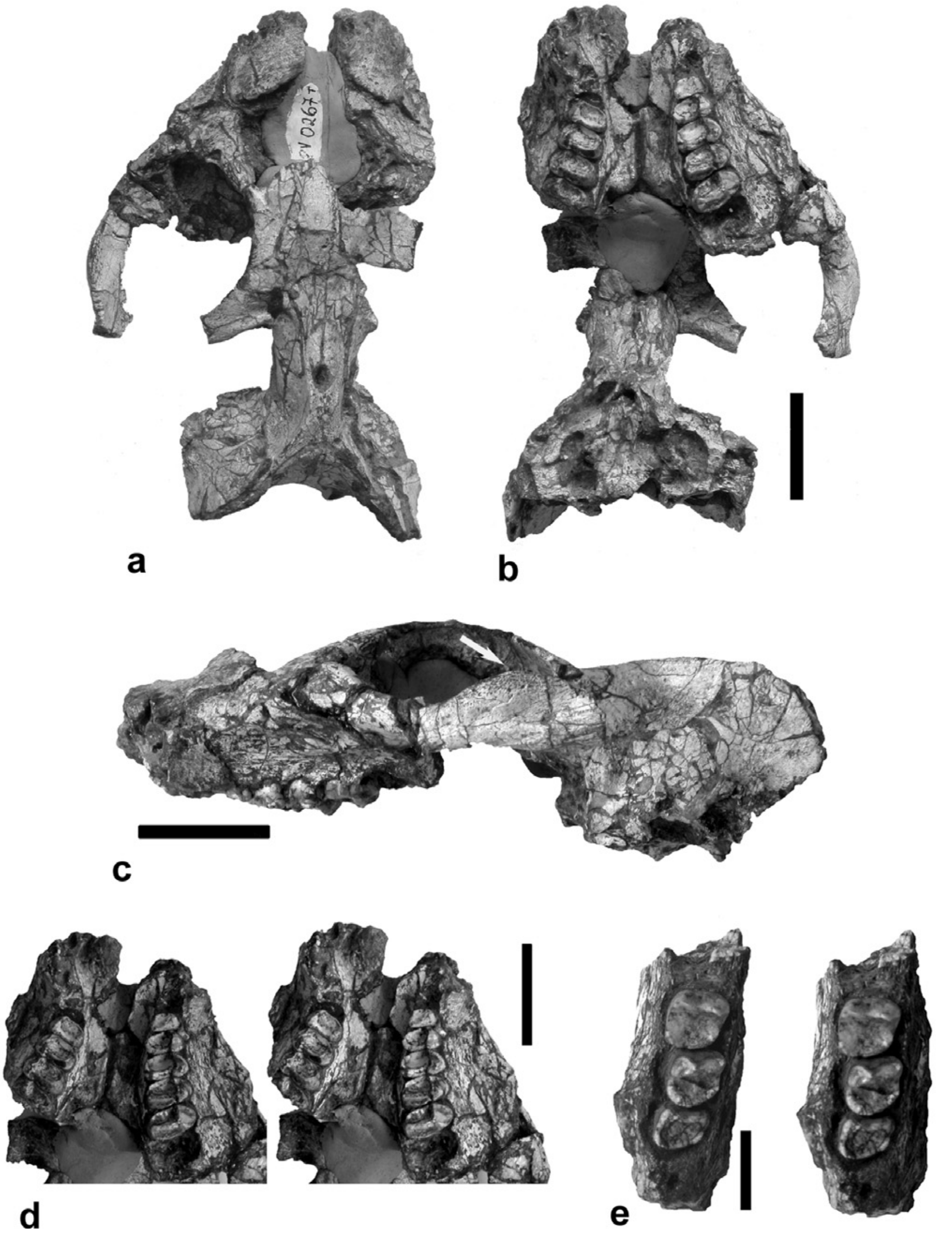

Figure 2. *Luangwa sudamericana,* UFRGS 267PV; **a**, dorsal, **b**, ventral and **c**, left lateral views of skull; **d**, stereopair of the upper postcanines; **e**, stereopair of lower postcanines. Scale bars = 20 mm (a, b, c, d) and 10 mm (e).

Fig. 8a,b); UMCZ T.908; T.909; T.910; T.911; T.912; T.913; T.914; T.915; T.916; T.917; T.918. All these specimens are skull and/or lower jaw fragments, with UMCZ T.910 showing the best-preserved upper and lower postcanines (Fig. 8c,d). They come from the locality B 29 of Stockley (1932), between Gingama and Tschikonge, Ruhuhu Valley, Tanzania and were described by Crompton (1955) as *S. angustifrons.*

Diagnosis

A traversodontid most similar to *Luangwa drysdalli* Brink 1963 and *Scalenodon angustifrons* (Parrington 1946). As in these species the upper postcanines are oval-outlined and feature an anterolabial cingulum. As in *L. drysdalli* the new species has a posterior cingulum with tiny cuspules behind the transverse crest of the upper postcanines, but less developed in *L. sudamericana* where it does not extend along the entire posterior border of the tooth. It also has tiny cuspules in front of the anterior transverse crest of the lower postcanines forming an incipient cingulum. Other similarities with *L. drysdalli* include a short snout and temporal region, large orbits and angle of the dentary slightly projected posteriorly. Differentiating *L. sudamericana* from *L. drysdalli* and *S. angustifrons* is a well-defined posterior accessory cusp on the labial crest of the upper postcanines. The presence of one anterior accessory cusp on the labial (sectorial) crest of the upper postcanines is a difference with the holotype of *L. drysdalli* (BP/1/3731), but not with OUMNH TSK 121.

Description

Specimen MCP 3167PV preserves the snout and part of the right orbit, while UFRGS 267PV is an almost complete skull, lacking the anterior and dorsal part of the snout, and showing an incomplete right orbit and temporal region on both sides. The snout is notably short, while the orbits

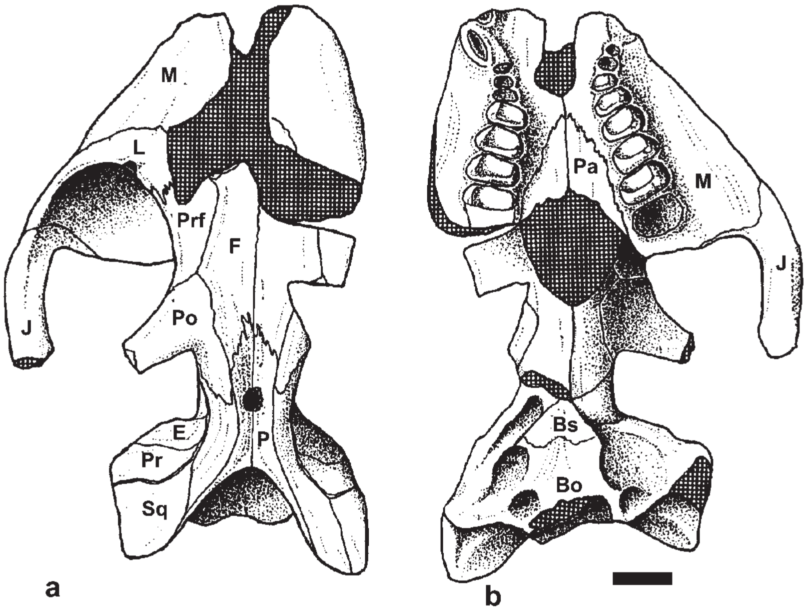

Figure 3. *Luangwa sudamericana,* UFRGS 267PV; **a**, dorsal and **b**, ventral view of skull. Abbreviations: Bo, baisoccipital; Bs, basisphenoid; E, epipterygoid; F, frontal; J, jugal; L, lacrimal; M, maxilla; P, parietal; Pa, palatine; Po, postorbital; Pr, prootic; Prf, prefrontal; Sq, squamosal. Scale bar = 10 mm.

are large in both specimens (Figs 1a, 2a, 3a). A well-developed ascending process of the premaxilla is present in MCP 3167PV (Fig. 1a). The right maxilla in the specimen is displaced from its original position, and the vertical vomer separating the nasal canals is visible. The maxillary labial platform is well developed in UFRGS 267PV (Figs 2b, 3b) and seems to be comparatively less developed in MCP 3167PV, but deformation in the specimen prevents certainty of the platform's original extent (Fig. 1b). The temporal region is remarkably short in UFRGS 267PV,

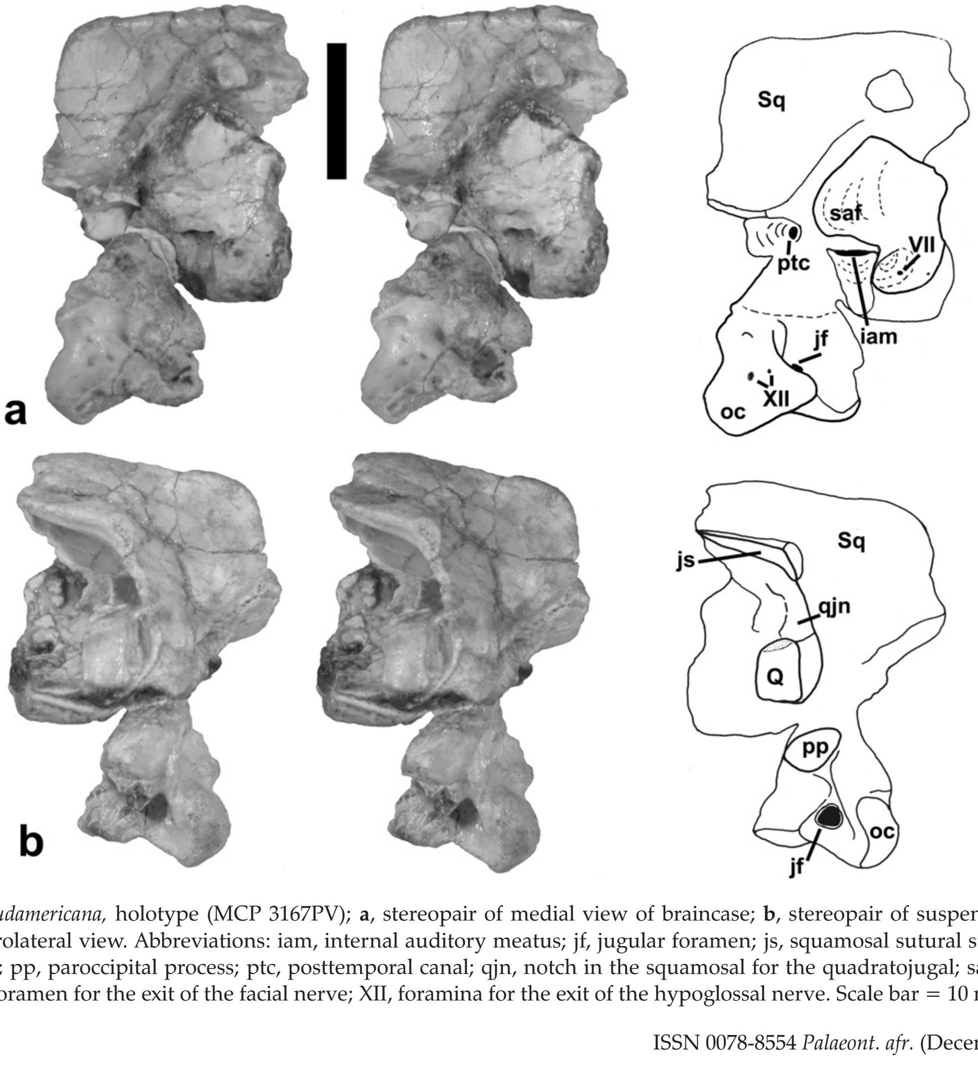

Figure 4. *Luangwa sudamericana,* holotype (MCP 3167PV); **a**, stereopair of medial view of braincase; **b**, stereopair of suspensorium and part of basicranium in ventrolateral view. Abbreviations: iam, internal auditory meatus; jf, jugular foramen; js, squamosal sutural surface for the jugal; oc, occipital condyle; pp, paroccipital process; ptc, posttemporal canal; qjn, notch in the squamosal for the quadratojugal; saf, subarcuate fossa; Sq, squamosal; VII, foramen for the exit of the facial nerve; XII, foramina for the exit of the hypoglossal nerve. Scale bar = 10 mm.

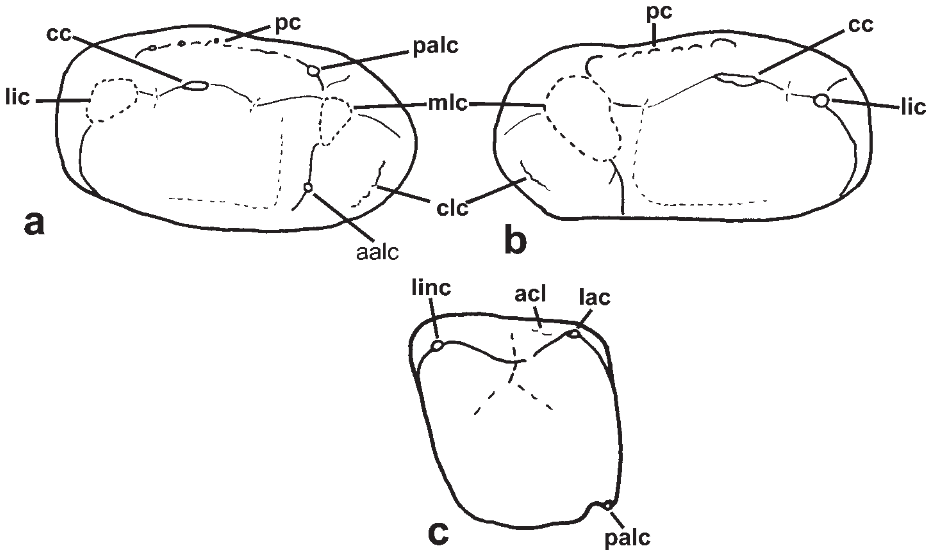

Figure 5. Postcanines of *Luangwa sudamericana,* MCP 3167PV; **a**, occlusal view of eighth upper right postcanine with some traits added considering also the ninth tooth (labial, right; anterior, bottom); **b**, occlusal view of ninth upper left postcanine (labial, left; anterior, bottom); **c**, occlusal view of seventh lower right postcanine (labial, right; anterior, top). The anterior cingulum represented in figure (**c**) was observed in UFRGS 267PV; Abbreviations: aalc, anterior accessory labial cusp; acl, anterior cingulum of the lower postcanines; cc, central cusp; clc, cingular labial crest; lac, labial cusp; lic, lingual cusp; linc, lingual cusp of the lower postcanine; mlc, main labial cusp; palc, posterior accessory labial cusp; pc, posterior cingulum.

displaying a wide parietal crest with the pineal foramen in the middle of the extension of the crest (Figs 2a, 3a). A slight ventral projection of the broken ventral edge of the zygomatic arch below the orbit in MCP 3167PV (Fig. 1a), suggests the presence of a descendant process of the jugal. This is confirmed in UFRGS 267PV where a portion of the right zygomatic arch was mistakenly glued upside down to the left side. The 'dorsal' border of the zygoma shows an extended and convex descendant process (arrow in Fig. 2c).

In the left cranio-mandibular joint region of MCP 3167PV, the squamosal accommodates the quadrate and shows a deep notch for the quadrato-jugal. Close to this notch, the squamosal shows a ventromedial surface for articulation with the posterior extension of the jugal (Fig. 4b). Another small surface on the posterior extremity of the squamosal appears to be for supplementary articulation with the surangular of the lower jaw. The posterior portion of the squamosal sulcus behind the quadrate is shallow compared with that of BP/1/3731. In anterior view, the quadrate shows a high dorsal plate directed dorso-laterally, ending in a pointed dorsal angle. The trochlea is wide anteroposteriorly (Fig. 4b), slightly convex ventrally, and the medial trochlear condyle is not medially projected from the body of the quadrate. The lateral condyle and the quadrato-jugal are not preserved.

A small portion of the lateral wall of the skull, corresponding to the prootic, is preserved medial to the

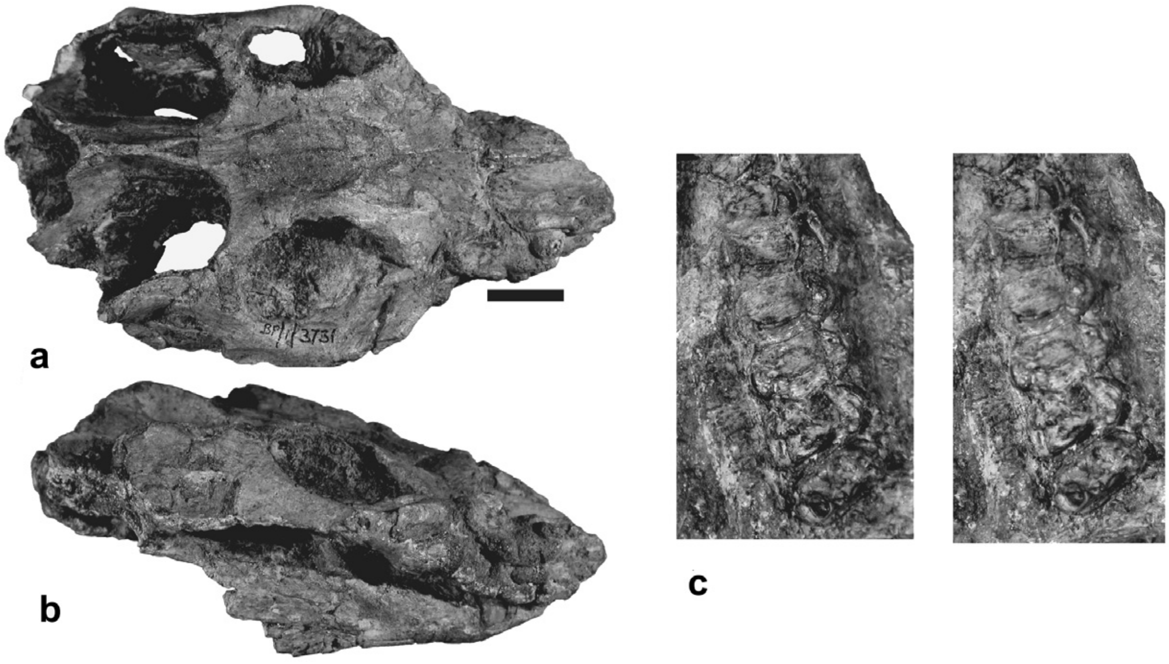

Figure 6. *Luangwa drysdalli* holotype (BP/1/3731); **a**, dorsal, **b**, right lateral view of skull; **c**, stereopair of left upper postcanine series. Scale bar = 20 mm.

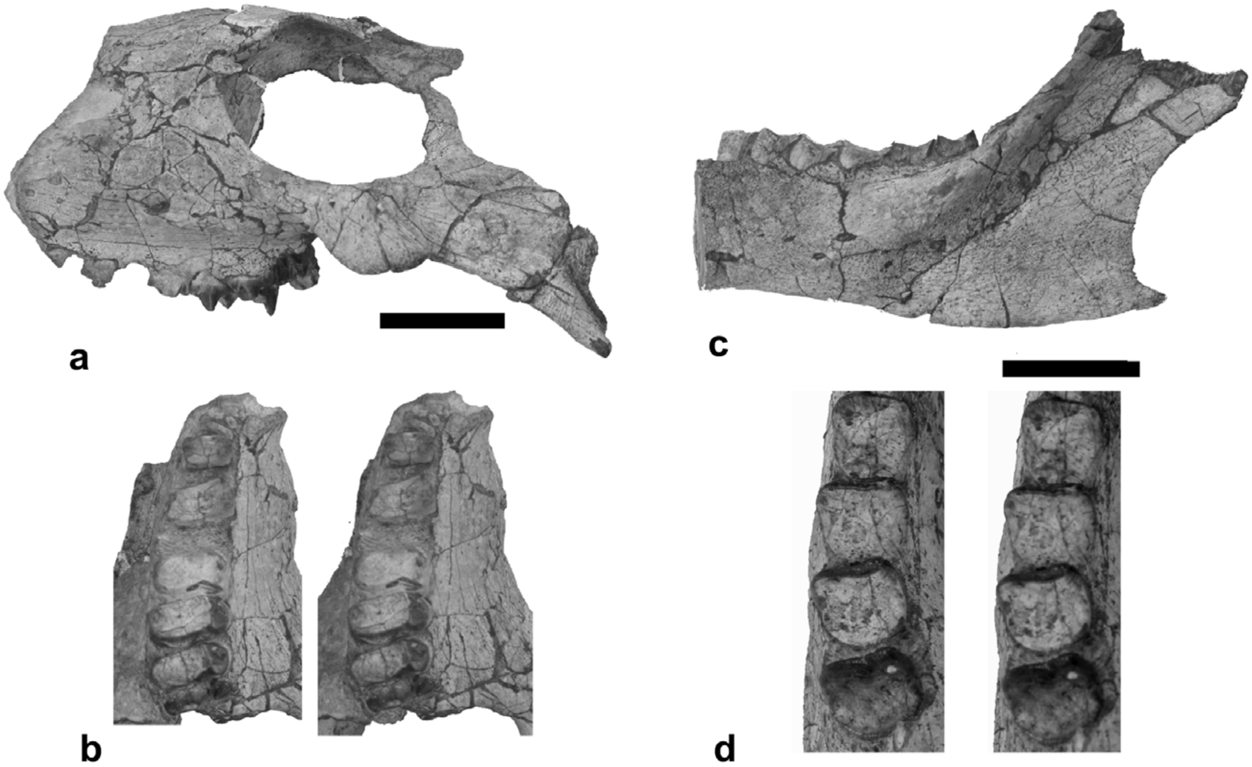

Figure 7. *Luangwa drysdalli,* OUMNH TSK121; **a**, left lateral view of snout and orbit; **b**, stereopair of left upper postcanine series; **c**, lateral view of the left mandibular ramus; **d**, stereopair of the four last right lower postcanines. Scale bars =20 mm

zygomatic process of the squamosal. Only the inner part of the wall is visible (Fig. 4a), with the fossa subarcuata, separated from the internal auditive meatus by a strong horizontal ossification. There exists a high vertical crest that separates the internal auditive meatus from a recess containing a foramen, probably for the facial nerve (VII). Part of the left basicranium, including the occipital condyle and paroccipital process, is also preserved (Fig. 4). Immediately above the condyle is a swelling probably for articulation with the proatlas, while medially there are two foramina for the hypoglossal nerve (XII). The paroccipital process is well developed with its distal end ventrally directed, and without division into anterior and posterior processes.

The dental formula in MCP 3167PV is 4/3 incisors, 1/1 canine and 9-10/8-9 postcanines, while 7–8 upper postcanines are present in UFRGS 267PV. Most of the upper incisors are broken, with the roots showing that the first, second and fourth are rounded in outline, while the third is more ellipsoid (Fig. 1b). The crown of the left third incisor is partially preserved, being canine-like, with a thick enamel layer labially that seems to be absent lingually. Faint denticulations are present on the posterior edge of this tooth, while the anterior edge appears to be smooth. A small diastema exists between the fourth incisor and the canine, the paracanine fossa being anteromedial with respect to the upper canine (Fig. 1b). This tooth is ellipsoid and is erupting on both sides. The enamel layer covers the canine both labially and lingually, and well-developed serrations are present on its anterior and posterior edges. The upper postcanines are ovoid in outline, and increase progressively in size posteriorly (Figs 1b; 2b,d; 3b). Shouldering (i.e. the anterolabial border of the upper postcanine extending forward, and producing a 'shoulder'-like process on the preceding tooth) is absent and the tooth series diverge slightly posteriorly (Figs 2b,d; 3b). The six anterior teeth in MCP 3167PV are badly worn, and the original structure of the postcanines can be seen in the posterior elements of the row (Fig. 5a,b). A main labial cusp, located posteriorly, and smaller anterior and posterior accessory cusps form the sectorial crest of the postcanine, which is positioned medially with respect to the labial border of the crown. A cingular crest occurs antero-labially, lateral to the anterior accessory cusp. Three cusps form a transverse crest of the tooth: a main labial cusp, a wide central cusp and a closely positioned small lingual cusp (Fig. 5a,b). The crest is situated near the posterior border of the tooth and a poorly developed posterior cingulum exists behind it.

The mandible displays a fused symphysis, a well-developed ascending ramus that partially covers the last postcanine in lateral view, and an incipient backward-projected angle of the dentary (Fig. 1c). The masseteric fossa in the dentary extends anteriorly to the level of the sixth or seventh postcanine. The lower incisors are roughly circular (Fig. 1d), and a thick enamel layer apparently disposed only laterally, is observed on the second left tooth. A reduced diastema is present between the third incisor and the canine. The canine is oval-shaped, slightly larger than the incisors, and covered by enamel both labially and lingually. It is not possible to see whether serrations occur on its edges. There is no diastema between the canine and the first postcanine. As in the upper series, the six anterior postcanines are badly worn (Fig. 1d). The last ones show the anterior crest formed by a wide lingual cusp and a narrow, taller labial one (Fig. 5c). An accessory labial cusp is present on the

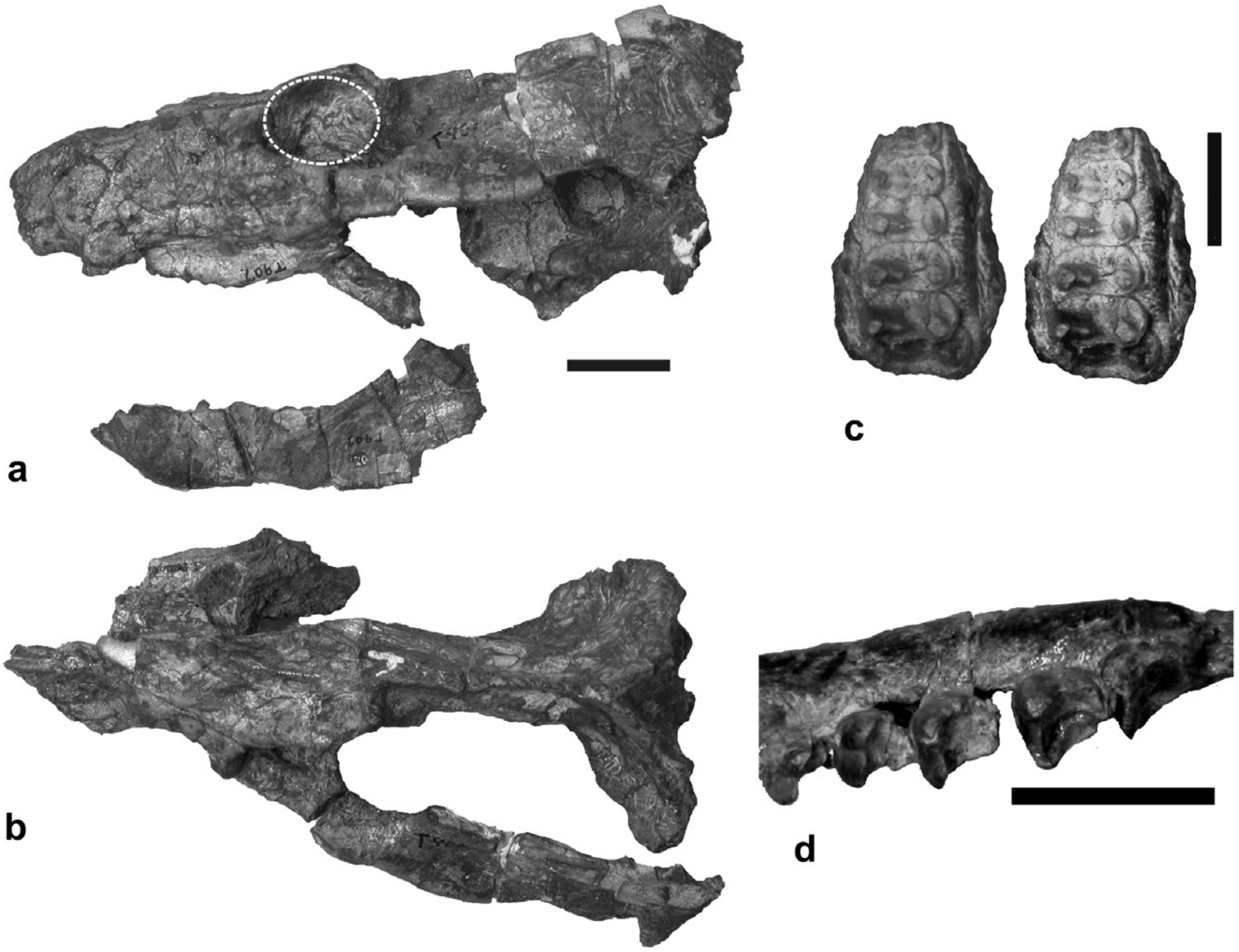

Figure 8. *Scalenodon angustifrons*; **a**, lateral view of the skull and mandible of holotype (UMCZ T.907), with the orbit outlined; **b**, dorsal view of the same skull; **c**, stereopair of left upper postcanine series (UMCZ T.910); **d**, dorsolateral view of right lower postcanine series (UMCZ T.910). Scale bars = 20 mm (a, b) and 10 mm (c, d).

posterior border of the tooth. There is no indication of an anterior cingulum in front of the transverse crest in MCP 3167PV, but two tiny cuspules occur anterior to the labial cusp of the transverse crest in the most anterior lower postcanine preserved in UFRGS 267PV (Figs 2e, 5c).

DISCUSSION

Two species of Anisian traversodontid from east Africa, *Luangwa drysdalli* from the Upper Ntawere Formation and *Scalenodon angustifrons* from the Manda Formation, appear to be more similar to the new South American traversodontid. These African species were proposed as co-generic by Battail (1991), but two recent phylogenetic analyses suggest that they do not form a monophyletic group (Hopson & Kitching 2001; Abdala & Ribeiro 2003).

Skull features of *L. sudamericana* similar to *L. drysdalli* - include a short snout, enormous orbits, and a short temporal region, while the lower jaw displays a high coronoid process with its antero-dorsal edge strongly reflected laterally, and the angle of the dentary slightly projected posteriorly from the ventral edge (Figs 1, 2, 3, 6 & 7). Proportions of the skull regions in *S. angustifrons* (UMCZ T.907) are different, with comparatively less developed orbits, longer snout and particularly longer temporal region (Fig. 8a,b). The lower jaws in the sample of *S. angustifrons* at the UMCZ are poorly preserved and not complete enough to allow a close comparison. The only specimen of *S. angustifrons* with an almost complete skull is the holotype (UMCZ T.907, Fig. 8a,b; see also Parrington 1946: fig. 8). The skull length is estimated at 13 cm and it bears nine postcanine alveoli. Considering the growth series proposed for the species by Crompton (1955: fig. 12), the maximum number of postcanines attained in specimens somewhat larger than the holotype is eleven. The holotype of *L. drysdalli,* approximately the same size as the *S. angustifrons* holotype (see Table 1), presents seven postcanines, while the specimen described by Kemp (1980) is somewhat larger than the holotype and features nine postcanines. The two individuals of the new Brazilian species are small compared to *L. drysdalli* (see Table 1), but present the same number of upper postcanines (between seven and nine).

The incisors of the new Brazilian taxon show some common traits with the African species, such as thick external enamel layer, while lingually this layer is thin in *Luangwa drysdalli* (Kemp 1980) and *S. angustifrons* (F. Abdala, pers. obs.), and absent in *L. sudamericana.* Incisors lacking enamel lingually were also reported in the Carnian traversodontid *Exaeretodon* (Chatterjee 1982; Abdala *et al.* 2002). *L. sudamericana* features serrated edges, weak on the incisors and more developed on the canines. Serrated edges are present on incisors and canines of

Table 1. Measurements (in mm) of *Luangwa* specimens.

	MCP 3167PV	UFRGS 267PV	BP/1/3731	OUMNH TSK121
Basal length of the skull		*94	136	
Dorsal length of the skull, to end of the parietal crest		*86	126.3	
Snout length	50.2	*32	60	
Length from the tip of the snout to the posterior border of the orbit		*65	93.9	
Orbital region length		22.9	38.7	
Length of the row of upper postcanines	33.6	33.7	38.6	41.1
Length from the anterior tip of the dentary to the articular process	*84.3		116.5	
Length from the anterior tip of the dentary to the angle	69.6		*88	94.2
Maximum vertical height of dentary	*53.9		*58.2	59.1
Height of dentary at anterior postcanines	13		15.7	19
Length of the row of lower postcanines	37.9/35.2			49.1

*Estimated.

S. angustifrons (Crompton 1955) and are also described for incisors of *L. drysdalli* (Kemp 1980). The holotype of the latter species shows serrated edges on the tips of the emerging canines (F. Abdala, pers. obs.). Other traversodontids from the Manda Formation, such as *'Scalenodon' hirschsoni* and *'S.' attridgei,* present instead smooth-edged incisors and canines (Hopson & Kitching 2001; F. Abdala, pers. obs.).

In the upper postcanines the new species is comparable to *L. drysdalli* and *S. angustifrons* in that the general outline of the teeth is somewhat ovoid, with the labial border slightly longer anteroposteriorly than the lingual border (Fig. 9a,b,e). This outline resembles the pattern of the teeth of *Diademodon* and the trirachodontid *Cricodon* (Crompton 1955, 1972), and is different from the more rectangular or trapezoidal teeth observed in late traversodontids (e.g. *Massetognathus, Exaeretodon,* contra Abdala & Ribeiro 2003: character 7). The external cingulum lateral to the anterior accessory cusp, recorded for the first time in a South American traversodontid, is also known in

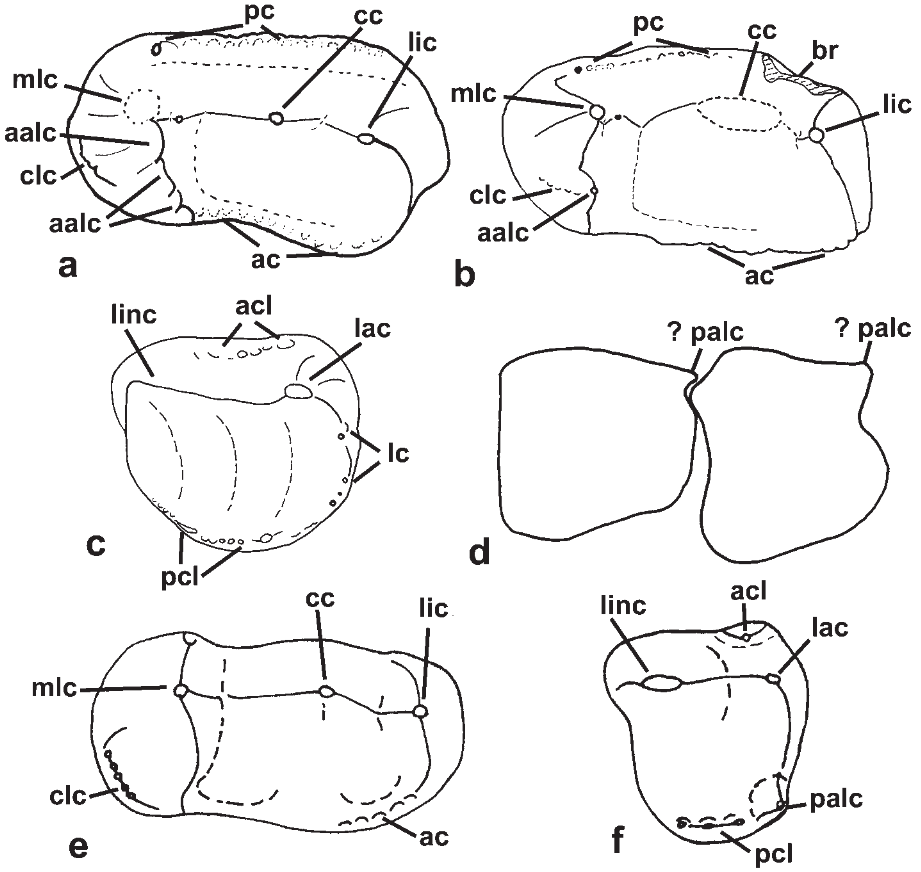

Figure 9. **a**, *Luangwa drysdalli,* BP/1/3731; occlusal view of last (seventh) left upper postcanine (labial, left; anterior, bottom); **b**, *Luangwa drysdalli,* OUMNH TSK121, occlusal view of last (ninth) left upper postcanine (in eruption process); hatching and 'br' indicate broken surface (labial, left; anterior, bottom); **c**, *Luangwa drysdalli,* OUMNH TSK121, occlusal view of last right lower postcanine (labial right, anterior up); **d**, *Luangwa drysdalli,* OUMNH TSK121, outline of lower right postcanines sixth and seventh to show the suggested posterior accessory labial cusps (labial up, anterior left); **e**, *Scalenodon angustifrons,* occlusal view of left upper postcanine; **f**, *Scalenodon angustifrons,* occlusal view of right lower postcanine. Abbreviations: aalc, anterior accessory labial cusp; ac, anterior cingulum; acl, anterior cingulum of the lower postcanines; cc, central cusp; clc, cingular labial crest; lac, labial cusp; lc, labial cingulum; lic, lingual cusp; linc, lingual cusp of the lower postcanines; mlc, main labial cusp; pc, posterior cingulum; pcl, posterior cingulum of the lower postcanines. Figures (e) and (f) from Crompton (1972).

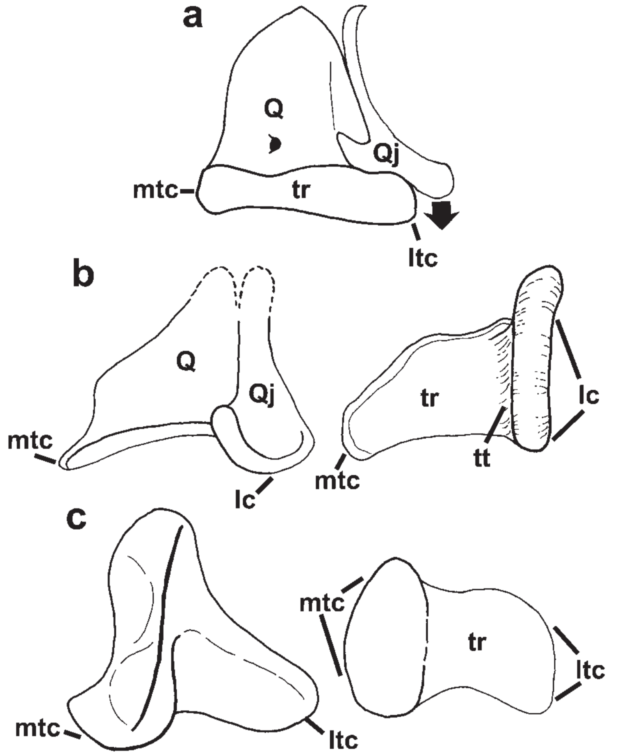

Figure 10. **a**, Anterior view of left quadrate/quadratojugal of *Thrinaxodon* (modified from Luo & Crompton 1994); **b**, anterior and anteroventral view of the left quadrate/quadratojugal of *Massetognathus.* In the anteroventral view the dorsal process of the quadrate was omitted (modified from Luo & Crompton 1994); **c**, anterior and ventral view of the left quadrate of *Lystrosaurus* (modified from Cluver 1971). Abbreviations: ltc, lateral trochlear condyle; lc, lateral condyle; mtc, medial trochlear condyle; Q, quadrate; Qj, quadratojugal; tr, trochlea; tt, trochlear trough. Arrow in (a) indicates the downward extension of the quadratojugal hypothesized to have produced the lateral condyle in *Massetognathus* (b).

L. drysdalli, S. angustifrons and in the recently described traversodontid *Dadadon isaloi* from Madagascar (Flynn *et al.* 2000; Abdala & Ribeiro, 2003). Others features of the upper postcanines of the new traversodontid similar to *L. drysdalli,* are the anterior accessory cusp on the labial crest, and the posterior cingulum with tiny cuspules behind the transverse crest (Figs 5a,b; 9a,b). Poorly developed anterior and posterior cingula were also described for *S. angustifrons,* probably based on specimen UMCZ T.910 (Crompton 1972, but see Crompton 1955). However, F.A. was not able to recognize cuspules or crenulations on the edges of the specimen at first hand examination. As in *L. drysdalli* and other traversodontids (e.g. *'Scalenodon' attridgei*: Crompton 1972: Plate 6; *Scalenodontoides macrodontes*: Gow & Hancox 1993: fig. 2), the upper tooth series curves slightly postero-laterally (Figs 2b, 3b). Features of the upper postcanines in *Luangwa drysdalli* not observed in the Brazilian material include: the presence of four cusps on the transverse crest, with a small cusp between the central and external cusps (Fig. 9a,b). The posterior cingulum in *L. sudamericana* is less developed and extends partially on the posterior border of the teeth (compare Figs 5a,b with 9a). Some traits of the upper postcanines are different in the two specimens of *Luangwa drysdalli.* BP/1/3731 presents four anterior accessory labial cusps in the last left upper postcanine, the only well preserved tooth in the specimen (Fig. 9a). In contrast, OUMNH TSK121 features one anterior accessory cusp (Fig. 9b; Kemp 1980), the same condition that characterizes *L. sudamericana* (Fig. 4a,b).

The lower postcanines of *L. sudamericana* (UFRGS 267PV) present a cingulum comprising two minute cuspules in front of the anterior transverse crest, while in *L. drysdalli* the cingulum is composed of many tiny cuspules (Fig. 9c; Kemp 1980) and a comparatively larger cusp in *S. angustifrons* (Fig. 9f). This anterior cingulum is also present in *'S.' hirschsoni* where the single cusp is extremely robust (Crompton 1972), and in the South American traversodontid *Andescynodon mendozensis* (Goñi & Goin 1988). The new species shows a narrow labial cusp and a transversely wide lingual cusp on the anterior transverse crest (Figs 1d, 5c), a trait also present in *Scalenodon angustifrons* (Figs 8d, 9f). It also has a well-differentiated accessory cusp on the postero-labial border of the tooth, a feature also present in *S. angustifrons* (Fig. 9f), *'S.' hirschsoni, Massetognathus* (Crompton 1972) and, apparently, in *L. drysdalli* (Fig. 9d, but see Fig. 9c). The absence of additional cusps on the sectorial border of the lower tooth is common to the new species and *S. angustifrons,* while *L. drysdalli* can present additional cusps, apart from the posterior one (Fig. 9c,f).

The quadrate morphology in traversodontid cynodonts

The quadrate in *L. sudamericana* is similar to that of *Massetognathus,* in the presence of a large, laterally directed dorsal plate ending in a pointed dorsal angle, and of an anteroposteriorly extended trochlea, (see Figs 4b, 10b). The dorsal plate is directed dorsally in *Procynosuchus* and *Thrinaxodon* (Fig. 10a) and slightly laterally in *Probainognathus,* while the trochlea is cylindrical in most non-mammaliaform cynodonts and in *Morganucodon* (Luo & Crompton 1994). Distinctive features in *Massetognathus* are the strong fusion of the quadratojugal with the quadrate, the presence of an anteroposteriorly elongated trochlea and a ventrally projected lateral condyle that limits externally the anteroposteriorly running trochlear trough (Fig. 10b; Luo & Crompton 1994). Besides *Massetognathus* and *L. sudamericana,* an anteroposteriorly-elongated trochlea is also present in the traversodontid *Exaeretodon* (Allin 1975: fig. 21). In addition, the latter genus also shows a well-developed ventrally projected lateral condyle delimiting the trochlear trough (MCZ 4493), a trait that is incipient in the carnivorous cynodont *Cynognathus* (NMQR 1444, SAM-PK-11264). When describing the suspensorium of the traversodontid *Massetognathus,* Luo & Crompton (1994: 348–349) interpreted the quadratojugal as fused to the dorsal plate of the quadrate, and the ventrally projected lateral condyle as produced by the quadrate trochlea. In *L. sudamericana* the quadratojugal is missing, and the trochlear trough and the lateral condyle are absent. This condition suggests that the quadratojugal was probably ventrally projected, fused at the level of the quadrate trochlea, and thus formed part of the trochlear trough and the lateral condyle. This is in agreement with the ventral location of the horizontal section of the quadratojugal in close apposition to the trochlear portion of the quadrate in

Thrinaxodon (Fig. 10a). In this scenario, the lateral trochlear condyle of *Thrinaxodon* and many other cynodonts would not be homologous with the lateral condyle of cynognathid and traversodontid cynodonts. Luo & Crompton (1994: 360) also pointed out that dicynodonts exhibited the same configuration of the trochlea as *Massetognathus.* A close inspection of the suspensorium in dicynodonts shows, however, that even when superficially similar because of the presence of an anteroposteriorly-oriented trough, the condition is reversed to that of traversodontids. Thus, in many dicynodonts (e.g. *Lystrosaurus*) the trough is located medially (Fig. 10c), limited by the quadrate medial condyle, which is directed downward, and the lateral condyle forms a long sheet that extends laterally (Cluver 1971). The pattern of the suspensorium in dicynodonts and traversodontid cynodonts seems to be oriented toward increasing the safety of the craniomandibular joint in relation to the anteroposterior movement of the lower jaw, extensive in the case of dicynodonts (Crompton & Hotton 1967; King 1990), and more restricted in traversodontids (Crompton 1972). While the two larger adductor externus muscles in dicynodonts tended to exert most of their force in the same line as the jaw ramus (Crompton & Hotton 1967), the pterygoideus, 'pterygoideus' posterior and pseudotemporalis, even when small (Crompton & Hotton 1967; King 1990), may have generated some medial traction on the lower jaw, opposed by the presence of the ventrally projected medial condyle. In most non-mammaliaform cynodonts, the zygoma is flared outward allowing for the presence of the powerful masseter complex, originated in the medial and ventral portion of the zygomatic arch, and inserted on the extensive masseteric fossa of the dentary (Barghusen 1968; Crompton 1995). The ventrally projected lateral condyle in traversodontid cynodonts is possibly related to balance forces directed laterally, generated by masseter muscles during lower jaw movements. In addition, the well-developed transverse process of the pterygoid in non-mammaliaform cynodonts, constrains severely any medially directed force exerted by muscles on the lower jaw, rendering unnecessary the presence of a ventrally projected medial condyle as in dicynodonts.

Biostratigraphic comments

Apart from the traversodontid cynodont *Luangwa,* the fauna of the upper levels of the Ntawere Formation includes the dicynodonts *Sangusaurus* and *Zambiasaurus* (Cox 1969, 1991; Cox & Li 1983), fragments of archosauriforms (Cox 1969, 1991), the mastodonsauroid temnospondyls (*sensu* Damiani 2001a) *Eryosuchus* and *Cherninia* (Chernin & Cosgriff 1975; Damiani 2001b) and the brachyopid temnospondyl *Batrachosuchus* (Chernin 1977). In addition, two cynodonts were reported from the same locality where the amphibians were recovered: 'the smaller perhaps belonging to the genus *Trirachodon* and the larger a *Scalenodon*-like form' (Chernin 1977: 90). The small cynodont mentioned by Chernin is probably BP/1/3733, a fragmentary snout of a juvenile *Luangwa drysdalli* (F. Abdala, pers. obs), while the 'Scalenodon-like form' is presumably the *L. drysdalli* holotype.

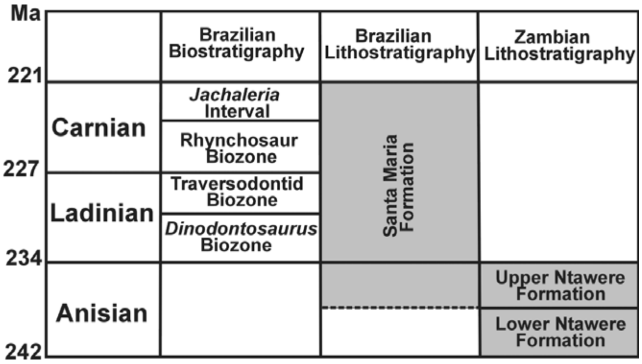

Figure 11. Stratigraphic chart showing the different faunas proposed for the Santa Maria Formation and the faunas from the Ntawere Formation in the Karoo System from Zambia. Time scale based on Gradstein & Ogg (1996). Brazilian faunas based on Abdala *et al.* (2001) and Zambian faunal ages based on Battail (1993).

Most authors interpret the upper portion of the Ntawere Formation as Anisian in age (Cox 1969, 1991; Anderson & Cruickshank 1978; Keyser & Cruickshank 1979; Anderson & Anderson 1993; Battail 1993; King 1993; but see Ochev & Shishkin 1989). The amphibian *Eryosuchus* has a Middle Triassic record (Damiani 2001a), being known also in the Manda Formation (Anisian, Tanzania), the Yerrapalli Formation (Anisian, India), and in the upper part of the Donguz formation (?Anisian-Ladinian, Russia). In addition, the dicynodont *Sangusaurus* is also present in the Manda Formation (Cox 1991).

The Santa Maria Formation of southern Brazil has been the subject of different biostratigraphical schemes of subdivision, all based largely on the tetrapod fauna (Barberena *et al.* 1985; Scherer *et al.* 1995; Schultz 1995; Schultz *et al.* 2000; Abdala *et al.* 2001; Lucas 2002). Four units were recently recognized for the Santa Maria Formation: the *Dinodontosaurus,* Traversodontid and Rhynchosaur biozones, plus the *Jachaleria* Interval, ranging from the Ladinian to the end of the Carnian (Abdala *et al.* 2001). The oldest of these faunas, the *Dinodontosaurus* Biozone, is chrono-correlated to the Chañares fauna from the Ischigualasto-Villa Union Basin in northwestern Argentina (Bonaparte 1982; Barberena *et al.* 1985; Schultz *et al.* 2000), and thus probably Early Ladinian in age (Rogers *et al.* 2001).

The presence of *Luangwa* in the Santa Maria Formation represents the second record of non-mammaliaform cynodonts that link Triassic faunas from South America and Africa. Previously, the carnivorous cynodont *Cynognathus,* a typical representative of the Late Scythian/Early Anisian *Cynognathus* Assemblage Zone of the South African Karoo (Kitching 1995; Hancox 2000), had been recorded from the Puesto Viejo Formation in western Argentina (Bonaparte 1969). Besides being the first traversodontid cynodont genus shared by Middle Triassic faunas of South America and Africa, the record of *Luangwa sudamericana* suggests an older Anisian age for some faunas of the Brazilian Middle/Upper Triassic (Fig. 11). Schultz (1995) and Scherer *et al.* (1995) also recognized a Late Anisian/Early Ladinian fauna for the Santa Maria Formation at the locality of Mariante, based on the record of a primitive rhynchosaur (Schultz & Azevedo 1990).

Nevertheless, in a more recent contribution, these authors (Schultz *et al.* 2000) regarded the afore-mentioned fauna as Ladinian.

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Early development of the mammalian superficial masseter muscle in cynodonts

Fernando Abdala* **& Ross Damiani**
Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand,
Private Bag 3, WITS, 2050 South Africa

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The masseter muscle is a hallmark of the jaw-closing mechanism of modern mammals, acting in concert with other mandibular adductor muscles to fine-tune oral food processing. The model explaining the origin of this muscle within non-mammalian therapsids involves the differentiation of a masseter-like muscle from a primitive external adductor, a downward migration of the masseter insertion on the mandible, and a division and distribution of the muscle to a condition that is similar to that in living mammals. The presence of a suborbital process of the jugal, which is interpreted as the site of origin for the superficial masseter, has been previously regarded as the earliest putative morphological evidence used to infer masseteric division. The suborbital process is first recorded in late Early Triassic (*c.* 245 Ma) cynognathian cynodonts. Here it is shown that primitive galesaurid cynodonts of earliest Triassic age (*c.* 251 Ma) display a distinct angulation of the zygomatic arch below the orbit, indicating the presence of a divided masseter amongst more basal cynodonts. This alters the timing of masseter muscle evolution by showing that the downward migration and division of the masseter occurred simultaneously, prior to the evolution of advanced cynodonts (=eucynodonts).

Keywords: masseter muscle, occlusion, Galesauridae, angular process.

INTRODUCTION

A suite of features present in late therapsids ('mammal-like reptiles'), especially non-mammaliaform cynodonts, is recognized as being unequivocally related to the acquisition of a feeding system typical of mammals. An outstanding feature of this system is the crown-to-crown postcanine occlusion (Crompton 1995) that results in the extensive mechanical reduction of food in the oral cavity (Hiiemae & Crompton 1985; Smith 1993). The most important modifications towards the mammalian system of feeding documented in late therapsids can be broadly summarized as follows: (1) a marked differentiation of the marginal teeth into incisors, canines and postcanines, with the acquisition of a more complex crown pattern in the latter; (2) the expansion of the temporal opening of the skull; (3) the enlargement of the dentary bone of the mandible with a concomitant elaboration of the angular, coronoid and articular processes of that bone, intimately associated with which is (4) the notable reduction of the postdentary bones and the quadrate/quadratojugal complex, resulting ultimately in the establishment of the craniostylic mandibular joint typical of mammals (Kemp 1982; Crompton 1995). The changes outlined in (2) through (4) are correlated with the development of the jaw adductor musculature, including the temporal and masseter muscles, and (4) is also linked with the elaboration of the auditory system (Allin 1975; Allin & Hopson 1992; Luo & Crompton 1994).

Adams (1919) carried out a detailed study on the jaw muscles in vertebrates. He interpreted the arrangement of the jaw-closing muscles in the cynodont *Cynognathus* as close to the mammalian pattern, with a large temporalis filling the temporal opening and a masseter originating from the zygomatic arch. Watson (1948) and Parrington (1955) proposed that a similar, mammal-like arrangement of the occlusal musculature was already present in basal synapsids such as *Dimetrodon*, a hypothesis supported by Crompton (1963). However, in a landmark study, Barghusen (1968) demonstrated that in *Dimetrodon* and basal therapsids the jaw-closing musculature filling the temporal fossa consisted of an adductor mandibulae externus, as in living reptiles. According to the widely accepted model for the origin and development of the masseter muscle proposed by Barghusen (1968), the earliest evidence indicating a superficial masseter muscle separated from the adductor mandibulae externus is the suborbital process of the jugal. This structure constitutes the origin for the superficial masseter and is present in advanced cynodonts such as *Trirachodon, Diademodon* and *Cynognathus* (Barghusen 1968).

In this paper we present new morphological evidence from basal galesaurid cynodonts which shifts our knowledge of the timing of origin of the superficial masseter muscle to earlier in the history of cynodonts, prior to the divergence of Cynognathia and Probainognathia, the major subclades of advanced cynodonts (=eucynodonts). We also discuss the possible homology of the pseudangular process of non-mammaliaform cynodonts and early mammaliaforms with the angular process of mammals.

Institutional abbreviations: AMNH, American Museum of Natural History, New York; BP, Bernard Price Institute for Palaeontological Research, Johannesburg; NMQR, National Museum, Bloemfontein; RC, Rubidge Collection, Wellwood, Eastern Cape Province, South Africa; SAM, Iziko Museums (South African Museum), Cape Town; TM, Transvaal Museum, Pretoria.

MATERIAL

The following galesaurid specimens were examined for this study: AMNH 2223 (described as *Glochinodontoides gracilis* by Boonstra 1935) and 2227; BP/1/4602 and 5064; NMQR 860 (described as *Platycraniellus elegans* by Brink 1954b), 1451 (referred to *Glochinodontoides gracilis* by Brink

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

1954a) and 3340; RC 845; SAM PK-K-1119, K-9954 (holotype of *Progalesaurus lootsbergensis* Sidor & Smith 2004) and K-9956.

EVOLUTION OF THE TEMPORAL FENESTRA, MASSETER MUSCULATURE, AND LOWER JAW IN CYNODONTS

Temporal fenestra

The reduction of the skull roof in the temporal region in late therapsids resulted in the development of a mammal-like temporal opening, first established in the Therocephalia-Cynodontia clade (Eutheriodontia), and subsequently expanded in non-mammaliaform cynodonts (Barghusen 1972). In basal cynodonts, such as the Late Permian *Procynosuchus* and *Dvinia,* widening of the temporal opening is achieved by an outward flaring of the zygomatic arch in the middle of the temporal region (Broom 1938, 1948; Tatarinov 1968). This basic temporal morphology appears to be highly conservative in the more advanced Probainognathia (e.g. *Lumkuia* and *Chiniquodon*), the group that ultimately gave rise to mammals. Departures from this basic pattern include the slightly smaller temporal opening present in the small-sized Early Triassic genera *Thrinaxodon* and *Galesaurus,* and the extensive flaring of the jugal along the entire temporal opening in the Middle Triassic *Probainognathus* (Crompton & Hylander 1986). On the other hand, members of the Cynognathia, the sister group of the Probainognathia, display a large temporal opening with the zygomatic arches diverging backward instead of flaring outward in the middle of the temporal region (Hopson 1991). In summary, the expansion of the temporal openings in a mammal-like fashion appeared in the latest Permian – minimally, 251 million years ago – and remained virtually unchanged in later probainognathians, basal Mammaliaformes (i.e. morganucodontids and other extinct taxa that are closely related to mammals; Luo *et al.* 2001), and even many extant mammals (for example *Didelphis*; Hiiemae & Jenkins 1969).

Masseter musculature

Masseter muscles derive from the reptilian mandibulae externus muscle (Barghusen 1968, see below) and are usually sub-divided in superficial and deep parts in extant mammals, although a more complex pattern can also be recognized (see Hiiemae & Jenkins 1969: 4). The superficial masseter generally extends along the ventral margin of the anterior portion of the zygomatic arch and, in some cases (e.g. *Ovis, Equus*), continue in front of the arch, attaching on the rostrum. The deep masseter has its origin along the entire ventral edge, or ventral and lateral facet (e.g. *Didelphis*; Turnbull 1970) of the lower edge of the zygomatic arch. Both muscles insert along the ventral border of the masseteric fossa, with the superficial attachment generally more ventrally and/or posteriorly located (Turnbull 1970).

The presence of well-developed sagittal and occipital crests in the large temporal opening of therocephalians and cynodonts indicate that the adductor mandibulae externus muscle originated from a temporal aponeurosis attached to the aforementioned crests (Barghusen 1968). In the Late Permian *Procynosuchus,* a lateral fossa is present high on the coronoid process of the dentary (Crompton 1963; Figs 1 & 2). The presence of this fossa on the mandible indicates a division of the adductor mandibulae externus muscle, and it was interpreted as an initial stage in the differentiation of the masseter, which originated on the temporal aponeurosis (Barghusen 1968). In lateral view, the zygomatic arch of *Procynosuchus* is oriented horizontally, whereas in the earliest Triassic (i.e. Induan) *Galesaurus* and *Thrinaxodon,* it displays an upward flexure (Figs 1, 2 & 3). Concomitant with this flexure in the zygoma is a notable increase in the size of the dentary, with a larger coronoid process, an extension of the lateral fossa (= masseteric fossa) to the base of the dentary, and the beginning of the development of the angular process. As a result of these changes, the masseter muscle extended its insertion, reaching the angle region in *Galesaurus* and *Thrinaxodon,* while its origin was located along the internal surface of the zygomatic arch (Barghusen 1968, 1972; DeMar & Barghusen 1972; Bramble 1978).

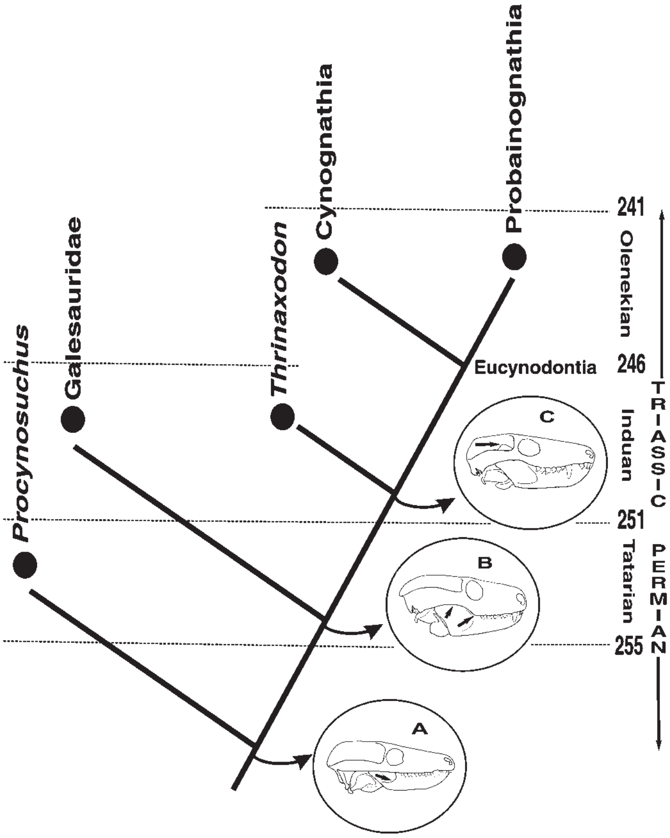

Figure 1. Phylogenetic relationships and morphological changes in the temporal region of the skull in basal cynodonts. Inset circles depict key morphological changes in the temporal region. **A**, In *Procynosuchus,* the zygomatic arch is straight and the masseteric fossa high on the dentary; **B**, in galesaurid cynodonts, the zygomatic arch shows an upward flexure and the development of a suborbital angulation; the masseteric fossa extends to the base of the dentary; **C**, In *Thrinaxodon,* the coronoid process of the mandible is significantly taller. Phylogeny follows Hopson & Kitching (2001); the clade Probainognathia includes mammals. *Procynosuchus* and *Thrinaxodon* modified from Hopson (1994).

In the Middle Triassic chiniquodontid probainognathians, there is a characteristic angulation below the orbit,

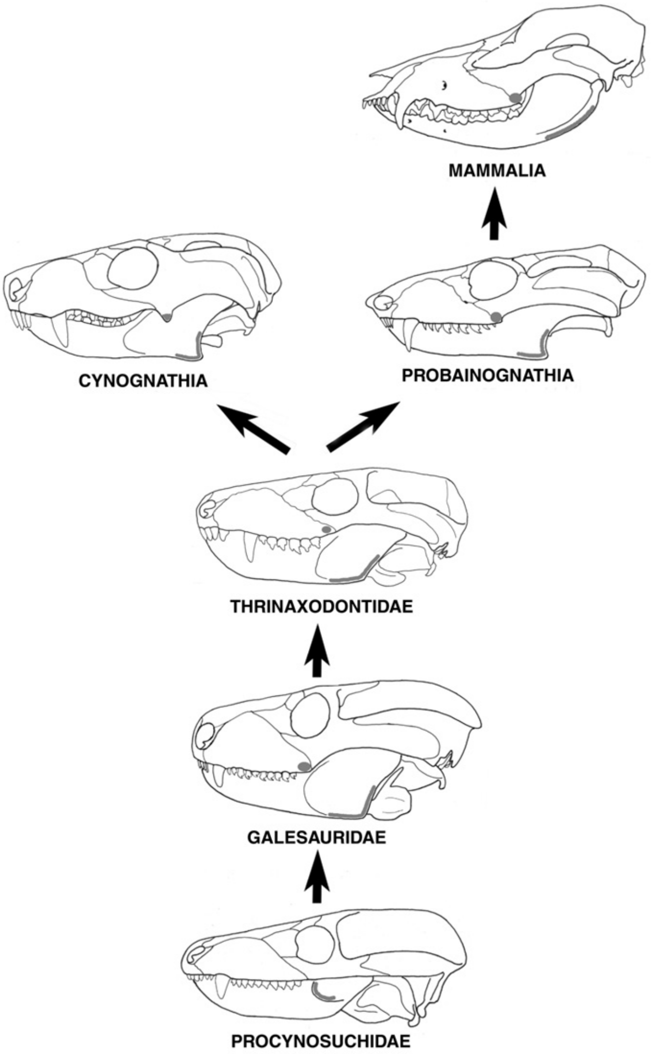

Figure 2. Evolution of the superficial masseter muscle in non-mammaliaform cynodonts and mammals. The origin and insertion points of the superficial masseter in the Galesauridae, *Thrinaxodon, Trirachodon* (representing the condition in Cynognathia), *Chiniquodon* (sensu Abdala & Giannini 2002; representing the condition in Probainognathia), and the extant mammal *Didelphis,* are depicted. In *Procynosuchus* the entire masseter, in its initial phase of differentiation, was inserted on the lateral fossa of the dentary. *Procynosuchus* modified from Hopson (1991), *Trirachodon* modified from Hopson & Barghusen (1986), and *Chiniquodon* modified from Romer (1969).

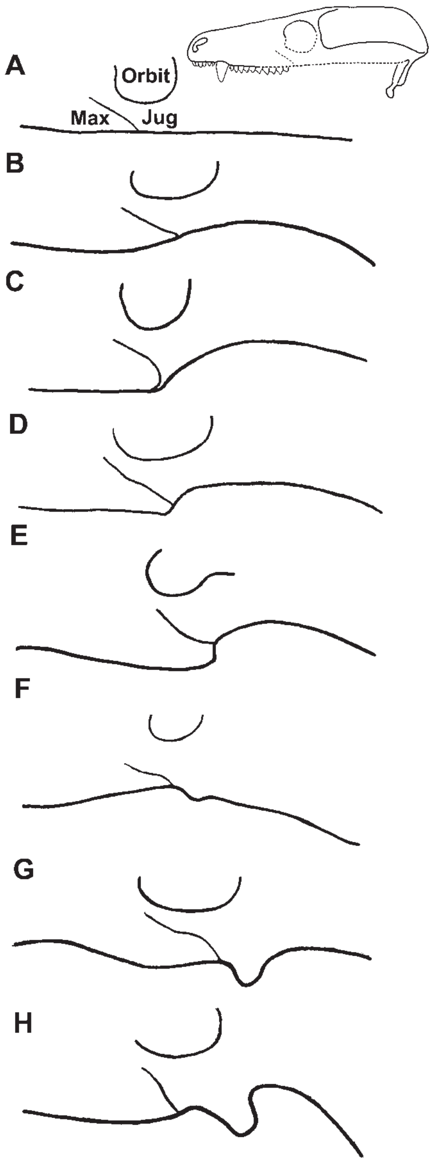

Figure 3. Lateral view of the suborbital region in different cynodonts. **A**, *Procynosuchus*; **B**, *Thrinaxodon*; **C**, Galesauridae; **D**, *Chiniquodon*; **E**, *Didelphis*; **F**, *Cynognathus*; **G**, *Trirachodon*; **H**, *Diademodon.* C, D, and E show the suborbital angulation; F, G and H show the suborbital process of the jugal. Abbreviations: Jug, jugal; Max, maxilla. Outline of *Procynosuchus* skull based on Hopson (1994).

hereafter termed the suborbital angulation. This feature is located at the junction between the anteroventral margin of the jugal and the zygomatic process of the maxilla (Hopson & Barghusen 1986; Hopson 1991; Hopson & Kitching 2001: character 41; Abdala & Giannini 2002; Figs 2 & 3), and seems a by-product of a higher upward flexure of the jugal (but see Hopson & Kitching 2001: fig. 2). A similar suborbital angulation is recognized in didelphid marsupials, and is manifested as a boss at the junction of the maxilla and the jugal on the anteroventral edge of the zygomatic arch (Hiiemae & Jenkins 1969; Figs 2 & 3). In both of these groups, the angulation is in a roughly similar position to the suborbital process of the jugal, a structure typical of late Early/early Middle Triassic cynognathian cynodonts (e.g. *Trirachodon, Cynognathus, Diademodon*). The suborbital process of the jugal in cynognathian cynodonts has been regarded as the earliest evidence of an independent origin for the superficial masseter muscle, according to the accepted model of evolution of the adductor musculature in therapsids (Barghusen 1968, 1972; DeMar & Barghusen 1972; Bramble 1978; Figs 2 & 3). However, a suborbital angulation identical to that of chiniquodontid cynodonts and didelphid marsupials is also present in large-sized galesaurid cynodonts of earliest Triassic age (Abdala 2003; Table 1, Figs 2 & 3). This evidence indicates that the differentiation of the superficial masseter muscle occurred first in members of the Galesauridae, some five million years earlier than currently recognized and prior to the evolution of advanced cynodonts (i.e. eucynodonts; Hopson & Kitching 2001; Figs 1 & 2). The differentiation of the superficial masseter in cynodonts thus occurred simultaneously with the downward expansion of the masseter insertion to the angular region of the lower jaw. Previously, these processes were considered to represent consecutive stages in the evolution of the mammalian

Table 1. Skull lengths in various galesaurid specimens, showing a correlation between larger skull size and the presence of a suborbital angulation.

Specimen	Skull length (mm)	Suborbital angulation
RC 845	69	Absent
SAM PK-K-1119	72	Absent
SAM PK-K-9956	73	Absent
AMNH 2227	79	Absent
BP/1/4602	82	Absent
NM QR1451	90	Present/Absent*
SAM PK-K-9954	92	Present
AMNH 2223	100	Present
NM QR3340	101	Present
BP/1/5064	103	Present
NM QR860	114	Present

*Angulation presents on the left zygoma but absent in the right.

occlusal complex (Barghusen 1968, 1972; Bramble 1978).

Intriguingly, the development of the suborbital angulation appears to be linked with the size of the animal. For instance, the suborbital angulation is absent in the small-sized cynodonts *Thrinaxodon* and *Probainognathus* with skull lengths up to approximately 80 mm, and in small individuals of the Galesauridae. An exception to this is the presence of the suborbital angulation in the small *Platycraniellus elegans* (TM 25; basal skull length 84 mm), which may be due to the remarkable development of the temporal opening in both longitudinal and transverse directions. In fact, this species exhibits the most widened temporal region amongst non-mammaliaform cynodonts (approximately 88% with respect to the basal skull length). In contrast, the suborbital angulation is present in large individuals of the Galesauridae with skull lengths above 90 mm (Table 1, Fig. 4), and in chiniquodontids with skull lengths up to 310 mm (Abdala & Giannini 2002). Evidence from ontogeny also supports a correlation between size and the suborbital angulation/suborbital process of the jugal. Tiny juveniles of *Trirachodon berryi* (BP/1/4534 and 4535) lack a suborbital process, whereas this process is well developed in adults. A similar ontogenetic trend is observed in the extant marsupial *Didelphis albiventris,* in which the maxillary boss, the homologue of the suborbital angulation in non-mammaliaform cynodonts, is absent in juveniles of *c.* 3.5 months (Abdala *et al.* 2001).

As a corollary of the evidence discussed above, we support the hypothesis of the presence of a differentiated superficial masseter in all epicynodonts (a monophyletic group including the common ancestor of Galesauridae and mammals, and all its descendants; Hopson & Kitching 2001). This hypothesis is favoured by the widely distributed suborbital process/angulation in non-mammaliaform cynodonts (Fig. 3), indicating that the superficial masseter remained differentiated in both Cynognathia and Probainognathia. Consequently, *Thrinaxodon,* which is phylogenetically placed between galesaurids and eucynodonts (Fig. 1), also possessed a differentiated superficial masseter. This hypothesis was advanced in muscular reconstructions of *Thrinaxodon* by Allin & Hopson (1992: figure 28.10C) and Crompton (1995: figure 4.4), although they did not provide supportive evidence to depart from the model proposed by Barghusen (1968).

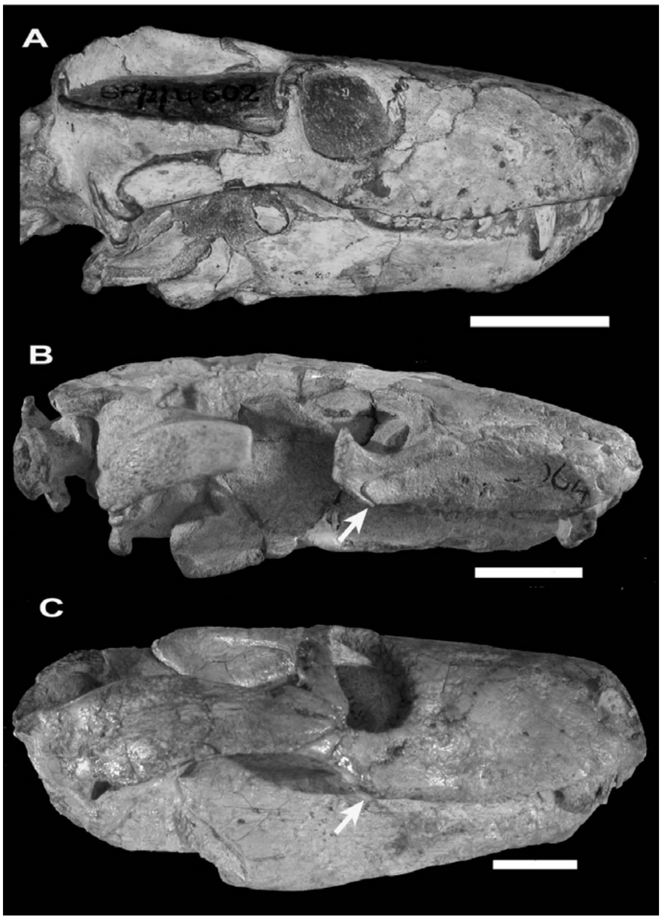

Figure 4. Lateral view of the skull of three specimens of Galesauridae. **A**, BP/1/4602 (skull length, 82 mm); **B**, BP/1/5064 (skull length 103 mm); **C**, NM QR860 (skull length 114 mm). Arrows in B and C indicate the suborbital angulation. Scale bars = 2 cm.

Many innovations associated with the feeding system in late non-mammaliaform cynodonts and early mammaliaformes are interpreted as safety devices that allow the postdentary bones and the quadrate to reduce in size while maintaining a viable, but weak, craniomandibular joint (CMJ). Modifications in the lower-jaw are related to increasing complexity of the external adductor musculature in the temporal fossa, which reduced mechanical stress exerted on the CMJ of non-mammaliaform cynodonts (Bramble 1978; Crompton & Hylander 1986). In this context, the anteriorly oriented fibres of the superficial masseter may have reduced compressive loading on the CMJ produced by the temporalis and deep masseter fibers (see Crompton & Hylander 1986: figs 5–9). The superficial masseter in non-mamaliaform cynodonts and early mammaliaformes seems to be shorter and dorsoventrally more obliquely orientated than in generalized mammals with relatively unspecialized masticatory apparatus such as *Didelphis* (Turnbull 1970), as a result of the anterior location of the angle of the dentary (see Fig. 2). The orientation and short fibres of the superficial masseter are also probably related to decreasing the stress on the weak CMJ by preventing exposure to anteroposteriorly directed tensile forces that could displace the joint. This sort of arrangement in the superficial masseter evidently restricted the muscle capacity in relation to mandibular protraction.

Lower jaw

Modifications to the temporal region of the skull in relation to the evolution of adductor musculature were initiated in the Late Permian therocephalians and basal cynodonts, leading to a basic mammal-like temporal design in the Early Triassic galesaurids. With the expansion of the temporal opening in basal cynodonts, the incipient coronoid process of the lower jaw was repositioned in the middle of that opening, increasing the space for adductor (i.e. masseter) musculature between the zygomatic arch and the lateral surface of the lower jaw (Barghusen 1968). Besides a repositioning of the coronoid process, modifications of the lower jaw towards the mammalian condition seem to have been somewhat delayed with respect to the skull transformations. Galesaurids share with *Thrinaxodon* a similar degree of development of the angle of the dentary. However, only *Thrinaxodon* shows the more mammal-like condition of a higher coronoid process and a slight reduction in the size of the postdentary bones and of the reflected lamina of the angular (Hopson & Kitching 2001; Figs 1 & 2). The morphology of the lower jaw attained in the Early Triassic *Thrinaxodon* was the basic pattern from which further modifications to the mandible were derived. These include an increase in the height of the coronoid process, an elaboration of the angular process, and a further reduction of the postdentary bones. The development of this 'derived' plan of the lower jaw has generally been interpreted as acquired independently in the Cynognathia and Probainognathia (Allin & Hopson 1992; Hopson & Kitching 2001).

MASSETERIC INSERTION AND ANGULAR PROCESS OF THE DENTARY

In our interpretation of the non-mammaliaform cynodont angle, and the angular process as a site of insertion of the superficial masseter, we concur with Luo *et al.* (2002: character 8) in recognizing them as homologous with the angular process of mammals. We would like to address here some aspects of the debate about the homology of the angle (pseudangular process of Patterson 1956) of therapsids and basal mammaliaforms (e.g. *Morganucodon, Sinoconodon*), and the angular process of late mammals. The initial proposal that a pseudangular process existed in late cynodonts and early mammaliaforms (Patterson 1956; see also Patterson & Olson 1961) was based on the comparatively long distance separating the angle from the CMJ in these groups. In contrast, Patterson & Olson (1961) indicated that the true angular process in therian mammals was at the same level as the CMJ. The functional correlate to this hypothesis was the suggestion that the pseudangular process was the insertion site for the mandibular depressor, based on the presence of a similar process in the lower jaw of the monotreme *Tachyglossus* (Patterson & Olson 1961). This muscular insertion was also suggested by the presence of a large, backwardly projecting process on the tip of the angle in cynodonts from the Ischigualasto Formation, concurrent with the supposed disappearance of the retroarticular process in these cynodonts. Two factors weaken the hypothesis of Patterson and Olson (1961): (1) the fact that only *Tachyglossus,* with the skull and lower-jaw highly modified, presents a structure 'homologous' to the pseudangular region/process of late therapsids and early mammaliaforms, supporting the putative insertion of the mandibular depressor; (2) a well-developed retroarticular process was later documented in advanced cynodonts, including those from the Ischigualasto Formation (Allin 1975, 1986), while the posteriorly projecting tip of the angle is known in quite a few non-mammaliaform cynodonts, including some traversodontids and tritylodontids (Bonaparte 1962; Kemp 1980; Sun 1984; Sues 1985; Flynn *et al.* 2000).

More recently, the presence of both the pseudangular and the 'true' angular processes have been documented in the mammaliaforms *Dinnetherium* from the United States (Jenkins *et al.* 1983) and *Megazostrodon* from South Africa (Gow 1986). Jenkins *et al.* (1983) interpreted the angular flange (true mammalian angle) as a neomorphic downward extension of the dentary for insertion of a part of the masseter, probably the superficial portion. They do not make any claim about the muscle attaching to the pseudangular process, but considering previous studies by these authors (e.g. Crompton & Jenkins 1979) it is clear that they interpret this process as a site for masseter attachment as well. This functional interpretation obviously indicates different homologies for the pseudangular process of these authors and that of Patterson & Olsen (1961). In contrast, Hopson (1994, see also Crompton & Luo 1993: fig. 4.4) has interpreted the pseudangular process of *Dinnetherium* as a reduced angular process, and the angular flange as a neomorphic lateral ridge behind the angular region. With respect to *Megazostrodon,* Gow (1986) also considered the 'true' angular process as a ventral extension of the lateral ridge of the dentary. Some early mammaliaforms such as *Hadrocodium* (Luo *et al.* 2001: fig. 3), and some specimens of *Morganucodon* (Crompton & Luo 1993: fig. 4.7), show the angular process (= pseudangular process of Patterson, 1956) closer to the CMJ when compared with non-mammaliaform cynodonts and other early mammaliaforms. In addition, an ontogenetic series of *Sinoconodon* shows the angular process clearly located more posteriorly in large specimens (Crompton & Luo 1993: fig. 4.2; Zhang *et al.* 1998: fig. 2). This evidence supports the homology between the angle and angular process of basal cynodonts and early mammaliaforms, and that of late mammals, as advanced by Hopson (1994). In addition, the evidence supports Parrington's (1959) hypothesis regarding the posterior migration of the angular process from the condition known in non-mammaliaform cynodonts and early mammaliaforms (morganucodonts in Parrington's view), to that present in 'typical pantotheres' (e.g. *Amphitherium,* Parrington 1959) and therian mammals.

CONCLUSION

The subdivision of the reptilian external adductor musculature into masseter and temporal muscles is linked with a strengthening of the mandible and with the more complex movements involved in mammalian mastication (Walker 1987). The presence of a differentiated superficial masseter in galesaurids implies that the morphology of the adductor musculature was already sophisticated in cynodonts lacking postcanine occlusion. This indicates that the first stages in the division of the adductor musculature (i.e. differentiation of the superficial masseter) was a prerequisite for crown-to-crown postcanine occlusion, albeit in a rudimentary fashion as in gomphodont cynodonts (Crompton 1972), or a more precise occlusion with consistent relationships between upper and lower molars, as later developed in Mammaliaformes (Crompton & Luo 1993).

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A juvenile coelophysoid skull from the Early Jurassic of Zimbabwe, and the synonymy of *Coelophysis* and *Syntarsus*

Anthea Bristowe* **& Michael A. Raath**

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

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Several authors have drawn attention to the close similarities between the neotheropod dinosaurs *Coelophysis* and *Syntarsus.* Reconstruction and analysis of a skull from a juvenile specimen of *Syntarsus* (collected from the Forest Sandstone Formation of Zimbabwe) show that cranial characters previously used to distinguish these taxa and justify their generic separation (namely the presence of a 'nasal fenestra' in *Syntarsus* and the length of its antorbital fenestra), were based on erroneous reconstructions of disassociated cranial elements. On the basis of this reinterpretation we conclude that *Syntarsus* is a junior synonym of *Coelophysis.* Variations are noted in three cranial characters – the length of the maxillary tooth row, the width of the base of the lachrymal and the shape of the antorbital maxillary fossa – that taken together with the chronological and geographical separation of the two taxa justify separation at species level.

Keywords: Dinosaurs, Neotheropoda, Coelophysoid, taxonomy, Triassic, Jurassic.

INTRODUCTION

Ever since the theropod *Syntarsus rhodesiensis* was first described (Raath 1969), a succession of authors have commented on the close morphological similarity between it and *Coelophysis bauri* (Raath 1969, 1977; Paul 1988, 1993; Colbert 1989; Rowe 1989; Tykoski 1998; Downs 2000). Paul (1988, 1993) went so far as to propose that the two taxa belong in the same genus, and that the differences advanced to justify their generic separation are questionable.

Recent work on a partially disarticulated skull of a juvenile specimen of *Syntarsus,* QG165, has made it possible to clarify details of the relationships between several critical cranial elements that were unclear in previous reconstructions. Reconstruction of the cranium allowed reassessment of the characters used by Raath (1977) to distinguish *Syntarsus* from the closely related *Coelophysis*. These characters included the 'nasal fenestra' (reported by Raath,1977, as present in *Syntarsus* but absent in *Coelophysis*); the nature of the contact between the lachrymal and the jugal bones; and Raath's (1977) observation that the antorbital fenestra in *Syntarsus* represented 43% of total skull length. Analysis of the newly discovered skull has demolished each of these purported characters, leading us to concur with Paul (1988 1993) that i) *Syntarsus* is a junior synonym of *Coelophysis,* and ii) that the recently proposed facetious replacement name for *Syntarsus* (*Megapnosaurus* Ivie, Slipinski & Wegrzynowicz, 2001) should not stand.

TAXONOMIC HISTORY

Coelophysis and *Syntarsus* have, until recently, been classified as ceratosaurian theropod dinosaurs, with *C. bauri* from the Late Triassic of North America and *S. rhodesiensis* from the Early Jurassic of Zimbabwe and South Africa. Following the work of Gauthier (1986), these taxa were suggested to belong to a monophyletic clade known as Ceratosauria. However, more recent works by a number of authors (Sereno 1997, 1999; Holtz 2000; Wilson *et al.* 2003; Rauhut 2003) have re-evaluated theropod interrelationships. For example, Rauhut (2003) proposed that Ceratosauria *sensu* Gauthier (1986) is paraphyletic and that the taxa usually grouped as ceratosaurs instead form two monophyletic clades that represent successive outgroups to the Tetanurae. The most basal clade is the Coelophysoidea from the Upper Triassic of the Chinle Formation in the U.S.A. to the Early Jurassic of 'Stormberg Group' equivalents in southern Africa. The second clade of basal theropods, comprising a more restricted Ceratosauria (*sensu* Rauhut 2003), includes *Ceratosaurus, Elaphrosaurus* and the abelisaurids.

Rauhut (2003) has argued that there are two fundamentally different approaches in the reconstruction of theropod phylogeny. He has pointed out that analyses such as those of Thulborn (1984), Gauthier (1986) and Sereno *et al.* (1996) are based on predetermined lists of synapomorphic characters. The result of this approach has been robust analyses with good resolution and exceptionally high consistency ratios. However, this method does not reflect the high degree of homoplasy that occurs in theropod phylogeny, and only partially represents a test of homology by congruence, the most reliable method of testing for homology (Rauhut 2003). The other method, preferred by Rauhut (2003), is to use as many characters as possible to test for congruence, and to establish synapomorphies in this way. Consistency ratios and cladogram resolution are not nearly as impressive, and the resulting phylogenies demonstrate abundant homoplasy (Rauhut 2003). However, the advantage of this approach is that it avoids preconceptions regarding the distribution of synapomorphic features on any particular

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*Author for correspondence. E-mail: bristowea@yahoo.co.uk phylogeny. While character choice will always be contentious, Rauhut (2003) maintains the second method results in a more objective analysis. We have followed Rauhut's approach in this study.

GEOLOGICAL SETTING OF THE QG165 SKULL

All known *Syntarsus*-bearing localities in Zimbabwe are in the fine-grained, pale, buff-coloured Forest Sandstone Formation (Raath 1969, 1977). Based on lithostratigraphic correlation, the Forest Sandstone Formation may be the equivalent of the upper part of the 'Stormberg Group' of the main Karoo Basin in South Africa (Olsen & Galton 1984). The 'Stormberg Group' comprises the Molteno, Elliot and Clarens formations, and the upper 'Stormberg' represents the Upper Elliot and Clarens formations (Olsen & Galton 1984). Olsen and Galton suggested on the basis of comparisons with European faunal assemblages that the lower 'Stormberg' assemblage was Late Triassic (Carnian-Norian) in age. However, on the basis of field evidence, Lucas & Hancox (2001) have assigned the prosauropod-dominated lower Elliot Formation a Norian age. The upper 'Stormberg' assemblage contains more diverse tetrapod assemblages than originally suggested by Kitching & Raath (1984), and Lucas & Hancox (2001) have conservatively assigned it an Early Jurassic age (Hettangian-Pliensbachian). They also considered the overlying Clarens Formation, which contains a limited fauna of taxa common to the underlying upper Elliot assemblages, to be Early Jurassic. The upper 'Stormberg' assemblage broadly correlates with the upper Newark Supergroup (eastern U.S.A.), the Glen Canyon Group (southwestern U.S.A.) and the Lower Lufeng Series (China). The African coelophysoid-bearing deposits are thus separated from the North American bone-beds by a significant period of geological time and a considerable continental distance.

One of the distinctive characteristics of coelophysoid deposits in both geographic locations is that they represent mass burials. One of the three localities in Zimbabwe preserves numerous individuals of *S. rhodesiensis* (Raath 1977, 1980). Two localities in the Kayenta Formation of Arizona, U.S.A., preserved at least three and eleven individuals of *S. kayentakatae*, respectively (Rowe 1989). The Ghost Ranch Quarry is one of the richest Mesozoic dinosaur burials yet discovered, although claims that it has yielded a thousand individuals (Schwartz & Gillette 1994) are difficult to substantiate because there are no data on minimum numbers of individuals recovered (Sullivan 1996). It is, however, accepted that the site has yielded at least hundreds of individuals of *C. bauri* that were buried en masse in the sediments of the Chinle Formation (Rowe *et al.* 1997).

These mass burials occur in a variety of depositional environments (Rowe & Gauthier 1990). The Ghost Ranch Quarry fossils are found in 1-metre-thick mudstone of fluvial origin (Rowe & Gauthier 1990). The *S. kayentakatae* burials are preserved in overbank deposits, and the mass burial of *S. rhodesiensis* was found in a thin fluvial lens within aeolian deposits (Raath 1977; Rowe & Gauthier 1990), but all localities suggest water-borne deposition of the vertebrate remains. By virtue of the numbers of individuals found at the Ghost Ranch and the Chitaki River sites, it can be concluded that these were catastrophic mass death events. Another exceptional feature of coelophysoid bone-beds is their monospecificity, supporting the conclusion that coelophysoids were gregarious (Raath 1977; Colbert 1989).

MATERIALS AND METHODS

In this account the following institutional abbreviations are used: AMNH, American Museum of Natural History, New York, U.S.A.; CM, Carnegie Museum, Pittsburgh, U.S.A.; GR, Ruth Hall Museum of Paleontology, Ghost Ranch, New Mexico, U.S.A.; MCZ, Museum of Comparative Zoology, Cambridge, U.S.A.; MNA, Museum of Northern Arizona, Flagstaff, U.S.A.; QG, Zimbabwe Natural History Museum, Bulawayo, Zimbabwe

Specimen QG165 was found in a detached block of Forest Sandstone from the Chitaki River bone-bed (approx. 16°07′S, 29°30′E), which was collected by one of the authors (M.A.R.) in 1972, and is now housed in the collections of the Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe. It consists of a partially disarticulated almost complete skull of a juvenile specimen, lacking only the snout, and is associated with a number of poorly preserved postcranial elements. This study focused on the skull.

The cranial elements of QG165 are closely associated, which is unusual for material from the Chitaki River site, where the bulk of the collection consists of isolated skeletal elements that have been randomly mixed together. In spite of this, the preservation of the often delicate and fragile bones is excellent and there is no clear evidence of abrasion or predation. Although partially disarticulated as a result of postmortem collapse and drifting by gentle currents, many of the individual elements are still close to their original life positions, providing new insights as to their articular relationships.

Other *Syntarsus* material (also collected by M.A.R.) was compared with QG165, including QG193, 194, 195, 196, 197, 202, 235, 241, 265, 278 and 307. All this material is also stored in the Zimbabwe Natural History Museum. Data on *Coelophysis* material used for comparison in this study was taken from Colbert (1989), in which he used AMNH 7223, 7224, 7227, 7228, 7230, 7239, 7240, 7241, 7242; MCZ4326, 4327, 4333; MNAV3315; YPM41196 and CM-C481. Other material referred to herein includes specimens of *C. bauri* (CM31374, a disarticulated juvenile with CM field number C-3-82-31, GR141, GR142 and GR1442: Downs 2000); and *S. kayentakatae* (MNA V2623: Rowe 1989; Tykoski 1998).

After initial mechanical preparation of QG165 to expose the extent of the skull, it was scanned at the Sunninghill Hospital, Sandton, Johannesburg, in a series of fine slices using a Philips Multidetector MX 8000 spiral CT scanner with effective slice thickness of 0.6 mm. The resulting images were manipulated on a Philips MxView workstation using maximal intensity projection imaging techniques and saved on CD in DICOM format. The formatted images were converted at the School of Mechanical,

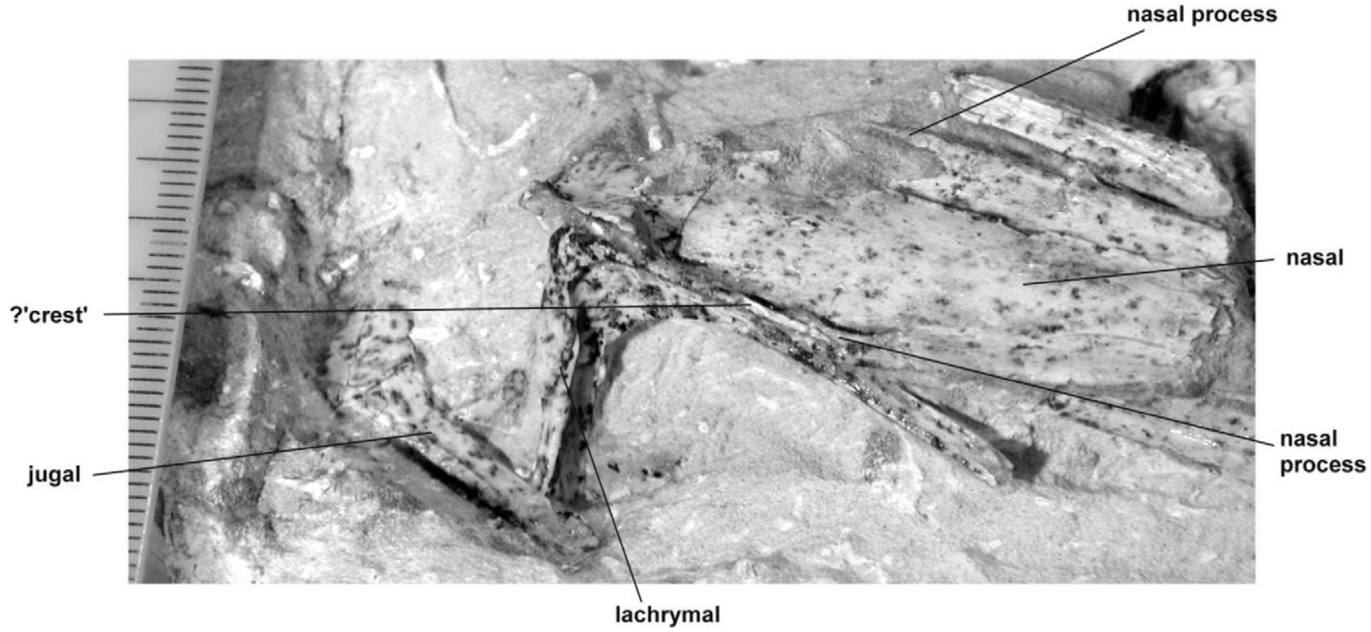

Figure 1. The right lachrymal of QG165 shown in partial articulation with the nasal and nasal process (or 'nasal fenestra' as described by Raath 1977) (scale divisions = mm).

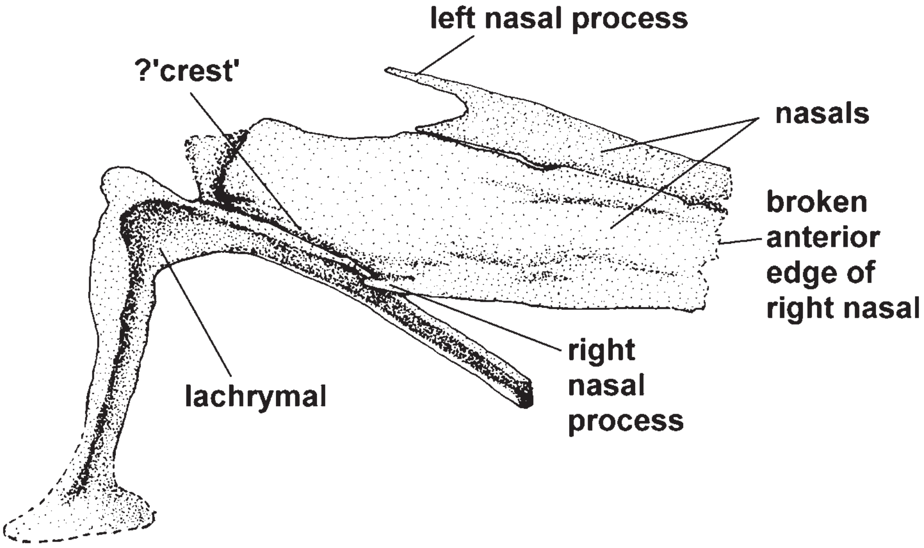

Figure 2. Interpretive drawing of right lachrymal of QG165 shown in contact with the nasal process and the body of the nasal, forming a small incipient crest.

Industrial and Aeronautical Engineering at the University of the Witwatersrand using the Mimics package Version 7.3, into a digital volume, which was exported to STL (stereolithographic) file format. The STL file was sent to a commercial prototyping company where a three-dimensional was replica was produced. This replica was used to supplement examination of those areas of QG165 which would have been endangered by further physical preparation.

DESCRIPTION

Raath (1977) identified a posterolateral nasal process – bordering what he termed the 'nasal fenestra' – as a defining character of *Syntarsus.* In QG165, the left nasal process is disassociated from the left nasal, but the distinctive V-shaped embayment is preserved (Fig. 1). However, the right nasal and the right nasal process are still essentially in articulation with the right lachrymal (Figs 1, 2). The nasal process is similar in every respect, other than size, to that seen in a juvenile *Coelophysis* specimen (C38231: Downs 2000, Fig. 3). The dorsal ramus of the right lachrymal and the lateral edge of the right nasal articulate to form what could be interpreted as a slightly raised incipient parasagittal crest, similar to the longitudinal crest described by Rowe (1989) in *S. kayentakatae,* but on a much smaller scale (Figs 1, 2). This 'crest' is slight, measuring no more than 3 mm in height and approximately 2 mm wide at the base. The right nasal process articulates with the anterior edge of this crest. Since there is no evidence of a similar crest on the left nasal, although the nasal process itself is preserved (Fig. 1), it seems likely that the small 'crest' on the right side is an artefact of slight displacement and distortion of the very thin and plastic lachrymal and nasal bones.

Compared with the flat, featureless appearance of most of the skull bones, the lachrymals are curved and sinuous. The right lachrymal articulates with the lateral margin of the right nasal and the nasal process. It is a slender L-shaped bone with an anteriorly projecting upper ramus and a ventrally projecting vertical process that expands into a footplate (Raath 1977). The base of the footplate is noticeably narrower anteroposteriorly than in *Coelophysis,* measuring less than 30 per cent of the height of the vertical arm of the lachrymal, compared to more than 30 per cent in a number of specimens of *Coelophysis,* most notably in the well-preserved complete skull CM31374 (Fig. 4). The medial and lateral margins of the vertical process of the right lachrymal border an anterior sulcus that tapers into a grooved lip along the lateral border as it reaches the ventral footplate. The footplate of the right lachrymal flares into a posterolateral process and an anterior process. The anterior process is cupped and expands outward around a noticeable sulcus. The footplate of the left lachrymal is not preserved. When restored, the footplate of the right lachrymal would have articulated with the dorsomedial margins of the jugal and maxilla.

The jugal is a long, flat, thin bone, reinforced by longitudinal ridges along the lateral surface (Figs 5, 6). It forms both the lateroventral border and part of the posterior border of the orbit. The bone divides into two rami posteriorly – a dorsal ramus that articulates with the ventral process of the postorbital, and a posterior ramus that overlaps the anterior ramus of the quadratojugal (Figs 5, 6). The anterior end of the jugal tapers to a finely pointed tip, and articulates with the posterior end of the maxilla and the ventral footplate of the lachrymal. It is excluded from the antorbital fenestra. The posterior end of the jugal is forked to receive the corresponding anterior process of the quadratojugal.

This reconstruction of the palatine presented herein takes into account research on palatine recesses by Witmer (1997) and by Harris (1998). The right palatine in QG165 is reconstructed as a tetraradiate element comprised of four conjoined processes (Figs 7, 8). There is a deeply excavated fossa (Fig. 7) on the dorsal surface of the palatine and the pterygoid that Witmer (1997) terms the muscular fossa. The muscular fossa is bordered by a pronounced ridge that reaches anteromedially from the maxillary contact in front of the suborbital fenestra to the vomeropterygoid contact. The vomeropterygoid process is expanded and extends both anteriorly and medially, creating a surface for the origin of the M. pterygoideus, pars dorsalis (Witmer 1997). A slender tapering maxillary process extends anteriorly, ventral to the vomeropterygoid process. The maxillary process and the vomeropterygoid process form the posterior borders of the choana. The fourth element of the palatine is what Harris (1998) terms the medial process, which like the maxillary process is long, tapering and laterally compressed. The medial process forms the ventral border of the palatine fenestra.

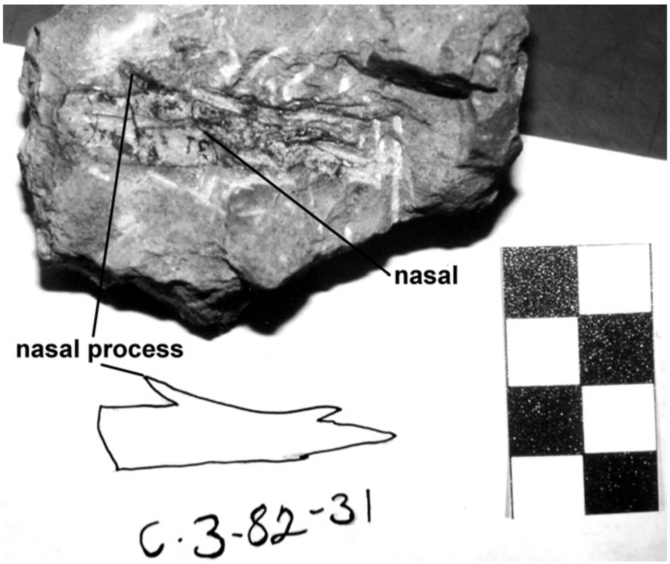

Figure 3. Isolated juvenile nasal of *C. bauri* C38231; anterior is towards the right of the figure (photograph: A. Downs) (scale divisions = cm).

It is clear from this reinterpretation that Raath (1977: fig. 4h,i) inverted the disarticulated right palatine in his reconstruction. If an image of the isolated palatine QG241 is rotated through 180 degrees (Fig. 9), the bone closely resembles the palatine in both QG165 (Fig. 7), and Witmer's (1997) reconstructions of *Coelophysis* (Fig. 10). In addition, the palatine in QG165 was found in close association with the pterygoid and the maxilla, suggesting that it was in, or close to, its natural position, adding further support to the reconstruction proposed herein. Witmer (1997) has used the palatine of *Coelophysis,* CM31374, to demonstrate the presence of a muscular fossa on the palatine and the sharply delineated ridge (Fig. 7). Witmer's

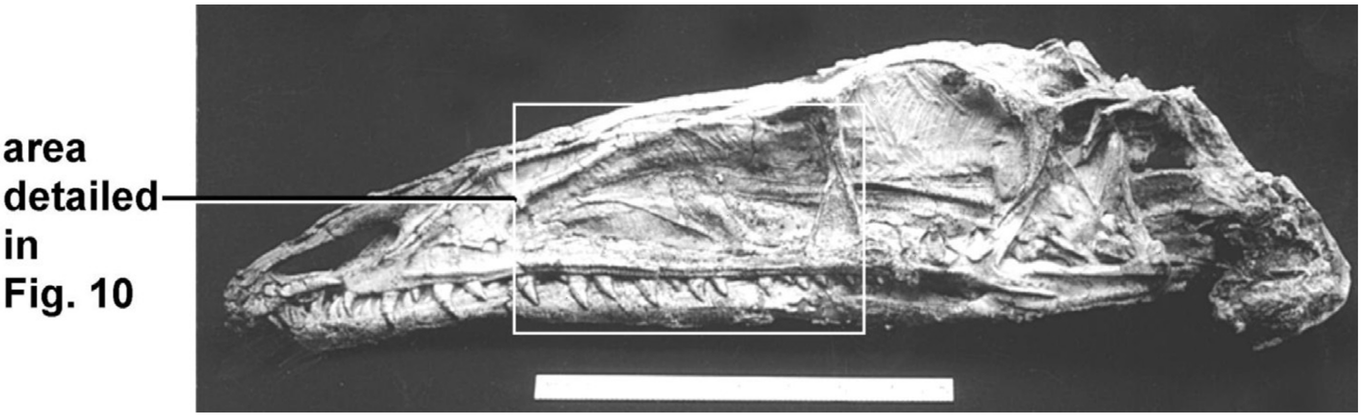

Figure 4. Subadult *Coelophysis* skull, CM31374, on which Witmer (1997) based his drawings in Fig. 10 (photograph: A. Downs) (scale bar = 8 cm).

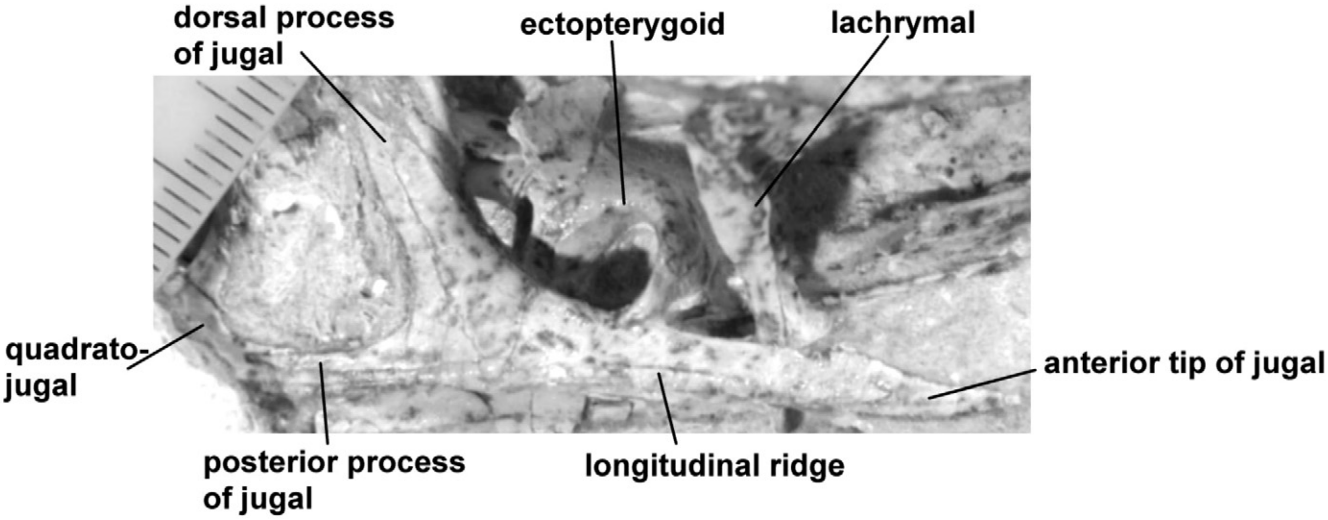

Figure 5. Right jugal of QG165, still in articulation with the quadratojugal. The right ectopterygoid articulates with the medial surface (scale divisions = mm).

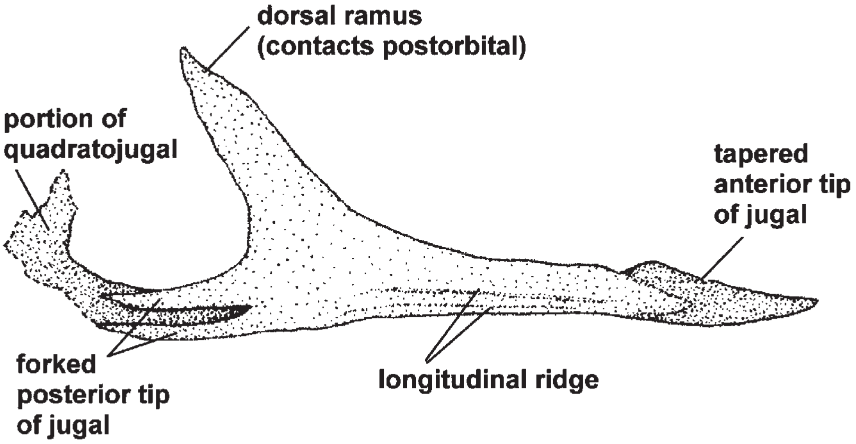

Figure 6. Interpretive drawing of the right jugal of QG165, with longitudinal ridges, a delicate anterior tip and forked posteriorly.

(1997) drawings are indistinguishable from the palatine of QG165 (Fig. 10). The vomer in QG165 was not preserved but the posterior ends of these long, slender elements would have contacted the elongate, anterior processes of the pterygoid.

A pair of hyoids that match those described in *C. bauri* (Colbert 1989) and in *S. kayentakatae* (Rowe, 1989) is preserved in QG165; they were not initially visible but were revealed in the rapid-prototyped replica. The hyoids in QG165 are long slender rods that are slightly bowed or angled toward the centre. They taper anteriorly, and expand and flatten posteriorly. One hyoid lies in close association with the ventral edge of the left dentary and the other in association with the right dentary. Because of damage to the left dentary, it is not possible to estimate the length of the hyoids as Rowe (1989) did in *S. kayentakatae,* but clearly these are long slender rods that could easily have reached one third of the length of the dentary. The hyoids of QG165 differ substantially from the elements identified by Raath (1977) as hyoids, lending support to the suggestion by Tykoski *et al.* (1993) that the latter elements are in fact furculae.

TAXONOMIC ANALYSIS

This analysis aims to test the validity of the historical distinctions between *Syntarsus* and *Coelophysis* to determine whether or not the former is a junior synonym of the latter. The technique of taxonomic analysis (comparison of the different character states of the two taxa) was preferred over cladistic analysis because a cladistic analysis would only reveal that *Syntarsus* and *Coelophysis* are sister taxa. However, the analysis is based on the list of theropod characters developed by Rauhut (2003) for his comprehensive cladistic analysis. He used 224 characters, 87 of which are cranial. Four additional characters have been added to his list of characters: (88) the presence or absence of a posterolateral nasal process (what Raath 1977, termed the 'nasal fenestra'); (89) size of the antorbital fenestra more than 40 per cent of total skull length, or less than 40 per cent; (90) width of the base of the vertical ramus of the lachrymal expressed as a percentage of its height; and (91) the presence or absence of interdental plates.

Overall, this analysis reiterates the remarkable similarity between *Syntarsus* and *Coelophysis.* Of the 91 cranial characters used, only 13 points of doubt or difference between the two taxa emerged, most of the uncertainty caused by preservational artefacts or missing data. The remaining 78 cranial characters were identical in the two taxa. For those 13 characters where differences were noted between the genera, ten characters were scored as uncertain in *Coelophysis* because they were either obscured or distorted, or

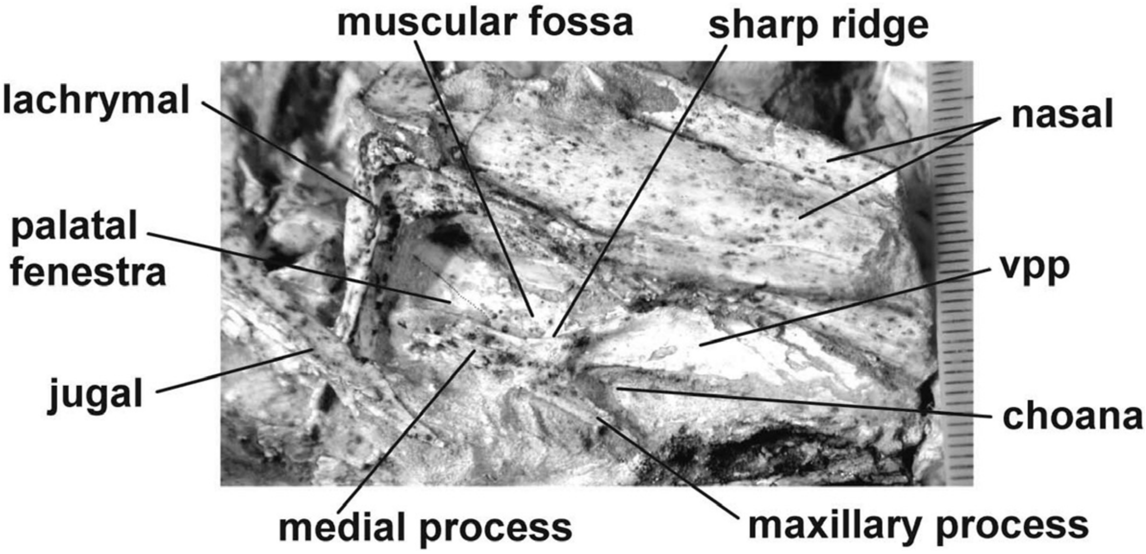

Figure 7. Tetraradiate right palatine bone of QG165 showing the deep muscular fossa and sharply delineated ridge as described by Witmer (1997). 'vpp' = vomeropterygoid process (scale divisions = mm).

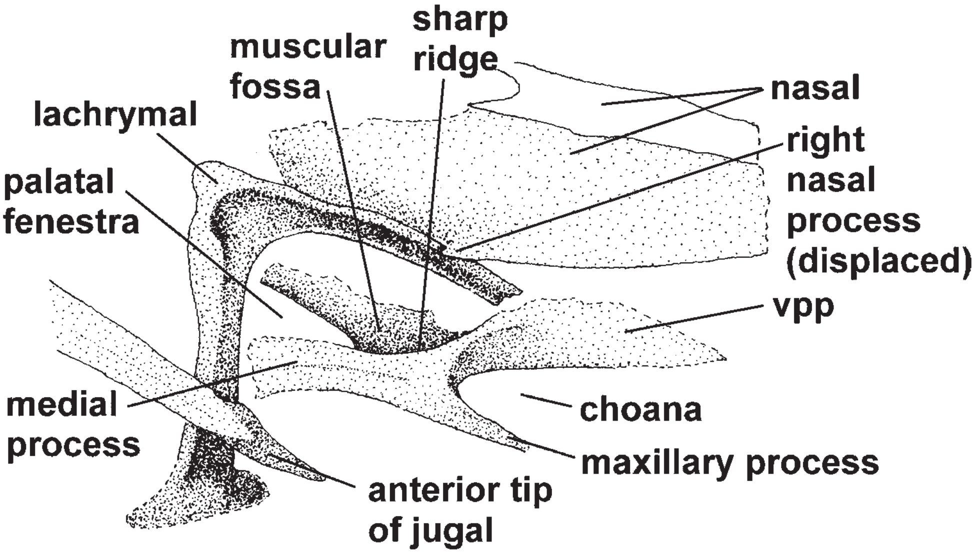

Figure 8. Interpretative drawing of palatine of QG165 in relation to surrounding elements (see also Figs 6 and 8).

there was insufficient information to score the character with confidence. Most *Coelophysis* skulls have been so bilaterally compressed that they provide information only in lateral view, and for this reason it is difficult to establish the nature of endocranial characters. Characters dealing with the pneumatization were difficult to score for the same reason, and because Colbert (1989) provided little detail on this aspect of the morphology. Characters of the dentary teeth in *Coelophysis* were problematic because the jaws of most specimens are clamped shut and the upper jaw tends to obscure dentary teeth. The ten uncertain characters in *Coelophysis* are: (37), (41), (49), (53), (60), (61), (63), (72), (74) and (83) (see Appendix 1). The three characters where points of distinction were confirmed are (13), (70) and (90). Character 13 relates to the shape of the maxillary antorbital fossa: in *Coelophysis* it is pointed, whereas in *Syntarsus* it is squared. Character 70 relates to the length of the maxillary tooth row and the posterior point at which it ends: the maxillary tooth row is longer in *Coelophysis* than in *Syntarsus.* Character 90 relates to the width of the ventral base of the vertical ramus of the lachrymal in relation to its height: in *Syntarsus* the width of the base of the lachrymal is less than 30 per cent of the height of the vertical ramus, whereas in *Coelophysis* it is more than 30 per cent.

DISCUSSION

There are no generally accepted criteria for distinguishing taxonomically significant differences from mere individual variation, and Molnar (1990) cautions against the assumption that taxonomically significant differences are always expressed in the skeleton, as there is a tendency to underestimate taxonomic diversity in fossils. However, an advantage when comparing *Coelophysis* and *Syntarsus* is that the taxa are based on samples of material that are quantitatively more than adequate and qualitatively excellent, especially where *Syntarsus* is concerned (Raath 1990).

The first step in assessing whether *Syntarsus* is a synonym of *Coelophysis* is to review Raath's (1977) list of thirteen characters that he considered diagnostic of the taxon. Five of these relate to differences in the length of a

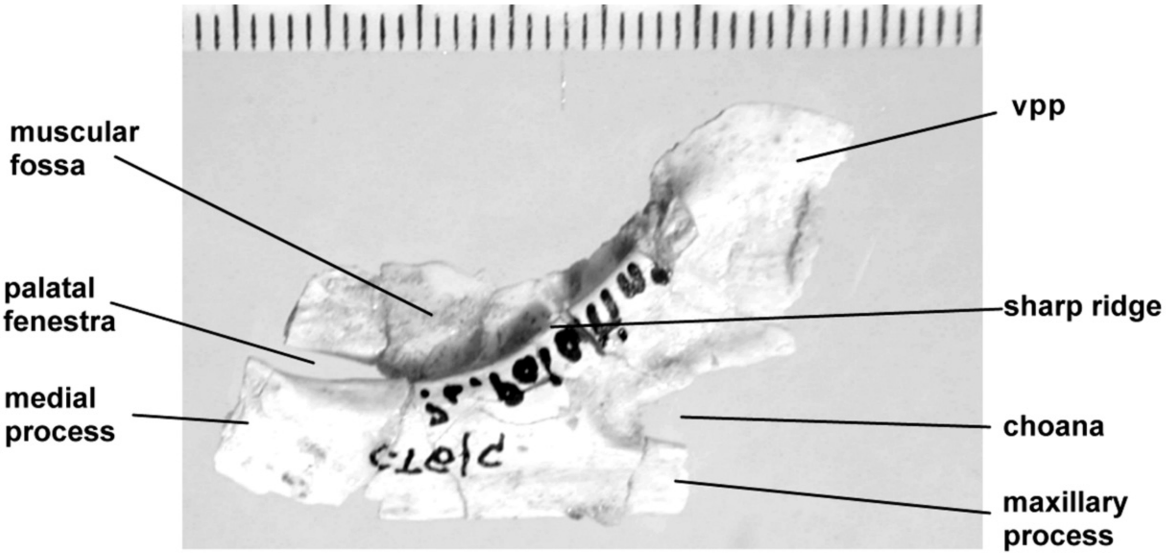

Figure 9. The right palatine of QG241, reversed left-to-right for comparison with QG165 in Fig. 7 (photograph: M.A. Raath) (scale divisions = mm).

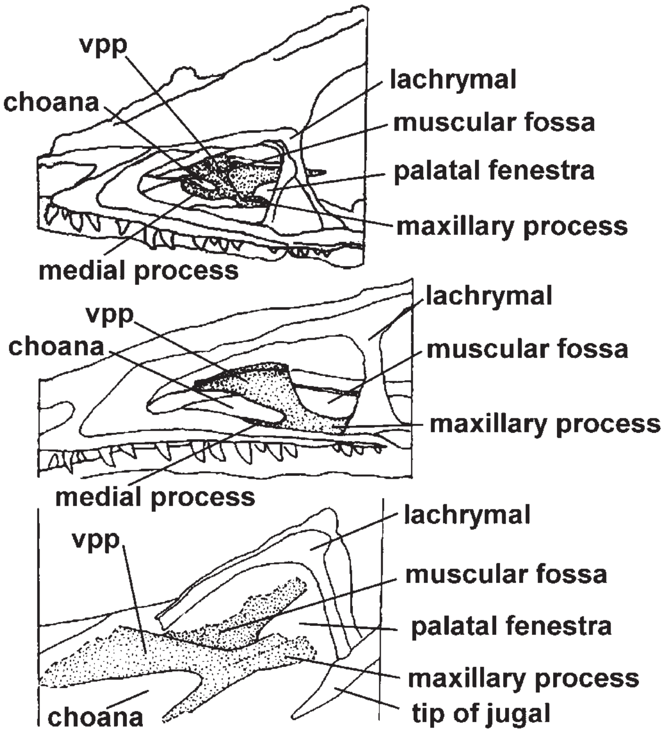

Figure 10. Comparison of tetraradiate coelophysoid palates illustrating the muscular fossa described by Witmer (1997). A. *C. bauri* (CM31375) redrawn from Witmer (1997); B. *C bauri* (CM31374), redrawn from Witmer (1997); C. *C. rhodesiensis* QG165. 'vpp' = vomeropterygoid process.

number of elements of the skull, expressed as percentages. Estimates given by Raath (1977) all indicate that *Syntarsus* is generally smaller than *Coelophysis,* except for the proportional length of the antorbital fenestra. Raath (1977) estimated the length of the antorbital fenestra at 43 per cent of total skull length in *Syntarsus.* Owing to the partial disarticulation of QG165 it is not possible to estimate the length of the antorbital fenestra, but Rowe (1989) estimated that the antorbital fenestra of S. *kayentakatae* was approximately 26 per cent of total skull length, which is similar to the figure obtained for *Coelophysis* (27 per cent: Colbert 1989). It is difficult to assess dental characters in QG165 because its jaws are incompletely preserved. However, Colbert (1989) noted that the upper tooth row in *Coelophysis* extends to a point beneath the middle of the orbit while in *Syntarsus* the upper tooth row extends to the posterior border of the antorbital fenestra. Also, it has not been possible to estimate ratios of skull height to length, or skull length to presacral length in QG165 because of its incompleteness: Raath's (1977) estimates have not been accepted because the new reconstruction of the nasal and lachrymal contact proposed here would affect his ratios, making the antorbital fenestra in *Syntarsus* proportionally significantly smaller than he estimated. As far as the palatine is concerned, it is noted that Raath's (1977) reconstruction was based on a disarticulated right palatine bone that was inverted in the reconstruction. The reconstruction proposed herein follows the pattern found in most non-avian theropods as described by Witmer (1997) and Harris (1998) – it is a tetraradiate bone consisting of four conjoined processes.

Secondly, the *Syntarsus* characters listed as definitive by Rowe (1989), (23) antorbital fenestra more than 40 per cent of total skull length, and (24) lachrymal overlaps the jugal laterally and reaches the alveolar border, must be re-examined. Both characters were based on Raath's reconstruction of disarticulated cranial elements. Rowe (1989) believed that if these characters were not sustained by articulated material, the diagnosis of *S. rhodesiensis* might need to be reconsidered.

Thirdly, it was found that *Syntarsus* and *Coelophysis* differed in only three of 91 phylogenetically informative cranial characters (see above). All these characters 13, 70 and 90 (see Appendix 1), relate to and affect the shape of the antorbital fenestra, subtly reducing its size in *Syntarsus.*

Previously contested characters were then re-evaluated using new evidence gleaned from the reconstruction of QG165. Because the right nasal and the right lachrymal of QG165 are still esentially in articulation, it is possible to propose a different reconstruction from that given by Raath (1977). The dorsal ramus of the right lachrymal and the lateral edge of the right nasal articulate in the region of the feature described above as an incipient parasagittal crest (although more likely an artefact of distortion) in a position comparable to the longitudinal crest described by Rowe (1989) in *S. kayentakatae.* The posterolateral nasal process (which Raath, 1977, suggested defined what he termed the 'nasal fenestra') articulates with the anterior edge of this slightly raised feature, which extends from the posterior end of the lachrymal to a point about midway along its dorsal ramus. The nasal process could be interpreted as a derived feature of neotheropods including the coelophysoids. The character is not found in basal theropods such as the Herrerasauridae, although this is not surprising since there are significant morphological disparities between the coelophysoids and the herrerasaurids (Sereno & Novas 1993; Rauhut 2003). A homologous structure is found in various other derived neotheropods such as the much younger *Tyrannosaurus rex* (Brochu, 2003). There is, however, an analogous structure in basal sauropodomorphs such as *Plateosaurus* (Galton 1984).

The footplate of the lachrymal is noticeably narrower in *Syntarsus* than in *Coelophysis,* measuring less than 30 per cent of the height of the vertical arm of the lachrymal, compared with more than 30 per cent in a number of specimens of *Coelophysis,* most notably CM31374 (see Fig. 4), but the extent of individual variation in this character remains unknown. In the reconstruction of QG165 proposed here, the lachrymal would articulate partially with the medial surface of the jugal and maxilla. In Raath's (1977) reconstruction the lachrymal overlaps the jugal and maxilla laterally, reaching the alveolar border, and shortening the height of the skull. In the light of the new evidence from QG165, this interpretation is patently incorrect.

There are different interpretations of the jugal in coelophysoids: according to Rowe (1989) the anterior process of the jugal of *S. kayentakatae* is forked; photographs of *Coelophysis* specimen CM 31374 show the jugal tapering to a fine point; the anterior end of the jugal in *Syntarsus* QG278 appears blunt, but the end is clearly broken; in Raath's (1977) reconstruction, the lachrymal overlaps and therefore obscures the anterior end of the jugal; and Colbert (1989) makes no mention of this character at all in his monograph on *Coelophysis.* In view of the excellent state of preservation of the right jugal and the anterior tip of the left jugal in QG165, this character was coded as 'tapering' in the taxonomic analysis.

This articulation between the jugal and the antorbital fenestra has also been variously interpreted but in QG165 the jugal is unambiguously excluded from the antorbital fenestra by the posterior end of the maxilla and the ventral footplate of the lachrymal. In *S. rhodesiensis,* Raath (1977) contended that the jugal was excluded from the antorbital fenestra by the lachrymal footplate, which overlapped the jugal. Rowe (1989) reported that the anterior end of the jugal in *S. kayentakatae* was excluded from the antorbital fenestra by the posterior end of the maxilla. In Colbert's (1989) reconstruction, the anterior tip of the jugal of *C. bauri* reaches the rim of the antorbital fenestra, whereas in photographs of CM31374 and other *Coelophysis* specimens, the tapered tip of the jugal is excluded from the fenestra and this is held to be correct.

The shape of the maxillary antorbital fossa (13): the snout of *Syntarsus* (BP/1/5278) is squared at the anterior margin, forming an angle of approximately 70 degrees to the horizontal dentigerous ramus, whereas the corresponding region of a cast of *Coelophysis* (CM31374) is pointed, forming an angle of approximately 50 degrees.

The next question to consider is whether the shape of a cranial cavity such as the antorbital fenestra represents a significant functional character in coelophysoids, important enough to justify generic separation between the two taxa. Witmer (1997) advances three hypotheses for the function of the antorbital cavity: it could be to house (1) a gland, (2) a muscle, or (3) a paranasal air sac. Having tested all three hypotheses, he concludes that only a paranasal air sac would involve all the bone structure associated with the antorbital fenestra, and that the function of the air sac is simply to pneumatize bone in an opportunistic way. According to Witmer (1997), factors such as weight reduction and optimizing design are secondary effects of air sacs. On this basis characters 13, 70 and 90 do not appear sufficiently significant to justify a generic separation of the taxa, although they might well be significant at species level.

There are other reasons for supporting a distinction at species level, such as the geographic and chronological separation between the two taxa. Geographic separation would not of necessity imply generic differentiation, although it might promote specific divergence. In the Late Triassic, coelophysoids represented the first successful worldwide radiation of theropods (Farlow 1993; Rauhut 2003). Coelophysoids are found in both the Late Triassic and the Early Jurassic, covering a span of around 15–20 million years, from the Carnian-Norian in North America (about 220 Ma) to the Hettangian in southern Africa (about 205.7 Ma to 201.9 Ma; Harland *et al.* 1990). Rauhut (2003) has identified four major theropod radiations in all, with coelophysoids being replaced by ceratosaurs (*sensu* Rauhut 2003) and tetanurans in the Middle Jurassic. Early Mesozoic theropod faunas lived in a world where the movement from one landmass to another was possible because of continental configuration and, as a result, faunas were globally rather uniform. The differences between theropod faunas became more marked with the subsequent fragmentation of Pangaea. The distinctions in faunas between Laurasia and Gondwana increased from the Triassic to the Cretaceous (Farlow 1993; Rauhut 2003), reflecting both early endemism, and the geographic separation of the continents. As an Early Mesozoic fauna, coelophysoids match the pattern of uniformity described by Fowler (1993) and Rauhut (2003), supporting the notion of an early Mesozoic supercontinental fauna (Paul 1993).

The chronological separation of *Coelophysis* (Late Triassic) and *Syntarsus* (Early Jurassic), might be responsible for some of the minor morphological differences that do exist. Niche adaptations to local (desert) conditions in the southern African portion of Gondwana undoubtedly also account for some part of this variation over time.

We therefore conclude that *Syntarsus* is indeed a junior synonym of *Coelophysis,* as first articulated by Paul (1988), but that the current species distinctions between the Laurasian form (*C. bauri*) and the Gondwanan form (*C. rhodesiensis*) remain valid. We acknowledge, however, that being limited to study of cranial elements only, and relying largely on a single incomplete skull, the foundation on which these conclusions are based is not as solid as we would have preferred. But we are confident that discovery of further articulated cranial material of the Gondwanan coelophysoid material will settle the matter and show that these conclusions are correct.

SYSTEMATIC PALAEONTOLOGY

Class Dinosauria Owen, 1842
Order Saurischia Seeley, 1887
Suborder Theropoda Marsh, 1881
Superfamily Coelophysoidea Welles, 1984 (*sensu* Holtz, 1994)
Family Coelophysidae Paul, 1988

Genus *Coelophysis* Cope, 1889

Type species

Coelophysis bauri Cope 1889 (by designation: Colbert, Charig, Dodson, Gillette, Ostrom & Weishampel 1992). A holotype was not designated by Cope in 1887 and was subsequently selected by Hay in 1930. Specimen AMNH 2722, four sacral vertebrae and an associated pubic process of an ilium, was selected as the lectotype (Colbert 1989).

Synonyms

Tanystropheus von Meyer 1855; (partim; non *T. conspicuus* von Meyer 1855; *T. longobardicus* (Bassani, 1886); *T. antiquus* von Huene, 1905; *T. meridensis* Wild, 1980).
Coelurus Cope 1887
Podokesaurus Talbot 1911
Syntarsus Raath 1969 (non *Syntarsus* Fairmaire 1869)
Longosaurus Welles 1984
Rioarribasaurus Hunt & Lucas 1991
Megapnosaurus Ivie, Slipinski & Wegrzynowicz 2001

Diagnosis (Rauhut 2003)

The diagnosis of the genus *Coelophysis* is founded on a hypodigm consisting of the specimens discovered by Cope and attributed to *C. bauri* and the species regarded as synonyms, *C. longicollis* and *C. willistoni,* as well as complete skeletons of *C. bauri* excavated at Ghost Ranch, New Mexico, by Colbert. *Coelophysis* differs from *Eoraptor, Herrerasaurus* and *Staurikosaurus* in the presence of pleurocoels in the dorsal vertebrae, the more elongated dorsal vertebrae, five fused sacral vertebrae, dolichoiliac ilium, presence of a small lateral projection on the distal end of the tibia and the functionally tridactyl foot with metatarsal I that is attached to metatarsal II and does not reach the ankle joint (Rauhut 2003). It differs from *Gojirasaurus* in the relatively lower dorsal neural spines and the significantly smaller size, from *Liliensternus* in the absence of the broad ridge that extends from the posterior end of the diapophyses to the posterior end of the vertebral centra in cervical vertebrae and the smaller size, from *Procompsognathus* in the considerably larger overall size, and from *Shuvosaurus* in the lack of any derived cranial features of the latter taxon (Rauhut 2003). The posterolateral nasal process is the same in *C.bauri* as in *C. rhodesiensis* and *C. kayentakatae.*

Referred species

C. rhodesiensis (Raath 1969)
?*C. kayentakatae* (Rowe, 1989)

Distribution

U.S.A.: Chinle Formation, Arizona, New Mexico, Petrified Forest National Park, Arizona, Kayenta Formation, Rock Head, Willow Springs, Arizona

Africa: Zimbabwe (Nyamandhlovu, Chitaki River, Maura River); South Africa (northeastern Free State Province)

Europe: ?Wales (D. Warrener, pers. comm. to M. Raath 1984)

Stratigraphic range

Late Triassic: Carnian/Norian (227.4Ma 220.7Ma) – Chinle Formation

Early Jurassic: Hettangian (205.7Ma 201.9Ma) – Forest Sandstone Formation, Elliot/Clarens Formation

Coelophysis rhodesiensis (Raath 1969)

Synonyms

Syntarsus rhodesiensis Raath, 1969
Megapnosaurus rhodesiensis Ivie, Slipinski & Wegrzynowicz, 2001

Holotype QG1 housed in the Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe.

Locality and horizon of the holotype

From exposures in the Kwengula stream on Southcote Farm at 19°58′S; 28°24′ 35″E, about 38km northwest of Bulawayo, Zimbabwe (Raath 1969). The Forest Sandstone of Zimbabwe correlates with the upper ‘Stormberg Group’ in South Africa, and is thus Early Jurassic in age.

Revised diagnosis

C. rhodesiensis is a small bipedal coelophysoid dinosaur (*sensu* Rauhut 2003) that can be distinguished from *C. bauri* by the following cranial characters: the anterior margin of the maxillary antorbital fossa in *C. rhodesiensis* is blunt and squared; the width of the base of the vertical ramus of the lachrymal is less than 30 per cent of its height; and the maxillary tooth row ends at the anterior rim of the lachrymal with the lower tooth row corresponding. These three characters define the margins of the antorbital fenestra, which would be proportionally smaller than the fenestra in *C. bauri.*

We gratefully acknowledge the co-operation of the National Museums and Monuments of Zimbabwe, and especially of the Curator of Palaeontology at the Zimbabwe Natural History Museum, Darlington Munyikwa, in permitting us to borrow the specimen QG165 on which this study relies so heavily. We are similarly grateful to Alex Downs of the Ruth Hall Museum of Paleontology, Ghost Ranch, New Mexico, for generously sharing with us some of his unpublished information on *Coelophysis.* Paul M. Barrett is thanked for his thorough, incisive and very helpful review of the manuscript. We are deeply grateful to Oliver W.M.Rauhut for his thoughtful comments on the MSc dissertation from which this paper is derived.

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APPENDIX I

Data matrix of cranial characters based on Rauhut (2003). [(Numbers in brackets are the values scored by Rauhut (2003)]

Character	*Coelophysis*	*Syntarsus*
1	0	0
2	1	1
3	0	0 (1)
4	1	1
5	1	1
6	2	2
7	0	0
8	1 (?)	1
9	1	1
10	0	0
11	0	0
12	1	1
13	0 (1)	1
14	0	0
15	1	1
16	0	0
17	0	0
18	0	0
19	0	0
20	0	0
21	0	0
22	1	1
23	0 (?)	0 (1)
24	1 (?)	1 (0/1)
25	0	0
26	0	0
27	1 (0)	1 (0)
28	1	1
29	1	1
30	0	0
31	0	0
32	0	0
33	0	0
34	0	0
35	0	0
36	0 (?)	0 (1)
37	?	0
38	0	0
39	0	0
40	0	0
41	? (?)	0
42	0	0
43	0	0
44	0	0
45	0	0
46	1 (?)	1
47	0	0
48	0 (?)	0
49	?	1 (?)
50	0 (?)	0
51	0	0
52	1 (?)	1
53	?	0
54	0	0
55	0 (?)	0
56	1	1
57	1	1
58	0	0
59	0 (?)	0 (1)
60	?	0
61	?	0
62	0	0
63	?	0
64	0 (?)	0
65	1 (?)	1
66	1 (0)	1 (0)
67	1 (?)	1
68	1	1 (?)
69	1 (0)	1 (0)
70	(0)	2 (0)
71	0	0
72	? (0)	1 (0)
73	(0)	(0)
74	? (0)	? (0)
75	0	0
76	0	0
77	0	0
78	?	?
79	0 (?)	0 (?)
80	?	0
81	0	0
82	0	0
83	?	0 (1)
84	1	1
85	0	0
86	0	0
87	0	0
88	0	0
89	1	1
90	0	1
91	1	1

A description of the sedimentology and palaeontology of the Late Triassic–Early Jurassic Elliot Formation in Lesotho

E.M. Bordy*, P.J. Hancox & B.S. Rubidge

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

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Sedimentological studies of the Late Triassic to Early Jurassic Elliot Formation (Karoo Supergroup) in Lesotho have proved to be a fundamental element in our research into the development of the main Karoo Basin of southern Africa. Complementing previous research in South Africa, studies of the architecture of the sedimentary units in the Elliot Formation reveal that there are two contrasting types of sandstone body geometries, each resulting from different fluvial depositional styles. In the lower part of the formation, the sandstones resemble multi-storey channel-fills, interpreted as deposits of perennial, moderately meandering fluvial systems. On the other hand, the upper part of the formation is characterized by mostly tabular, multi-storey sheet sandstones which resulted from ephemeral fluvial processes. Based mainly on changes in the fluvial style and palaeocurrent pattern within the formation, the regional lithostratigraphic subdivision applied to the Elliot Formation in South Africa is applicable in Lesotho as well. This study adds detail and therefore refines the stratigraphic subdivision documented for the South African succession, and as such forms an important framework for palaeontological, palaeoecological and biostratigraphic studies in Lesotho.

Keywords: Lesotho, facies architecture, palaeocurrents, main Karoo Basin.

INTRODUCTION

The Late Trassic–Early Traissic is an important time both palaeontologically and geologically, and the excellent exposures in Lesotho have proven to be crucial to our understanding of this period of the geological history of Gondwana, which preceded the break-up of the supercontinent. This paper presents the results of a field-based sedimentological investigation of the Elliot Formation (Karoo Supergroup) in the southern and western half of Lesotho, which forms part of a regional research project focussed on the development of the main Karoo Basin in southern Africa. The investigation of the Elliot Formation in South Africa predated the present study, and its results are described in three papers by the same authors (Bordy *et al.* 2004a,b,c). Although various aspects of this work overlap with the descriptions of the South African succession, this work is warranted because of the high-quality exposures in Lesotho, which have not been described in terms of modern sedimentology and which allow for the intrabasinal correlation of the southern and northern outcrops of the formation within southern Africa. In addition, these exposures often show the elemental architecture better than their South African counterparts, a fact that is especially true for the upper part of the formation. Furthermore, these sedimentological descriptions will aid current palaeontological and biostratigraphic work being undertaken in Lesotho.

Numerous important fossils have been collected from Lesotho including holotypes of cynodonts *Tritylodon* (Owen 1884) and *Scalenodontoides* (Crompton & Ellenberger 1958), mammals *Erythotherium* (Crompton 1964) and *Megazostrodon* (Crompton & Jenkins 1968), as well as numerous well-preserved dinosaur and crocodilomorph specimens. Furthermore, Lesotho has the best exposures of Late Triassic to Middle Jurassic vertebrate trackways in southern Africa (Ellenberger 1970; Olsen & Galton 1984). Previous palaeontological collections were, however, often not stratigraphically well-constrained, many important palaeontological specimens are unprovenanced, and the Lesotho exposures have lacked the extensive methodological sampling of their South African counterparts (e.g. Kitching & Raath 1984). This is changing, however, and there is a renewed interest in the numerous dinosaurs trackway sites, as well as in the Triassic and Jurassic faunas of Lesotho (Smith & Battail, pers. comm.). With many specimens still *in situ,* the Lesotho exposures presently offer some of the last virgin ground for controlled, detailed taphonomic and biostratigraphic collecting. Although the Elliot Formation in Lesotho presents a vast potential for new and biostratigraphically significant findings, without a well-established geological framework the advancement of palaeontological research in Lesotho will be hampered. This paper therefore documents, for the first time, the stratigraphy, detailed sedimentary facies architecture, thickness and palaeocurrent patterns, as well as brief notes on new fossil localities in the Elliot Formation of Lesotho.

Geological background

The Elliot Formation is part of the Late Carboniferous to Middle Jurassic Karoo Supergroup (Fig. 1) which outcrops in the main Karoo Basin of South Africa and Lesotho, as well as in several other separated outcrop areas in central and southern Africa (Johnson *et al.* 1996; Bordy 2000; Bordy & Catuneanu 2001). The main Karoo Basin is a retro-arc foreland basin which developed in front of the

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*Author for correspondence. E-mail: emese_bordy@yahoo.com

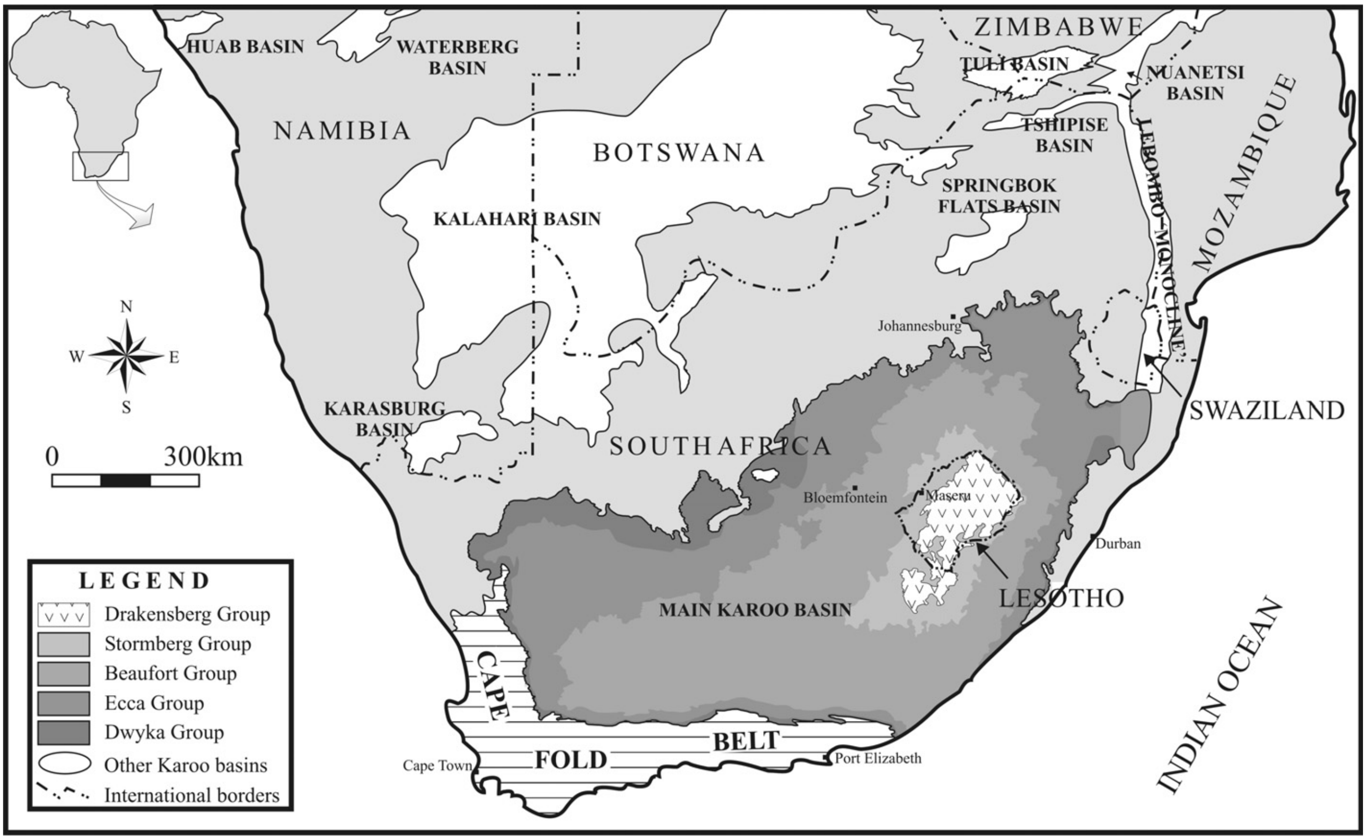

Figure 1. Geological map of the Karoo Supergroup in the main Karoo Basin (Lesotho and South Africa), and other outcrop areas with Karoo-age deposits in southern Africa (modified after Johnson *et al.* 1996; Catuneanu *et al.* 1998).

Cape Fold Belt (Fig. 1) in response to the late Palaeozoic–early Mesozoic subduction of the palaeo-Pacific plate beneath the Gondwana plate (e.g. Johnson 1991; Catuneanu *et al.* 1998; Pysklywec & Mitrovica 1999; Catuneanu & Elango 2001). Together with the underlying Molteno and overlying Clarens formations, the preserved succession of the Elliot Formation (Fig. 2) was deposited during the final stages of the basin history, in a foresag setting (Catuneanu *et al.* 1998).

Previous research

In spite of the excellent Elliot Formation outcrops in southern Africa, to date, there are only a few field-based geological investigations dealing with the sedimentological relations of the formation. Most of these studies were undertaken in South Africa and have shown the formation to consist of continental red beds of fluvial, lacustrine and aeolian origin (e.g. Botha 1968; Le Roux 1974; Johnson 1976; Visser & Botha 1980; Eriksson 1983 1985; Kitching & Raath 1984; Smith *et al.* 1993; Johnson *et al.* 1996; Johnson *et al.* 1997; Smith & Kitching 1997). The only detailed description of the Elliot Formation of Lesotho is a general geological report complied by Stockley more than fifty-five years ago (Stockley 1947). Although there is a reasonable database of the dinosaur fossils and footprint locations in Lesotho based primarily on work done by P. Ellenberger over two decades from the 1950s to 1970s (Ellenberger 1970), the sedimentology and exact stratigraphic position of a number of the sites are largely unknown. Ellenberger (1970), however, utilized the stratigraphic position of the various trackway sites to establish a subdivision for the Molteno, Elliot and Clarens formations in Lesotho. This nomenclature has not been internationally accepted, and it should be noted that it has also not been rigorously tested.

DATABASE AND INTERPRETATIONS

Stratigraphy

The present study undertaken in Lesotho confirmed most of the findings of the previous South African survey (Bordy *et al.* 2004a,b,c). The most important analogy between the South African and Lesotho records is that the lithostratigraphic distinction between the lower and upper part of the formation documented in South Africa, is possible throughout Lesotho as well (Fig. 3). The formation therefore comprises two units on a basinal scale, which show different and characteristic facies assemblage, isopach and denudation patterns, and are referred to as lower Elliot Formation (lEF) and upper Elliot Formation (uEF), respectively. Apart from the geological differences, the boundary between the two units is also manifested in the geomorphology of the study area, as it forms a regionally traceable plateau. This break of slope is especially well developed in the southern outcrop area, but is also evident in the north (Fig. 3; Mauteng, Maseru District). Considering new fossil finding (Yates, written comm., 2004) it is unclear whether the two units (i.e. the lEF and uEF) correspond with the biostratigraphic units defined by Kitching & Raath (1984) as the *Euskelosaurus* and *Massospondylus* range zones, respectively. However, the tripartite lithostratigraphic subdivision (Lower,

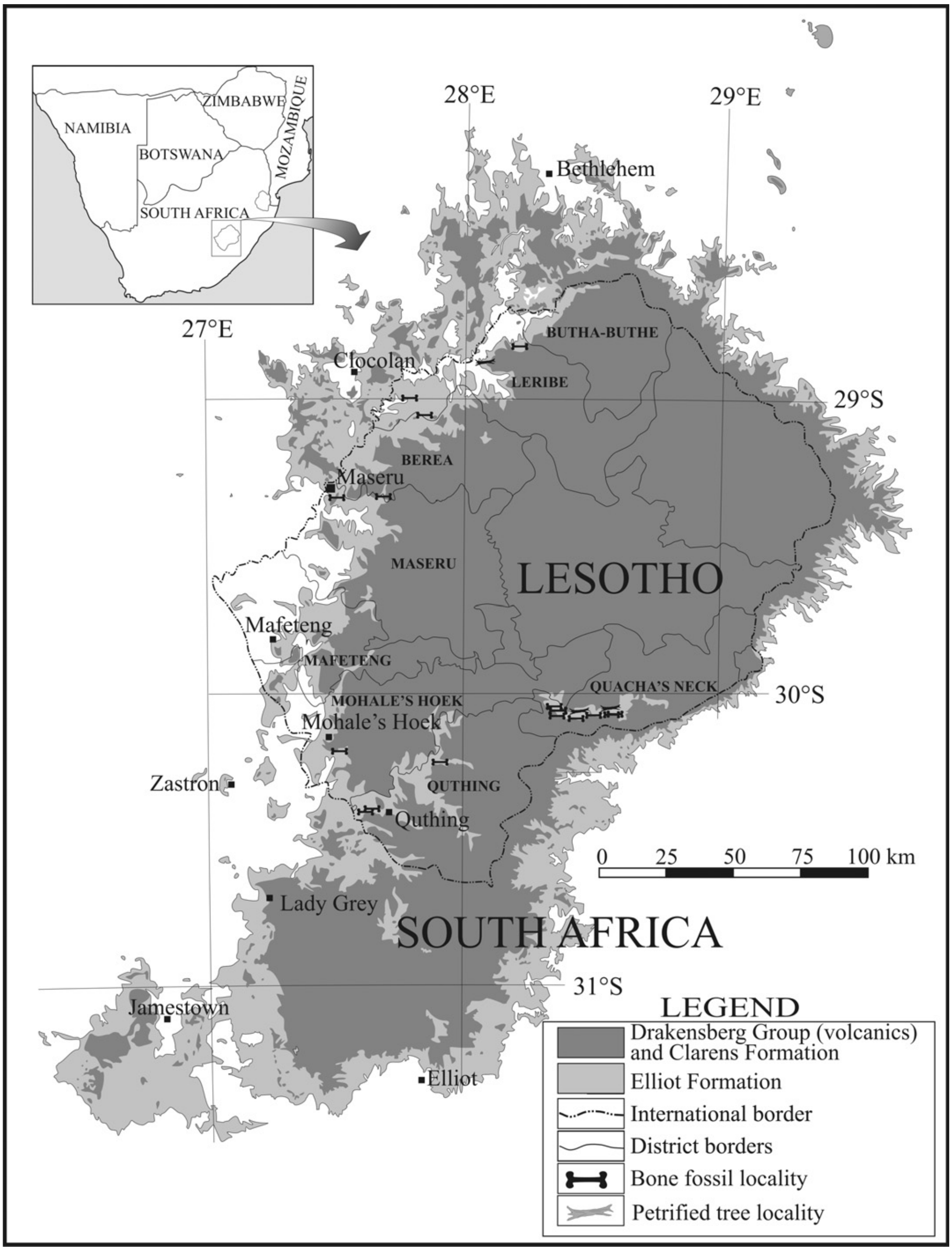

Figure 2. Geological map of the Elliot Formation in Lesotho and the Republic of South Africa (modified after the 1:1 000 000 geological map of South Africa, Swaziland and Lesotho, SA Geological Survey (1984) showing new fossil localities. See Table 1 for Global Positioning System (GPS) coordinates.

Middle and Upper Elliot formation) of Kitching & Raath (1984) could not be traced on a regional scale, and in our classification the Middle Elliot formation is included in the uEF. A tentative correlation of the lower and upper Elliot Formations, and the zones developed by Ellenberger (1970) suggests that the lEF comprises zones A4, A5 and A6, while the uEF coincides with zones B1, B2 and B3 of Ellenberger's (1970) terminology.

Sedimentology

Three major sedimentary characteristics, namely the colour, grain size and association of sedimentary structures (i.e. facies architecture) of the Elliot Formation are remarkably different in the lower and upper part of the formation in Lesotho. In addition to these characteristics, thin-section analysis of some fifty Elliot Formation sandstone samples from South Africa (Bordy *et al.* 2004c) showed that the petrography of the two units is also distinct with the uEF richer in feldspar than the lEF. The lEF lithologies are represented by various, lighter shades of red, and mottling of olive green, gray, yellow and purple, which contrast with the deep red or maroon, and sporadic light grey mottles of the uEF deposits (i.e. in general terms, lEF ~ light red, uEF ~ deep red). Generally, in a vertical section of the Elliot Formation, the fine- to medium-grained sandstones of the lEF are followed by very fine- to fine-grained sandstones in the lower part of the iEF and fine- to medium-grained sandstones in the

Figure 3. Outcrop scale differences between strata of the lower and upper Elliot Formations (lEF and uEF) are clearly visible due to the differential weathering of the dissimilar lithologies (Maseru).

upper part of the uEF. Locally (e.g. in the vicinity of Mount Moorsi, Quthing District), the uppermost uEF sandstones have medium to coarse grain sizes. As for the South African sections (Bordy *et al.* 2004b,c), the lEF sandstones become finer in grain size along a south–north profile, while the uEF sandstones lack lateral grain-size variations. Reference sections for the lEF are in the vicinity of Thabana Morena (southeast of Mafeteng, Mafeteng District), and for the uEF between Qacha's Neck and Sekake (Qacha's Neck District).

Facies architecture of the lower Elliot Formation

Architecturally, the lEF in Lesotho is characterized by lenticular, multi-storey, laterally impersistent (max. 100–150 m) sandstone bodies with maximum thicknesses of 20–25 m, and mudstone units of 20–30 m. The frequency of the sandstone bodies is constant within the lEF. Within the individual sandstone bodies, large- or medium-scale lateral accretion surfaces are common (Fig. 4A,B,C), separating slightly upward-fining successions (Lateral Accretion architectural element – LA) which are characterized by trough and planar cross-stratification, massive beds, and less commonly low-angle cross-stratification.

The quality of the lEF mudstone outcrops in Lesotho are inadequate for very detailed sedimentological interpretations, but in general sedimentary structures are rare, and most of the clay- and fine silt-rich mudstones are massive, or very rarely horizontally laminated. Pedogenic over-

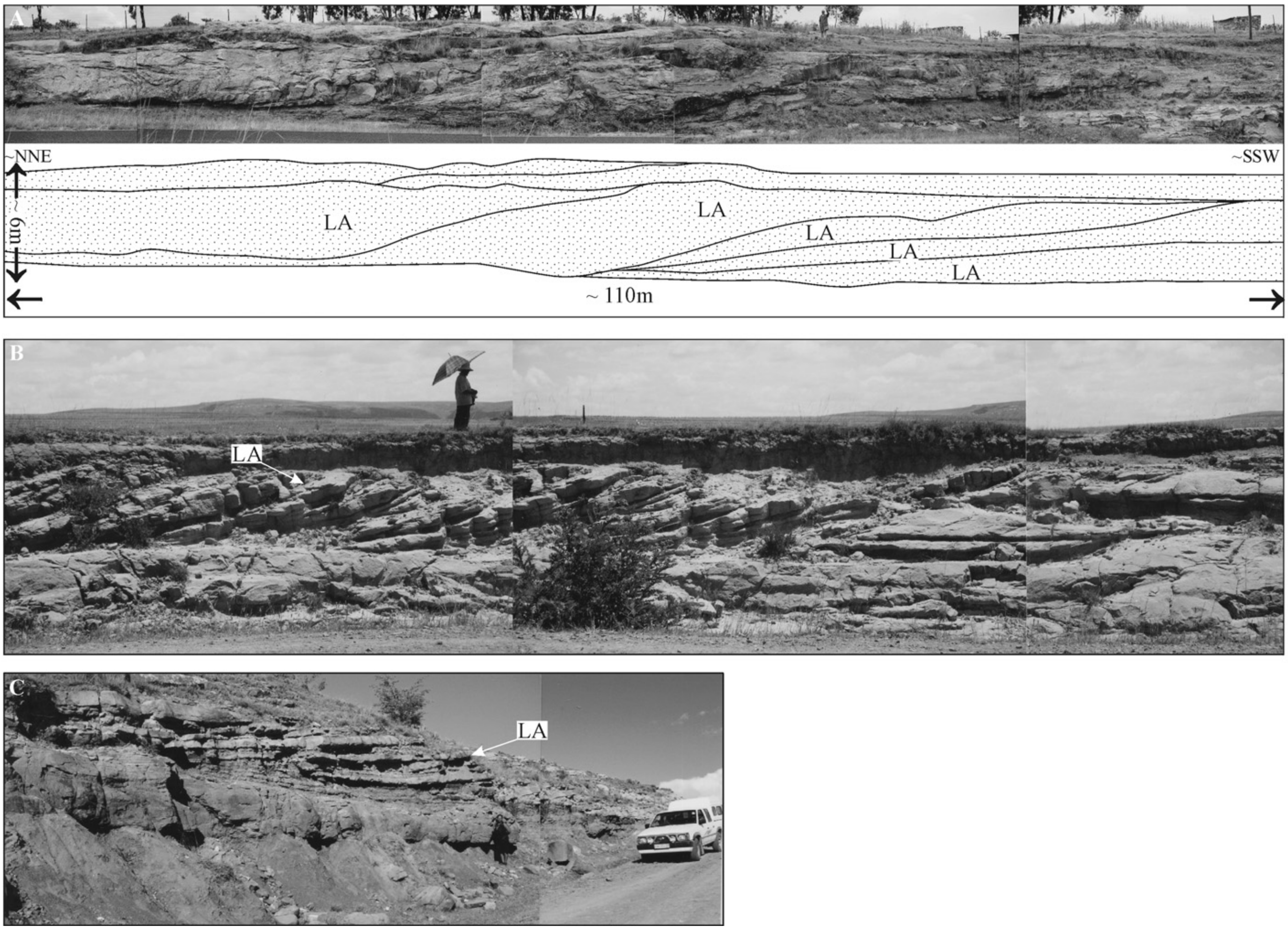

Figure 4. Gently inclined, large- (**A**, Hlotse, Leribe District) and medium-scale (**B**, east of Butha-Buthe, Butha-Buthe District; **C**, west of Ha Ntsekele, Leribe District; person for scale) lateral accretion surfaces (LA) in multi-storey sandstone bodies of the lower Elliot Formation. Person for scale.

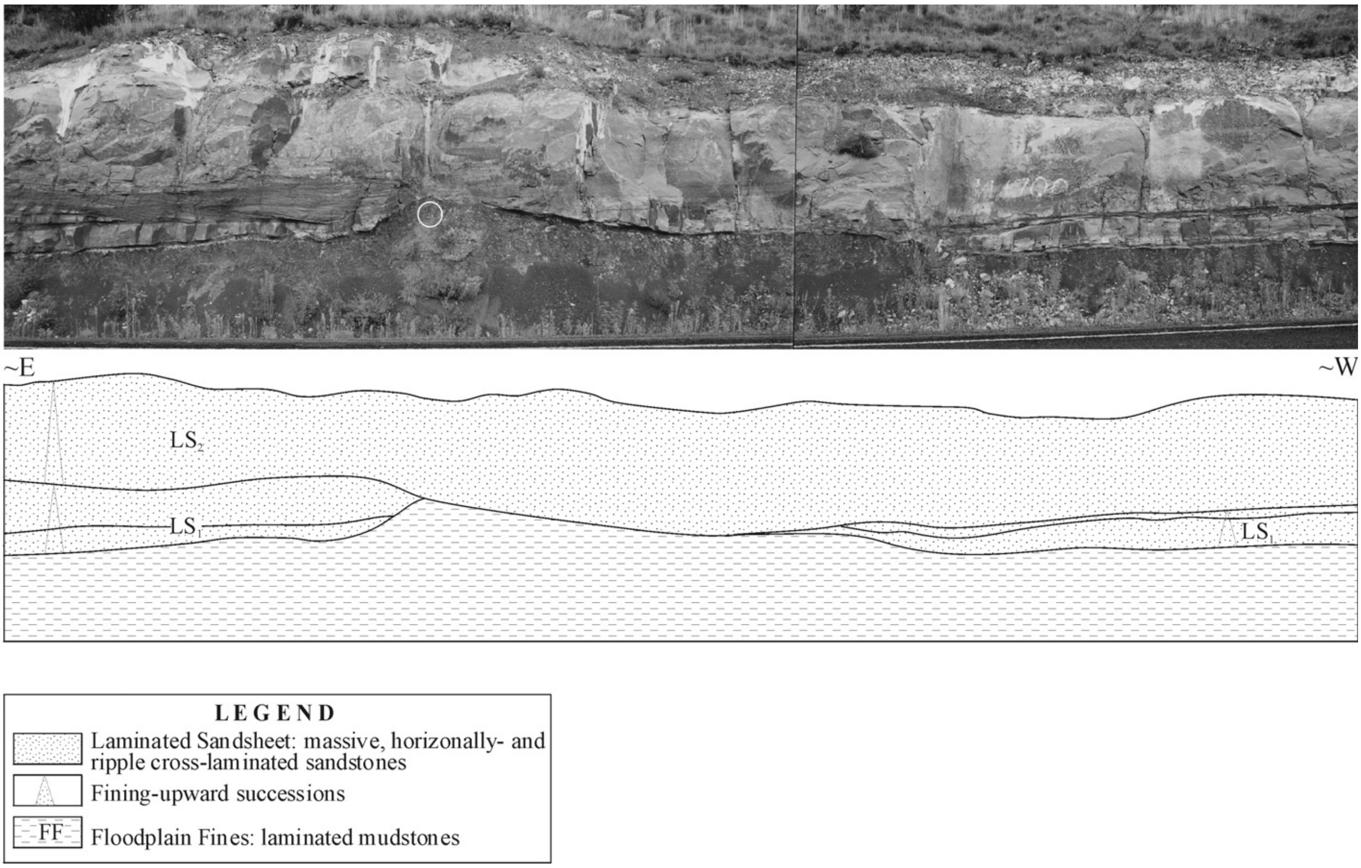

Figure 5. Sharp, laterally persistent bounding surfaces in a upper Elliot Formation tabular sandstone body. Note the lack of major irregularities at the base of the two slightly upward-fining successions (between Whitehill and Malimong, Qacha's Neck District). Hammer in white circle for scale = 28 cm.

printing is rare in the south, and even in the north, such alteration remains restricted to irregular mottles, a few dessication cracks, and rare calcareous glaebules. Small (max. 5–6 m thick), asymmetrical channel-shaped successions, and thin (0.2 to 1.2 m), laterally continuous tabular layers or rhythmically bedded units (<0.3 m) of sand- and mudstone are common features of the lEF mudstone units in South Africa (Bordy *et al.* 2004b) but have not been noted in Lesotho. However, their absence may simply be due to the limited number of lEF mudstone outcrops in Lesotho. The above mentioned sedimentary characteristics suggest a palaeoenvironmental interpretation that is identical to the scenario reconstructed for the lEF of South Africa (Bordy *et al.* 2004b), i.e. one of relatively narrow, fairly fixed, and meandering channels, and extensive floodplain areas. In addition, the diversity of large-bodied herbivores in the lEF suggests that the floodplains were well vegetated (Yates, pers. comm.). The reconstructed palaeomilieu is also consistent with the results of the previous researchers on the Elliot Formation (e.g. Botha 1968; Le Roux 1974; Visser & Botha 1980; Eriksson 1983, 1985; Smith *et al.* 1993) which all depicted a meandering river environment with associated floodplain areas for the depositional setting of the lower part of the Elliot Formation.

Facies architecture of the upper Elliot Formation

The uEF in Lesotho is characterized by sheet sandstone bodies several tens of metres wide, with maximum thicknesses of between 5 and 6 m, and 0.5 to 10 m thick mudstone units. The frequency of the sandstone bodies increases stratigraphically upwards in the uEF. Most sandstone bodies in the uEF are bound, and internally separated by, semi-horizontal, laterally persistent erosion surfaces, which lack basal irregularities larger than a few tens of centimetres (Fig. 5). In the uppermost part of the Elliot Formation, just below the junction with the Clarens Formation, amalgamated lenses of sandstones with cumulative thicknesses up to 15 m are present at places. These uppermost sandstone bodies are coarser in grain size (up to medium sand) than the other sandstones in the uEF, and at one locality (Levis Neck, Leribe District) gently inclined (shallow) lateral accretion surfaces are present (Fig. 6). The sandstone bodies of the uEF are generally characterized by couplets of horizontal and ripple cross-laminated (Fig. 7), or massive and ripple cross-laminated sandstone layers. Thicker massive beds, rare trough cross-stratification, small-scale water escape structures (Fig. 7), mud-drapes (Fig. 7), dessication cracks (Fig. 8A,B) and various bioturbation features were also observed. In addition, the uEF is characterized by a unique and fairly common lithofacies type which can be used as a regional 'hallmark' of the upper part of the Elliot Formation both in Lesotho and South Africa. In Lesotho, this lithofacies, which is a pedogenic glaebule conglomerate, occurs throughout the outcrop area (e.g. Malimong, Qacha's Neck District; Maphutseng, Mohale's Hoek District; Maseru; Ha Ntsekele, Leribe District), and is generally

Figure 6. Localized lateral accretion (LA) surfaces in the uppermost, lenticular sandstone bodies of the upper Elliot Formation (Levis Neck, Leribe District). Person for scale in white circle.

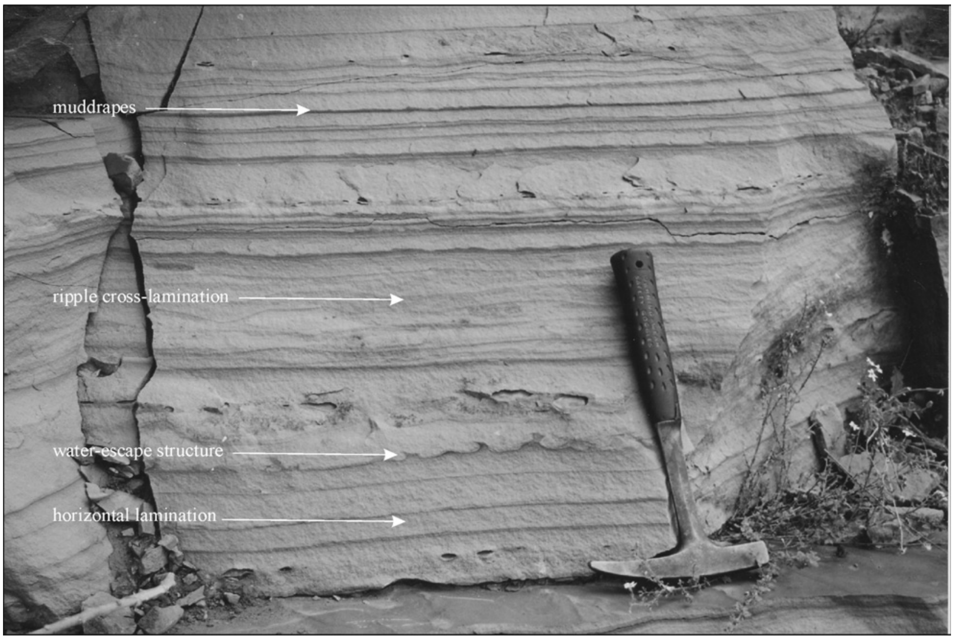

Figure 7. Horizontal lamination is commonly associated with ripple-cross lamination in the upper Elliot Formation sandstones. Small-scale water-escape structures and mud-draped surfaces are also present (along the Quthing River, Quthing District). Hammer for scale = 28 cm.

massive; however horizontal (Fig. 9) and cross-stratified beds were also observed. Apart from the granule- to pebble-sized, well-rounded carbonate and septarian nodules, other clasts, in decreasing frequency, include mudstone and sandstone, fossil bones and teeth, and occasional small quartz pebbles. Limited to the uEF, but less common than the pedogenic glaebule conglomerates, are red intraformational sandstone clast breccias and clast-rich sandstones with occasional soft sediment deformations. The angular clasts in these lithofacies are predominantly fine- to very fine-grained sandstones that show occasionally horizontal lamination. In addition, massive, very fine to fine-grained sandstone beds occur in conjunction with them. Examples of these lithofacies were documented in the south near Whitehill (Qacha's Neck District) and in the north near Ha Jonathane (Leribe District). As for the South African outcrops (Bordy *et al.* 2004b), these lithofacies are rarely found in association with the larger uEF sandstone bodies, but occur within uEF mudstone units at many places. Most of the mudstones in the uEF are massive, but horizontal lamination is more common than in the lEF mudstones. Other sedimentary structures encountered in these mudstone units are pedogenic alteration features, and include 0.2–3 m thick, laterally continuous (over 120 m) calcareous surfaces, calcretized root traces, calcareous concretions, large-scale calcretized and clay-lined shrinkage cracks and irregular, light grey mottles

Newly developed road-cuts in southern Lesotho (Qacha's Neck District), between Qacha's Neck and the area west of Sekake, present high-quality exposures of the different subunits within the uEF mudstones. Small, asymmetrical channel-shaped successions with shallow lateral accretion surfaces (Fig. 11) and laterally continuous, tabular sandstone intercalations (Fig. 12) are quite common in the upper part of uEF mudstone units, especially in association with the coarser grained, more channelized sandstone units with lenticular geometries.

The genesis of the sedimentary rocks in the lower and upper parts of the upper Elliot Formation are slightly different. The laterally persistent sheet sandstone bodies in the lower part of the uEF are seen as distal sheetflood deposits (*sensu* Hogg 1982), while the more channelized facies at the top of the uEF are interpreted as single thread, incised channels produced by successive streamfloods (*sensu* Hogg 1982). In both parts of the uEF, mudstones are explained as sediments accumulated in the floodplain environment in standing water bodies and/or abandoned watercourses. The various pedogenic alteration features and desiccation cracks in the mudstones suggest that calcareous palaeosol horizons were common, and that the floodplains were subject to long periods of dessication during the

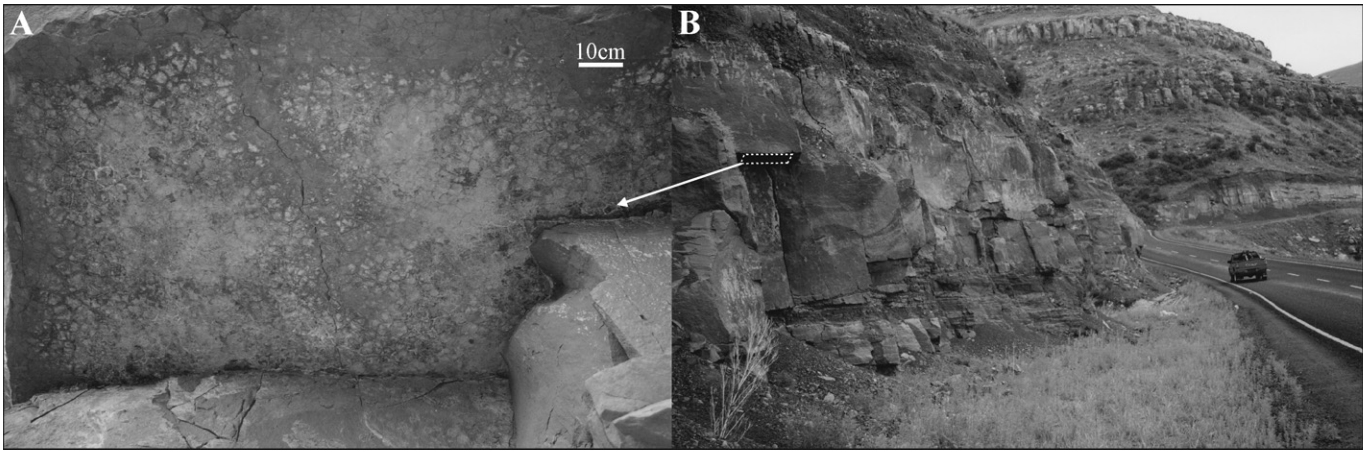

Figure 8. Cast of dessication cracks (**A**, lower bedding plane view; bar for scale) in the upper Elliot Formation found within (see arrow) a three metre thick sandstone unit (**B**, vehicle for scale) (between Whitehill and Malimong, Qacha's Neck District).

deposition of the uEF. The other, uniquely uEF lithofacies, the pedogenic glaebule conglomerates, the matrix-supported intraformational sandstone breccias, and the clast-rich sandstones, are interpreted as having been formed through the denudation of the floodplains and other penecontemporaneous strata. During severe storms (suggested by upper flow regime sedimentary structures), the uEF floodwaters were vigorous enough to erode the floodplain, thus removing the pedogenic nodules from the soils as well as parts of other semi-consolidated formations. These were later incorporated as lag material in the uEF sheet sandstone bodies, or became deposited as colluvial fills of smaller, rainstorm-eroded gullies and other irregular depression on the floodplain. The massive, very fine to fine-grained sandstone beds associated with these strata are interpreted as the first manifestations of aeolian processes during the sedimentation of the uEF.

Although a similar palaeoenvironmental picture has already been proposed for the uEF in South Africa (Bordy *et al.* 2004b), the present study not only reinforces previous interpretations, but due to the better quality road-cuts also provides a more sophisticated picture of the depositional setting of the uEF, and an improved control of the three dimensional architecture of the succession. For instance, the observed shallow, lateral accretion surfaces in the lenticular sandstone bodies of the uppermost uEF are the only indication that the later streams were slightly meandering. Also, the dessication cracks within the sandstone units characterized by couplets of horizontal (or massive) and ripple cross-laminated beds indicate that short-lived flood events with pulsating discharges were separated by periods of non-deposition and dessication. In addition, the good-quality exposures of the uEF mudstones in the Qacha's Neck District, aid the interpretation of the various sandstone subunits found

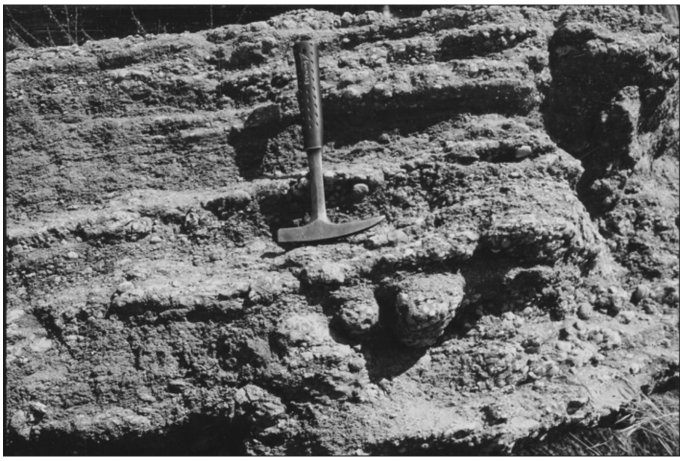

Figure 9. Clast-supported pedogenic glaebule conglomerates are unique to the upper Elliot Formation (Maphutseng, Mohale's Hoek District). Hammer for scale = 28 cm.

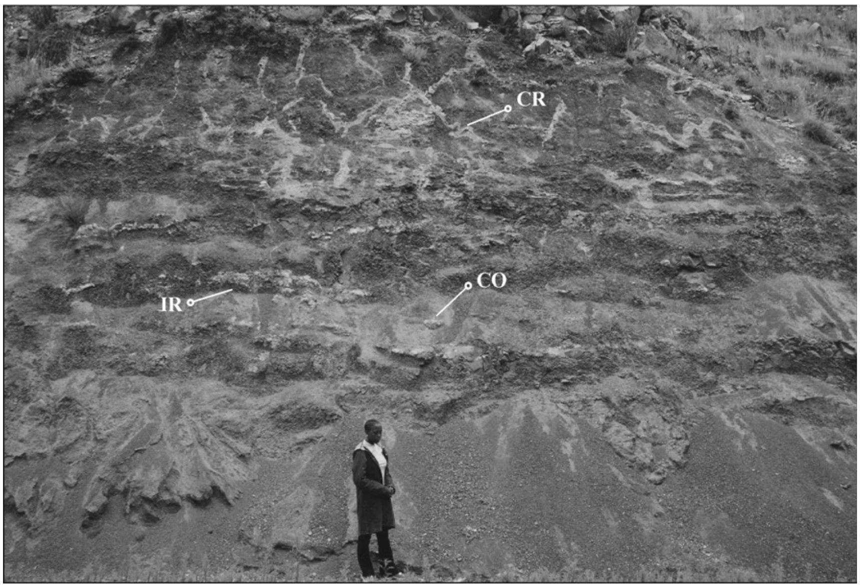

Figure 10. Calcareous concretions (CO), irregular mottles (IR), and large-scale calcretized and clay-lined shrinkage cracks (CR) in upper Elliot Formation mudstones (between Whitehill and Malimong, Qacha's Neck District). Person for scale.

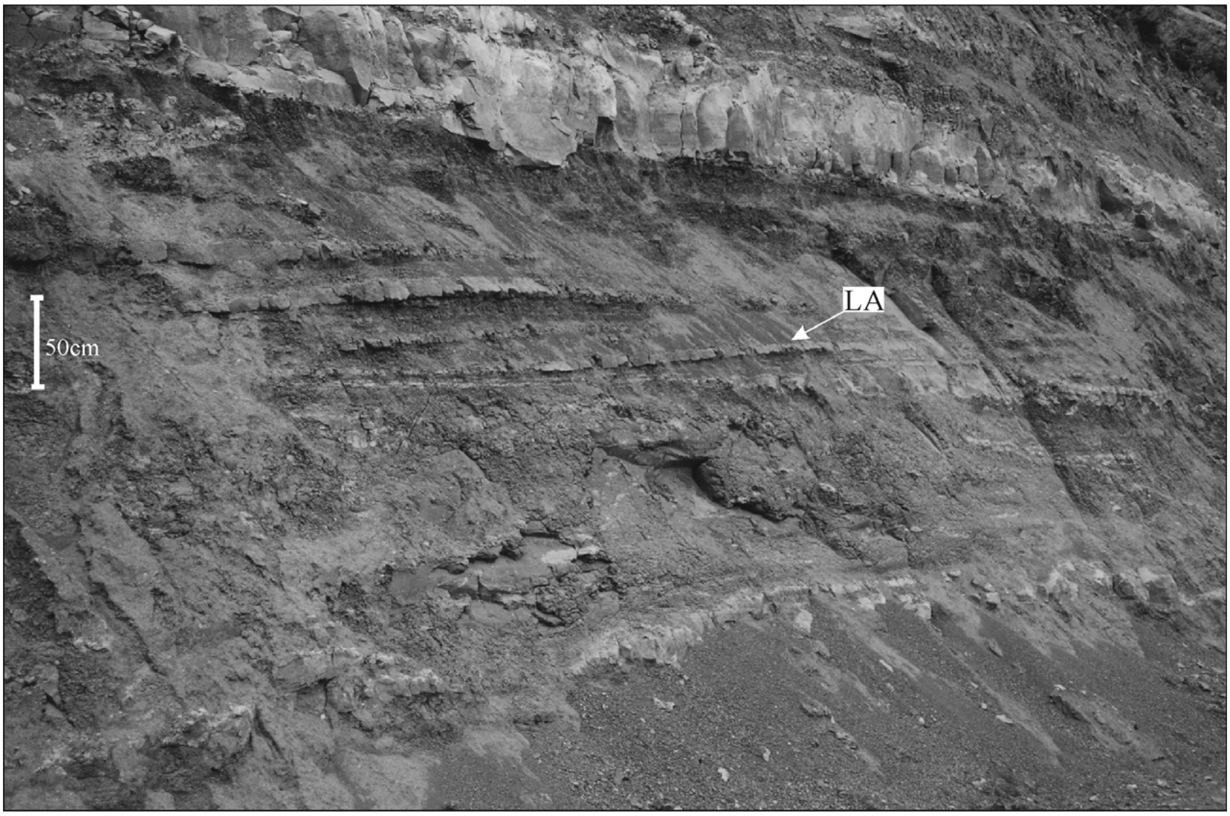

Figure 11. Shallow, lateral accretion (LA) surfaces in the channelized sandstone intercalations of the upper part of upper Elliot Formation mudstone units (between Whitehill and Malimong, Qacha's Neck District). Bar for scale.

within the floodplain deposits. In this way, it is clear that the lenticular sandstone bodies of the uppermost uEF were characterized by frequent crevassing, as demonstrated by the sharply bounded, tabular, thin sandstone strata with uneven upper surfaces that are situated in close proximity to the lenticular sandstone bodies (e.g. Fig. 12). Furthermore, the various size of the asymmetrical, channel-shaped deposits, with laterally accreted layers (e.g. Fig. 11) which were identified as secondary, sinuous channels of the floodplain, show that these secondary channels existed in various sizes from rivulets to 2–3 m deep watercourses.

Thickness variations

In order to determine the regional thickness pattern of the Elliot Formation, the correct recognition of the lower and upper boundaries of the formation is paramount. The basal contact of the Elliot Formation is easily identified in the western and northern outcrop areas where the underlying Molteno Formation is characterized by grey, gritty

Figure 12. Laterally continuous (outcrop scale), tabular sandstone intercalations in the upper part of the upper Elliot Formation mudstone units (between Whitehill and Malimong, Qacha's Neck District). The upper surfaces of these thin sandstone strata are characteristically uneven. Vehicle for scale.

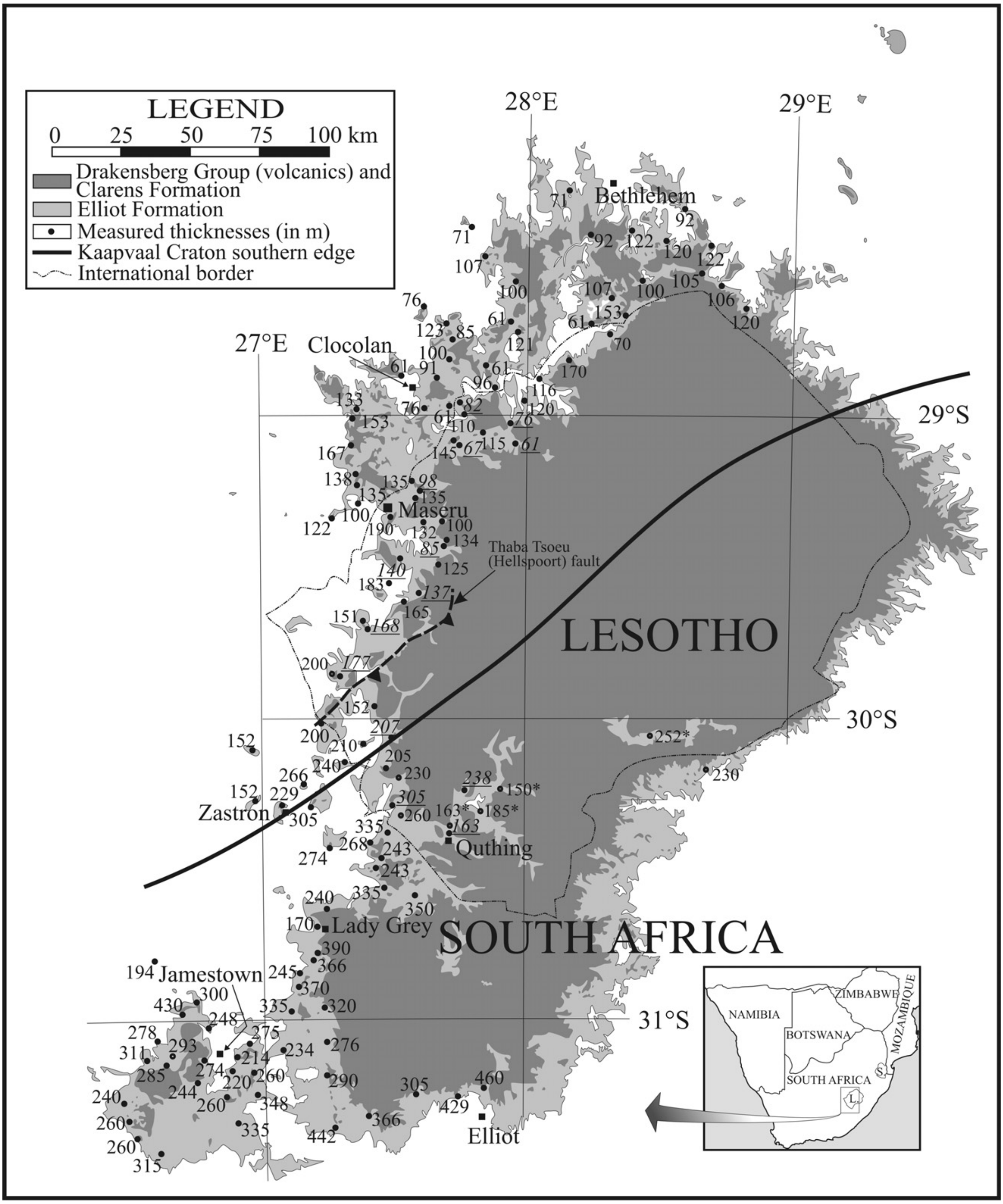

Figure 13. Thickness measurements of the Elliot Formation in Lesotho (underlined data in italics based on Stockley (1947); * marks incomplete Elliot Formation thicknesses) and South Africa. South African measurements are from Bordy *et al.* (2004a).

sandstones in contrast to the dusty yellow, medium-grained sandstones of the lEF. Here, as a general rule, the strata of the Molteno Formation form virtually flat plains above which the lEF sequence appears as terraced slopes.

The upper boundary of the Elliot Formation in Lesotho is either gradual (e.g. at Malimong, Qacha's Neck District), where the uEF terminates in sandstones (either fluvial or aeolian) or sharp (e.g. Qualo, Butha-Buthe District), where the uEF terminates in mudstones. In some places (e.g. Qacha's Neck District), there is a transitional zone between the red uEF sandstone and mudstones units, and the yellow-white, massive Clarens Formation sandstones. This zone consists of an inter-bedded succession of deep or light purple, massive, fine- to very fine-sandstones and mudstones, and yellow-white, massive sandstones. The architecture of these beds (e.g. erosion surfaces resulting in channel-shaped sandstones bodies) suggests some of them are fluvial, rather than aeolian in origin, and they were therefore considered as part of the uEF during the thickness measurements.

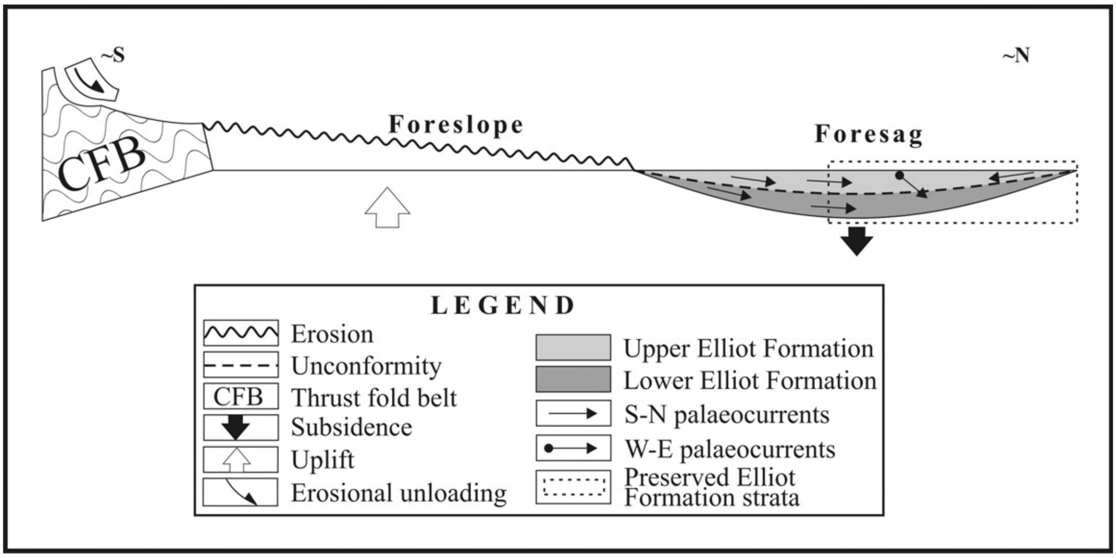

Figure 14. Hypothetical cross-section of the Karoo foreland system during the deposition of the Elliot Formation showing the dominant palaeocurrents in both lower and upper Elliot formations (after Catuneanu *et al.* 1998; Catuneanu & Elango 2001).

The well-documented (e.g. Botha 1968; Le Roux 1974; Johnson 1976; Visser & Botha 1980; Kitching & Raath 1984; Eriksson 1985; Smith & Kitching 1997) regional (from south to north) thickness decrease of the Elliot Formation in South Africa, was first demonstrated in Lesotho by Stockley (1947), and the present study has merely confirmed and quantified this finding (Fig. 13). It must be emphasized, however, that in the southern regions, especially along the Senqu River in Quthing and Qacha's Neck Districts, the base of the Elliot Formation is not exposed, and most of the thickness measurements in this area represent only part of the formation (i.e. are minimum values only).

The gradual thickness decrease of the Elliot Formation from south to north was explained by Catuneanu *et al.* (1998) as a consequence of the late stage development of the main Karoo Basin. These authors envisaged that the Elliot Formation, together with the underlying Molteno and overlying Clarens formations (i.e. the old 'Stormberg Group') constituted the foresag fill of the Karoo foreland system (i.e. main Karoo Basin and Cape Fold Belt). These formations with their northward tapering thicknesses thus represent the northern half of the Late Triassic–Early Jurassic foresag (Fig. 14). In the general northward thinning of the formation, there is a marked thickness reduction in the area between Zastron (South Africa) and Mohale's Hoek (Lesotho) which seems to coincide with the southern margin of the Kaapvaal Craton (Fig. 13).

Although the Lesotho data south of this zone are incomplete, measurements south and north of the Kaapvaal Craton southern edge show large discrepancies. North of Kaapvaal Craton southern boundary thicknesses are usually below 200 m both in Lesotho and South Africa, whereas south of this zone the gross thickness is usually considerably more than 200 m. In addition, the few measurements that were carried out south of this zone show large thickness variations within short distances (Fig. 13).

We suggest that the development of the variable thickness patterns in this area was probably controlled by a structural zone related to the margin between the southern edge of the Kaapvaal Craton and the northern edge of the Natal–Namaqua Mobile Belt. It is also noteworthy that the only major, post-Karoo fault in Lesotho, the Thaba Tsoeu fault of Stockley (1947) (also known an the Hellspoort fault) runs parallel to the southern edge of the Kaapvaal Craton (less than about 30 km north of this zone), reinforcing the idea that this area is a long lived, tectonically important region (Fig. 13). In addition, at Mohale's Hoek, a set of two dolerite dykes, each approximately a hundred metre wide, also parallels the aforementioned zone.

Palaeocurrents

To reconstruct the palaeodrainage during the Elliot Formation, the dip direction of one hundred and eighty-four foresets of planar cross-stratified sandstones were measured. The data were collected from medium- and large-scale planar cross-stratified units in major sandstone bodies only, because more reliable trough cross-stratified sandstones are rare. It is important to mention that rare trough and larger channel axis orientations were found to be consistent with the main orientation direction of planar cross-bedded sets.

Current indicators show that the major sediment supply directions were from south to north and southwest to northeast in the lEF, and from the south, southwest and west in the uEF (Figs 15, 16 & 17). Differences in the sediment supply patterns are not only traceable between the southern and northern regions (Fig. 15), but also between the lEF and uEF (Figs 16 & 17). Fig. 16A shows that the mean current vector was to the ~N in the lEF, while Fig. 16B indicates that this vector diverted to the ENE during uEF times. Palaeocurrent patterns of the Elliot Formation in Lesotho are strikingly similar to those measured in the South African outcrop areas (Bordy *et al.* 2004c), and the palaeocurrent data suggest that throughout the deposition of the Elliot Formation, sediment was supplied from the south, probably from the Cape Fold Belt. In the uEF, especially in its northern regions, sediments were also derived from a source in the west. Considering the findings of Bordy *et al.* (2004c), this source

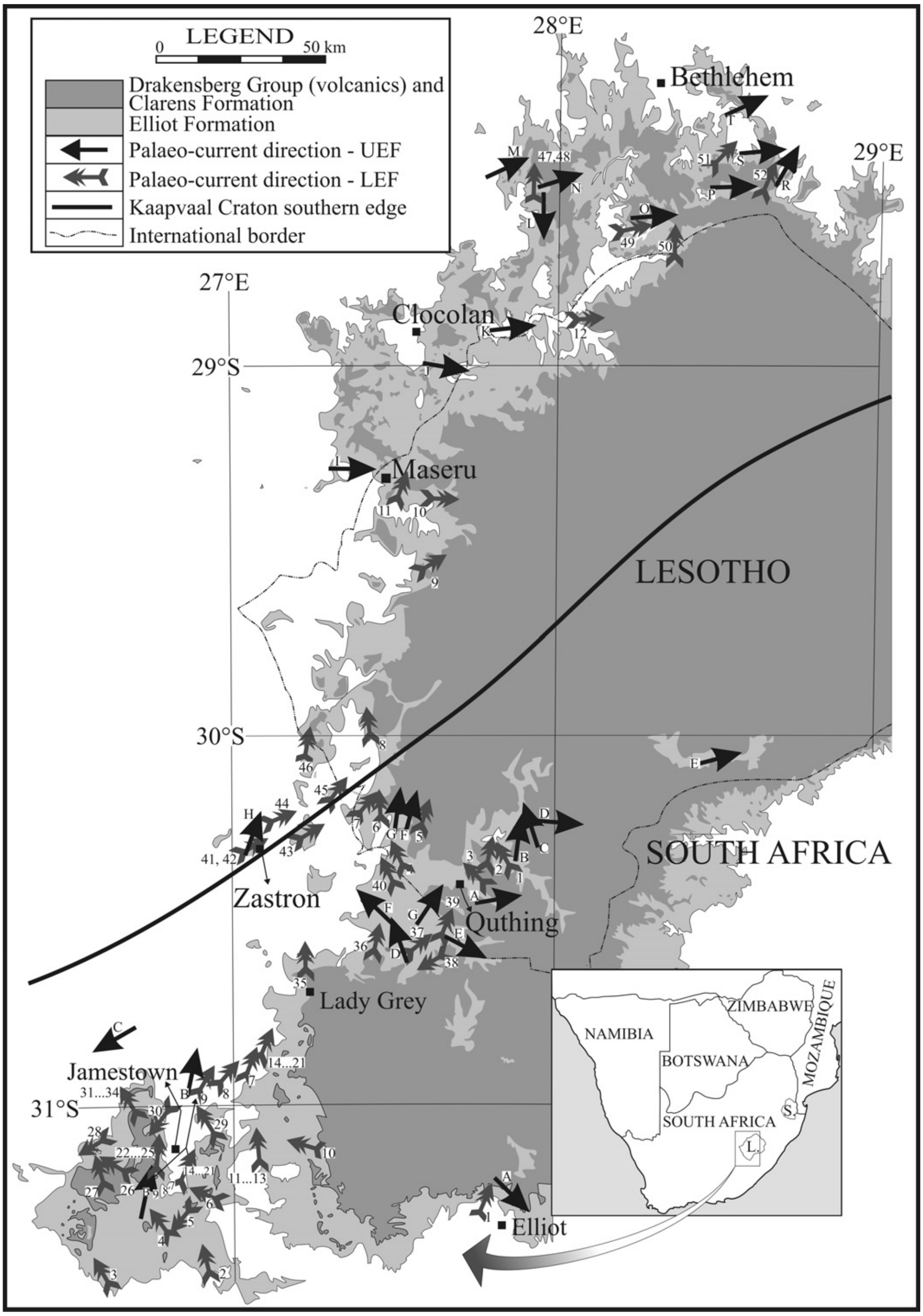

Figure 15. Palaeocurrent map of the Elliot Formation (numbers showing lower Elliot Formation measurements; letters showing upper Elliot Formation measurements – see Fig. 17 for more detailed information) in South Africa and Lesotho. South African measurements from Bordy *et al.* (2004c).

in the west may have been partially responsible for the higher feldspar content of the uEF sandstones. On these grounds, it is speculated that a palaeobasement high existed west of the present outcrop area.

Fossils

As a result of permit requirements, fossils discovered during this investigation could not be collected, but a few, highly weathered specimens (Table 1) were submitted to the Director of Culture at the Ministry of Tourism, Culture and Environment in Lesotho. The abundance of the material observed, and left *in situ,* in the field has once again highlighted how imperative it is that these fossils be removed and preserved. Cracked, disarticulated and fragmented fossil bones were found in the overbank deposits of both the lEF and uEF (Table 1, Fig. 18A–F). Fossils were not found in channel-fill sandstones; however channel-lags often contain fragmentary fossil bones, mainly in association with carbonate glaebule conglomerates in the uEF (e.g. Maseru, Maputseng). Large dinosaurian bones observed in the uEF at Peka (Leribe District) (Fig. 18A,B) are important in light of the recently documented

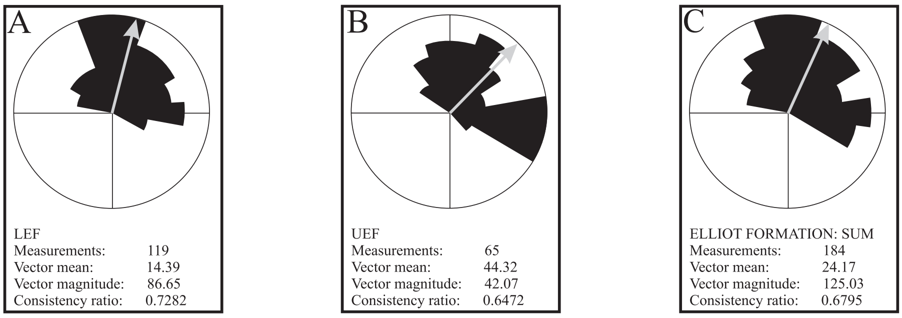

Figure 16. Summary palaeocurrent rose diagrams for planar cross-bedded sandstones in the Elliot Formation of Lesotho. **A**, lower Elliot Formation; **B**, upper Elliot Formation; **C**, Elliot Formation (all measurements).

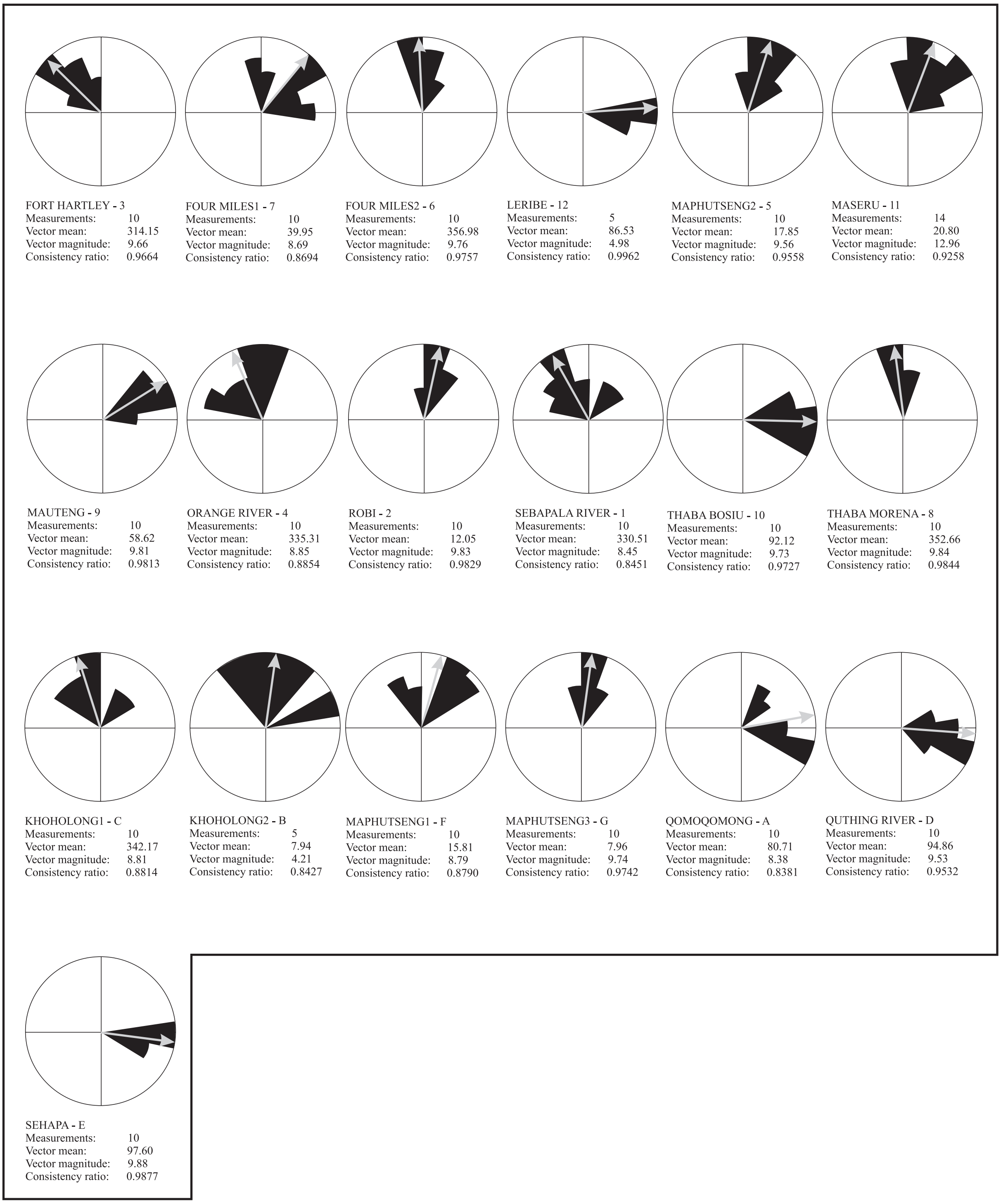

Figure 17. Palaeocurrent rose diagrams for planar cross-bedded sandstones in the Elliot Formation (Lesotho). Numbers refer to lower Elliot measurements, letters indicate upper Elliot Formation data. Roses are listed in alphabetic order of the locality names.

occurrence of a large sauropod (*Sauropoda* indet.) in the uEF of the northern part of the Karoo Basin (Yates *et al.* 2004) as well as the occurrence of large theropod footprints in the rocks of the lower Clarens Formation in South Africa. Fossil wood fragments were collected in two outcrops near Sekake (along the Senqu River), at the base of the uEF sequence.

Most invertebrate trace fossils in the Elliot Formation occur as relatively rare, but strongly bioturbated, shallow bedding plane features. Such trace fossils are virtually absent from the lEF (Fig. 19A), while the uEF ichnofossils are of relatively higher diversity and abundance (Fig. 19B, C–F). Vertebrate tracks, especially dinosaurian footprints, were observed at several localities (e.g. Maputheng, Roma, Quthing) (Fig. 20A,B). However, it has to be emphasized that the vast majority of the fossil footprint localities mentioned by Ellenberger (1970) proved to be very difficult, or impossible to relocate because of the lack of precise site descriptions.

The occurrence pattern (as rare, but strongly bioturbated, shallow bedding plane features) of most of the Elliot Formation invertebrate trace fossils has been documented by Hasiotis (2001) within dryland river deposits as an indicator of rare, but intensive biological activities in dryland alluvial settings dominated by episodic rainfall. The reason for the relatively higher diversity and abundance of trace fossils in the uEF may therefore be explained by the fact that in a depositional environment characterized by punctuated episodic sedimentation, the land-derived organic debris is supplied more sporadically, but more intensively than in a more humid setting (e.g. lEF). Since bioturbation intensity reflects moisture availability, their absence from the floodplain deposits might mean that the overbank areas were moist for only short periods of time during the uEF.

CONCLUSIONS

Sedimentological and palaeontological studies of the Elliot Formation in Lesotho has provided new and crucial insights to the palaeoenvironmental setting in southwestern Gondwana during Late Triassic to Early Jurassic times. Our understanding of the depositional history of the upper Elliot Formation, in particular the details of the fluvial architectural elements is enhanced by the quality of the uEF exposures in Lesotho, most of which are in the new road-cuts of the Qacha's Neck District. New data on gross thickness of the Elliot Formation emphasize the importance of the southern boundary of the Kaapvaal Craton in basin development studies, and it highlights that it seems to have played a significant role in the development of thickness patterns during the deposition of the Elliot Formation. Palaeocurrent measurements in Lesotho complement those documented in South Africa (Bordy *et al.* 2004c), and indicate that the source of sediments shifted from a predominantly southern (i.e. Cape Fold Belt) to a mainly western source (probable basement high) from lEF to uEF times.

The fact that the transition between the different sedimentation styles corresponds to changes in palaeocurrent trends (and sandstone petrography for the South African

Table 1. List of fossil bone localities identified during this study (collected specimens are stored at the Lesotho National Museum, Ministry of Tourism, Culture and Environment, Maseru, Lesotho).

Geographical coordinates in degrees (S/E)	Nearby locality	Altitude in m	Short description	Notes
28°47.405′/28°13.159′	Ha Rampae	1770	Fossil bone fragments	Upper Elliot F. mudstones. See sample collected RAM1
29°19.950′/27°42.5′	Qiloane	1670	Fossil bone fragments	Upper Elliot F. mudstones. No sample collected
29 20.615′/27°29.51′	Ha Thetsane	1755	Fossil bone fragment in pedogenic nodule conglomerate	Upper Elliot F. conglomerates. See sample collected THE1
28°58.70′/27°45.98′	Peka	1578	Fossil bone fragments (long, toe, etc.)	(?Upper) Elliot F. mudstones. See samples collected PEK1 and PEK2
29°02.284′/27°48.705′	Ntsekele	1639	Fossil bone fragments	Upper Elliot F. mudstones. See sample collected NTS1
28°51.650′/28°04.133′	Leribe	1734	?Fossil wood	Upper Elliot F. mudstones. See sample collected SEB1
30°01.579′/28°19.72′	Sekake	1863	Fossil bone fragments	Upper Elliot F. mudstones. No sample collected
30°04.044′/28°25.363′	Sekake	1600	Fossil wood	Upper Elliot F. mudstones. See sample collected SEK3
30°03.973′/28°25.648′	Sekake	1602	Fossil wood	Upper Elliot F. mudstones. See sample collected SEK4
30°03.732′/28°28.432′	Tebellong	1628	Fossil bone fragments	Upper Elliot F. mudstones. See sample collected SEK5
30°04.135′/28°28.937′	Whitehill	1683	Fossil bone fragments	Upper Elliot F. mudstones. No sample collected
30°03.249′/28°29.071′	Whitehill	1680	Fossil bone fragments (+ 1 vertebra)	Upper Elliot F. mudstones. See sample collected SEK7
30°03.812′/28°31.353′	Whitehill	1666	Fossil bone fragments (+ 1 vertebra)	Upper Elliot F. mudstones. See sample collected SEK8
30°03.793′/28°31.562′	Whitehill	1668	Fossil bone fragments	Upper Elliot F. mudstones. See sample collected SEK9
30°03.801′/28°31.828′	Ha Noosi	1676	Fossil bone fragments	Upper Elliot F. mudstones. See sample collected SEK10
30°13.548′/27°52.603′	Orange and Quthing rivers confluence	1500	Fossil bone fragments	Upper Elliot F. mudstones. See sample collected QUTH2 and QUTH3
30°23.331′/27°37.013′	Alwynskop	1520	Fossil bone fragments	Upper Elliot F. mudstones. See sample collected ALW2 and ALW3

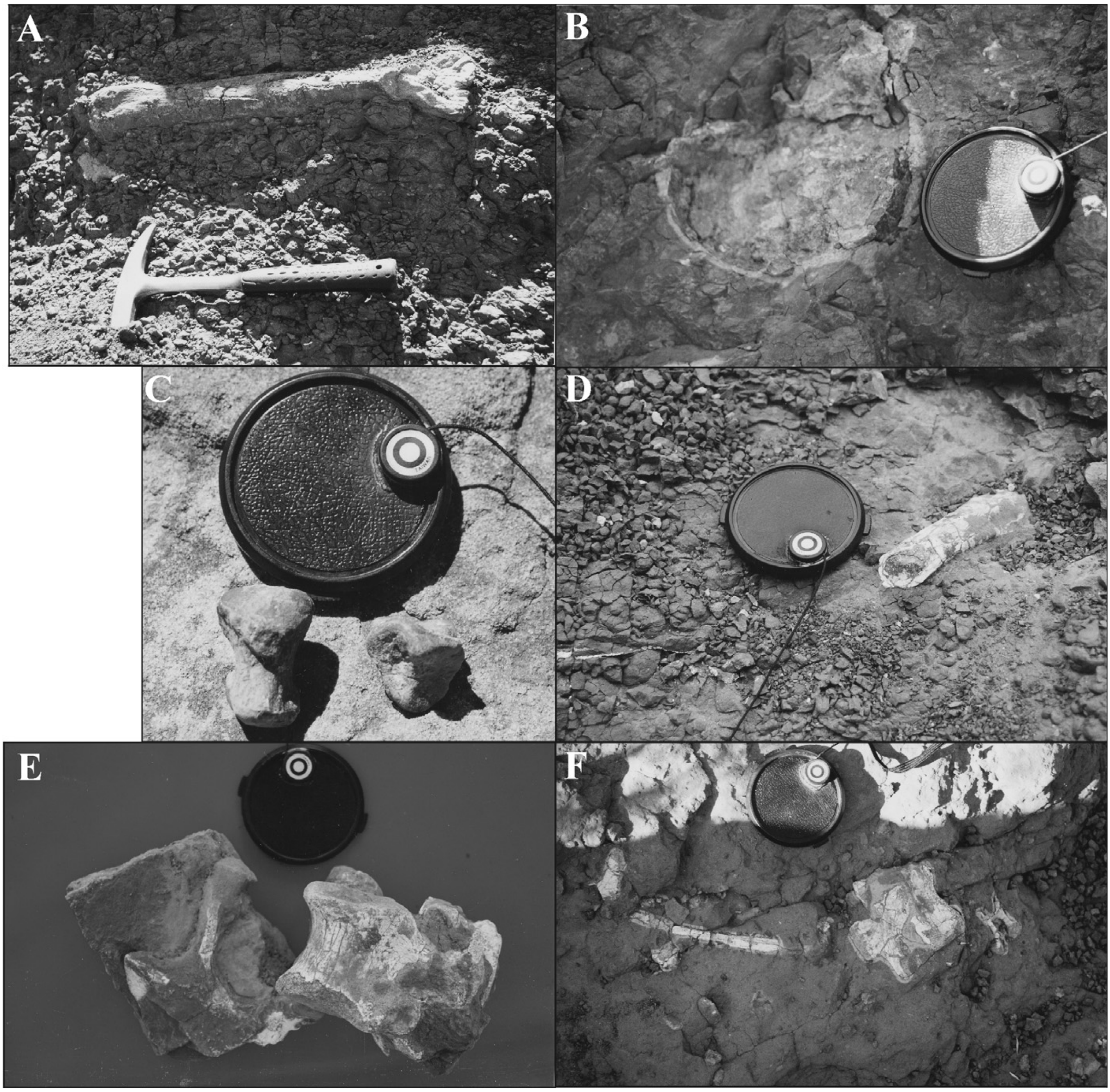

Figure 18. Fossil bones from the upper Elliot Formation. (**A, B, C**, Peka, Leribe District; **D**, Ha Noosi, Qacha's Neck District; **E**, Sehapa, Qacha's Neck District; **F**, Sekake, Qacha's Neck District. (Hammer (= 28 cm) and lens cap (= 5.8 cm) for scale.

samples) implies that the changes in the fluvial style in the Elliot Formation are primarily tectonic in nature. In particular, the geometry of the sandstone bodies (laterally impersistent lEF *vs* continuous uEF) and frequency of pedogenic alterations (rare in lEF *vs* common in uEF) indicate that the tectonic subsidence rate became reduced by the time of the uEF deposition. On the other hand, the increasing sandstone body frequency (e.g. amalgamated sandstones at the uEF/Clarens junction) and coarser grain-sizes in the upper part of the uEF suggest periods of slightly higher subsidence rates that were outpaced by even higher sediment supply rates (i.e. accommodation rapidly consumed by the overwhelming clastic input). The coarser grain sizes are explained by the gradual steeping of the foreslope which resulted in higher fluvial energy and thus in the supply of coarser sediments than in the lower part of uEF.

We suggest that in the light of the stratigraphic framework outlined above, the fossil trackway sites of Lesotho should be restudied, since their preservation and abundance may allow for a reinterpretation of Ellenberger's work, and once correctly stratigraphically positioned, would aid in biostratigraphical and palaeoecological studies of this important period of Gondwana's evolutionary history.

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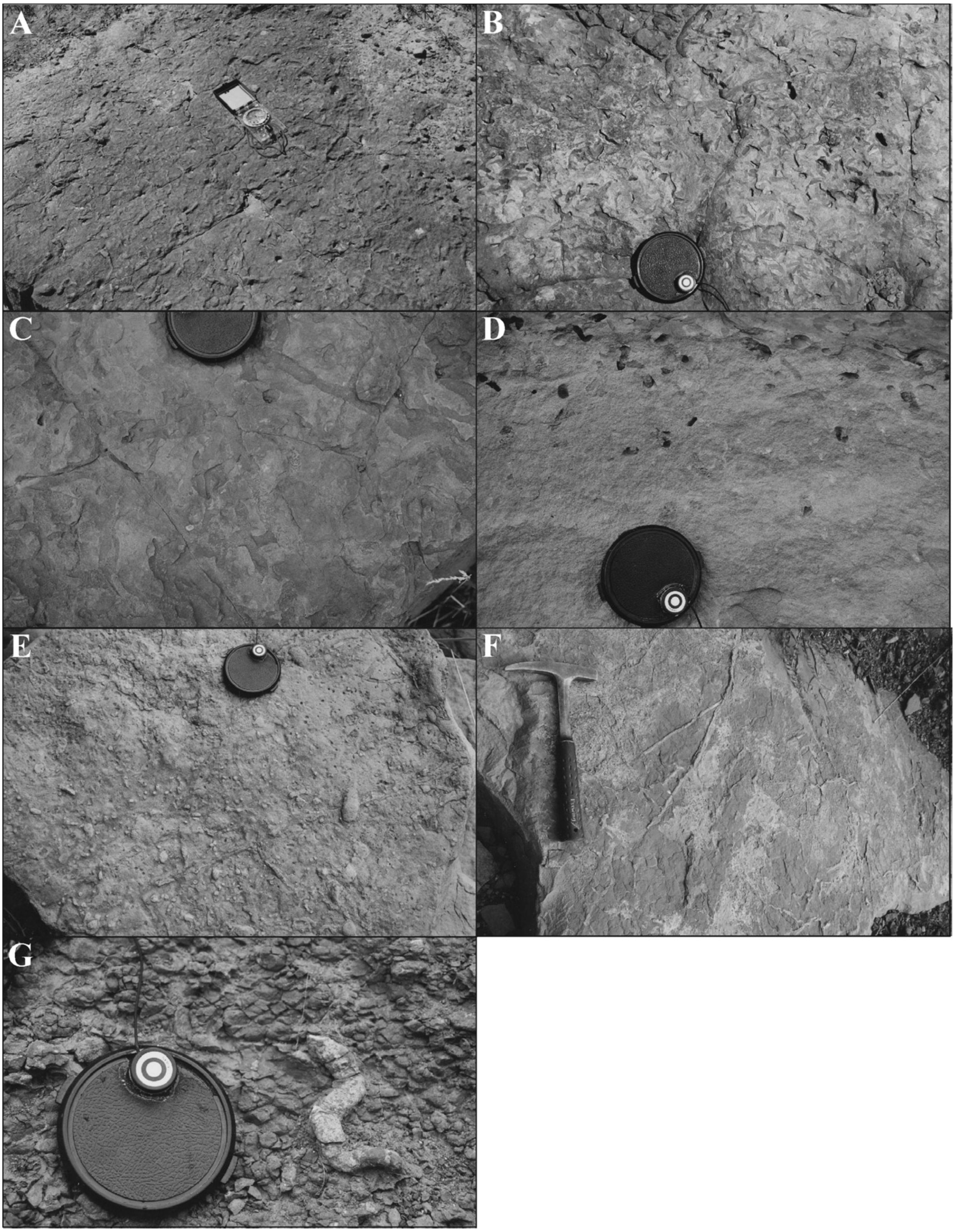

Figure 19. Bioturbation on upper bedding planes of sandstones are extremely rare in lower (**A**, Mauteng, Maseru District) and common in the upper Elliot Formation (**B**, Thaba Bosiu, Maseru District; **C, D, E**, Whitehill, Qacha's Neck District; **F**, between Whitehill and Malimong, Qacha's Neck District). Invertebrate trace fossils are also more frequent in upper Elliot Formation (**G**, between Whitehill and Malimong, Qacha's Neck District) mudstones than in the lower Elliot Formation. Open compass (= 14 cm), lens cap (= 5.8 cm) and hammer (= 28 cm) for scale.

regarding the Elliot Formation, and locating ichnofossil sites near Roma. Mrs N. Khitsane (Director of Culture: Ministry of Tourism, Culture and Environment, Lesotho) is acknowledged for her kind permission to undertake this study. The authors also wish to thank the late Prof. J.W. Kitching and Dr M.A. Raath for stimulating discussions regarding the palaeoenvironmental conditions of the Elliot Formation. We thank the two anonymous reviewers for their thoughtful comments on the original manuscript. Also, special thanks to Drs Mike Raath and Marion Bamford for their editorial support.

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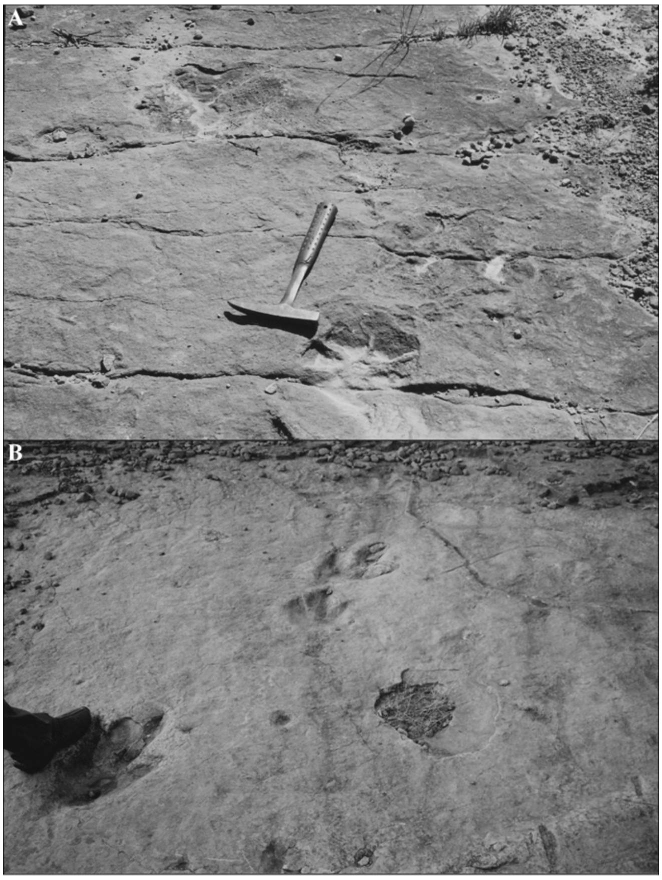

Figure 20. Footprints from the Elliot Formation. **A**, Four-toed(?) footprint in the lower Elliot Formation (Maphutseng, Mohale's Hoek District). Hammer for scale = 28 cm; **B**, Three-toed footprint in the uppermost upper Elliot Formation (Roma, Maseru District). Adult human foot for scale.

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The ultrastructure of Upper Palaeozoic and Mesozoic pollen from southern Africa and Asia

Michael S. Zavada
Department of Biology, Providence College, Providence, RI 02918, U.S.A.
E-mail: mzavada@providence.edu

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The dispersed pollen taxa *Cycadopites, Monosulcites, Bennetitteaepollenites, Pityosporites,* and *Inaperturopollenites* recovered from Permian to Jurassic sediments in southern Africa and Asia were examined ultrastructurally. *Cycadopites, Monosulcites, Bennetitteaepollenites* and *Inaperturopollenites* wall structure is characterized by homogeneous outer layer that is variously lacunate, and is underlain by a lamellated basal layer. Only one species of *Monosulcites* recovered from Jurassic sediments of Afghanistan showed a well-developed tectum, an infrastructural layer composed of columellae, or irregularly shaped columellae underlain by a basal layer. The saccate pollen of *Pityosporites* has an infrastructural layer of irregularly shaped anastomosing rods, the sacci are formed by an expansion of infrastructural layer in the region of the saccus (i.e. protosaccate *sensu* Scheuring). A majority of Permian, Triassic and Jurassic saccate and non-saccate monosulcate pollen is characterized by limited morphological diversity with regard to sculpturing and wall structure type compared to the diversity in angiosperm monosulcate pollen; however, there are pre-Cretaceous monosulcate pollen types that exhibit angiospermous pollen characteristics.

Keywords: ultrastructure, monosulcate pollen, Palaeozoic, Mesozoic, Africa, Afghanistan, China.

INTRODUCTION

Monosulcate pollen is one of the most ubiquitous pollen types found in the Mesozoic and has been recovered from sediments distributed throughout the world. The first appearance of this pollen type is in the Upper Palaeozoic. The common occurrence of monosulcate pollen and its wide distribution suggest that a number of vascular seed plant groups have derived this pollen aperture type (Walker 1974; Walker & Doyle 1975; Doyle 1978; Crane 1985; Doyle & Donoghue 1993; Brenner 1996; Dilcher 2001a,b). Monosulcate pollen occurs in every major extant vascular seed plant group, including the angiosperms. The common occurrence of this pollen type in the basal dicots and the monocots suggests that this aperture type is also shared by the angiosperm sister group, which at present has not been unequivocally identified based on anatomical, morphological, fossil or molecular evidence (APG 1998; Judd *et al.* 2002).

This paper is part of an ongoing investigation to assess and document pollen variation of monosulcate pollen from Upper Palaeozoic and Mesozoic localities throughout the world using characters obtained by light, scanning electron and transmission electron microscopy. This paper describes selected saccate and non-saccate dispersed monosulcate pollen of unknown affinity from localities in southern Africa and Asia. Understanding the morphological diversity of non-angiospermous Upper Palaeozoic and Mesozoic monosulcate pollen can more clearly define the morphological transformation that may have taken place in the gymnosperm–angiosperm transition, clarify distributional patterns of pre-angiospermous monosulcate pollen, and permit the elucidation of pollen features restricted to and characteristic of angiosperm monosulcate pollen. The latter is especially useful for tracking the first appearance and geographical distribution of early angiosperms or their stem relatives.

MATERIALS AND METHODS

Three localities were sampled in South Africa (Table 1). Palynological samples from Lower and Middle Permian age sediments of the Ecca were recovered from Hammanskraal located in the northern Karoo Basin. The collection locality was previously described by Anderson (1977) and Anderson & Anderson (1985). Palynological samples from the Triassic Molteno Formation were collected from Little Switzerland near Bergville, KwaZulu-Natal. This locality was previously described by Anderson & Anderson (1983, 1985, 1989). Palynological samples from the Lower Cretaceous Kirkwood Formation were collected from Dunbrodie, a locality previously described by Anderson & Anderson (1985) (also see Scott 1976) along the Wit River in the Eastern Cape Province.

A single sample of a cannel coal was received from D.L. Dilcher of the Florida State Natural History Museum, Gainesville, FL, U.S.A. The sample was recovered from the undifferentiated Jurassic of Afghanistan (Table 1).

Six palynological samples of Triassic age (Norian) were recovered from the Xiaotangzi Member of the Xujiahe Formation, Sichuan Province, China (Shang & Li 1992). The samples were provided by Yuke Shang of the Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China (Table 1).

All palynological samples were processed following a modified version of the method of Barss & Williams (1973). The palynological residues were processed and prepared for SEM and TEM after Zavada (2003).

SYSTEMATIC PALYNOLOGY

Cycadopites type, Figs 1–4, 13–14

Cycadopites is characterized by the osteoid shape of the sulcus (Figs 1, 3), i.e. the sulcus margins are narrow in the central region and flare at the distal ends of the sulcus (Figs 1, 3). Dispersed pollen grains range from ellipsoidal

Table 1. List of individual pollen types examined in this study, their country of origin, age of the formation they are extracted from, and figures. Each entry represents a pollen type examined with light, scanning electron and/or transmission electron microscopy.

Pollen type	Locality	Age	Figures
Cycadopites	Hammanskraal, South Africa	Permian	1, 2
Cycadopites	Hammanskraal, South Africa	Permian	3, 4, 13, 14
Monosulcites	Little Switzerland, South Africa	Triassic	24
Monosulcites	Little Switzerland, South Africa	Triassic	25
Monosulcites	Little Switzerland, South Africa	Triassic	26, 36
Monosulcites	Little Switzerland, South Africa	Triassic	27
Monosulcites	Little Switzerland, South Africa	Triassic	28
Monosulcites	Dunbrodie, South Africa	Early Cretaceous	41
Monosulcites	Dunbrodie, South Africa	Early Cretaceous	42, 46, 47
Monosulcites	Dunbrodie, South Africa	Early Cretaceous	43
Monosulcites	Sichuan, China	Triassic	48
Monosulcites	Sichuan, China	Triassic	49
Monosulcites	Sichuan, China	Triassic	50
Monosulcites	Afghanistan	Jurassic	51, 56
Monosulcites	Afghanistan	Jurassic	52
Monosulcites	Afghanistan	Jurassic	53
Monosulcites	Afghanistan	Jurassic	54, 57, 58
Bennettiteaepollenites	Little Switzerland, South Africa	Triassic	30, 31, 32, 35
Pityosporites	Hammanskraal, South Africa	Permian	5, 6, 15, 16
Pityosporites	Hammanskraal, South Africa	Permian	7, 8, 17
Pityosporites	Hammanskraal, South Africa	Permian	9, 10, 19, 22, 23
Pityosporites	Hammanskraal, South Africa	Permian	11, 12, 18, 20, 21
Pityosporites	Little Switzerland, South Africa	Triassic	29, 38, 39, 40
Pityosporites	Dunbrodie, South Africa	Early Cretaceous	44, 45
Inaperturopollenites	Little Switzerland, South Africa	Triassic	33, 34, 37
Inaperturopollenites	Sichuan, China	Triassic	55, 59, 60

to sub-circular in shape (Figs 1–4). Pollen size varies, ranging from 18 to 40 μm. Pollen sculpturing ranges from psilate to scabrate-granulate (Figs 1–4). Pollen wall structure is homogeneous to slightly lacunate (Figs 13–14), and in many taxa a lamellated basal layer is present (not shown).

This taxon is distinguished from other monosulcate taxa by lacking folds or sacci flanking the conspicuous sulcus. In *Monosulcites* the sulcus is ellipsoidal and lacks the conspicuous osteoid appearance of the sulcus in *Cycadopites.* This pollen type ranges from the Upper Palaeozoic to the Late Cretaceous and has a cosmopolitan distribution (Zavada 1984, 1990).

***Monosulcites* type**, Figs 24–28, 36, 41–43, 46–47, 48–54, 56–58

The sulcus in *Monosulcites* is straight and narrow to somewhat wide and ellipsoidal (Figs 24–28, 41–43, 48–54). Dispersed pollen grains are generally ellipsoidal (Figs 24–28, 41–43, 48–50, 53) but may occasionally be subcircular (Figs 51, 52) to circular in shape (Fig. 54). Pollen size varies, most frequently ranging between 18 and 40 μm. Pollen sculpturing is psilate (Figs 24–27, 41, 42, 48–53) to scabrate-granulate to psilate (Figs 28, 43, 54).

Pollen wall structure is primarily homogeneous (Figs 36, 46–47) to slightly lacunate (Fig. 56); however, a number of taxa have numerous lacunae (Zavada 1984, 1990). In one dispersed taxon recovered from Afghanistan (Fig. 54) the wall structure is composed of a well-developed tectum (Fig. 57), an infrastructural layer composed of columellae, irregularly shaped rods and occasional granules (Fig. 57). The infrastructural layer is underlain by a thin, homogeneous basal layer (Fig. 57).

Although *Monosulcites* exhibits a number of similarities to other non-saccate monosulcate dispersed pollen, this Mesozoic morphotype has the greatest wall structure diversity. This taxon ranges from the Upper Palaeozoic to the Late Cretaceous, and has a cosmopolitan distribution.

***Bennettiteaepollenites* type**, Figs 30–32, 35

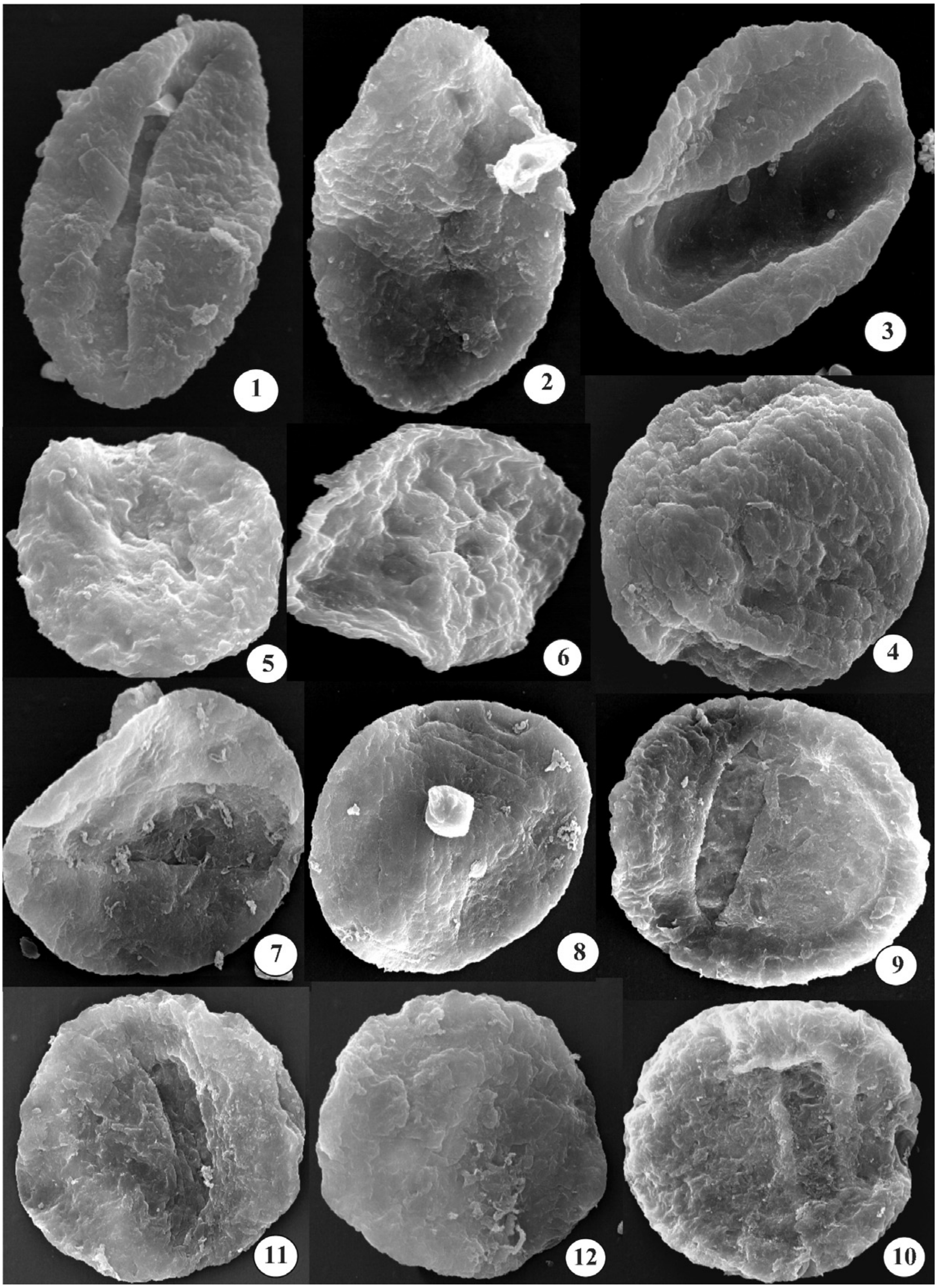
The sulcus is straight and ellipsoidal (Figs 30, 31). Dispersed pollen grains are ellipsoidal to sub-circular in shape (Figs 30–32). Pollen varies in size but most frequently ranges between 18 and 40 μm. Pollen sculpturing is psilate (Figs 30–32) to granulate-scabrate (Zavada 1984). Often long conspicuous folds flank both sides of the sulcus.

Pollen wall structure is homogenous to slightly lacunate (Figs 35). The outer homogenous layer is underlain by a differentially staining basal layer that occasionally exhibits lamellations (Figs 35). This taxon ranges from the Lower Mesozoic to the lower Upper Cretaceous, and has a cosmopolitan distribution. This taxon differs from *Cycadopites* and *Monosulcites* by the regular occurrence of exinal folds on both sides of the sulcus (Figs 30, 31).

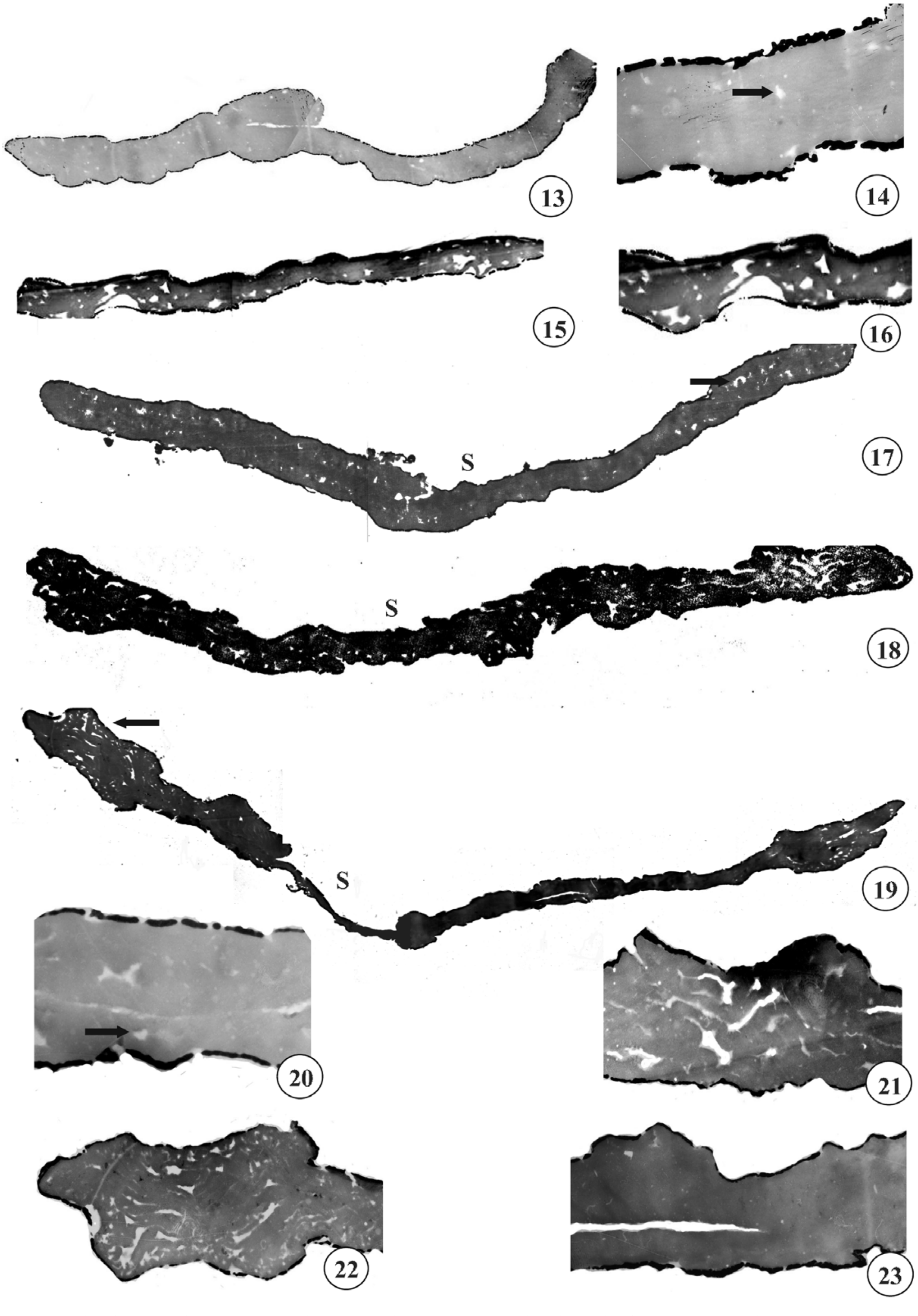
***Pitysporites* type**, Figs 5–12, 15–23, 29, 38–40, 44–45

This taxon encompasses a large and diverse group of dispersed pollen types. Pollen is monosulcate, circular to slightly elongate (Figs 5–12, 29, 44–45). Exine sculpturing is psilate (Figs 5–6, 9–12, 29, 44–45); however, a few species are reported to be striate (Figs 7–8) (Anderson 1977). Pollen is generally interpreted to be saccate, the sacci forming a marginal fringe (Figs 9–12, 29, 44–45). Pollen ranges in size from 24 to 136 μm.

Pollen wall structure is composed of an outer tectum that varies in thickness and that is underlain by a struc-



Figures 1–12. SEM of pollen from the Permian Northern Karoo locality Hammanskraal, South Africa. **1–4**: *Cycadopites* type 1, distal view, ×2000; **2**, proximal view of the same grain in Fig. 1, ×2000; **3**, distal view, ×2100; **4**, proximal view of the same grain in Fig. 3, note the slightly rugulate sculpturing, ×2100. **5–12**: *Pityosporites* type; **5**, distal view, ×1800; **6**, proximal view of the same grain in Fig. 5, ×1800; **7**, distal view, ×1200; **8**, proximal view of the same grain in Fig. 7, note the regularly spaced exinal grooves at the top of the pollen grain, ×1200; **9**, distal view, note what appears to be an equatorial saccus, ×600; **10**, proximal view of the same grain in Fig. 9, ×600; **11**, distal view, ×1400; **12**, proximal view of the same grain in Fig. 11, note the slightly rugulate exine sculpturing, ×1400.



Figures 13–23. TEM of pollen from the Permian Northern Karoo locality Hammanskraal, South Africa. **13–14**: *Cycadopites* type; **13**, TEM of the whole pollen grain in Figs 3 and 4 showing the homogeneous wall structure that is occasionally interrupted by small lacunae; in similar grains a thin, differentially staining, lamellated basal layer is present, ×4100; **14,** high-magnification TEM of the same grain in Figs 3, 4 and 13 showing the small occasional lacunae (arrow); the black outer layer on the wall is the gold coating applied for SEM, ×20 000. **15–23**: *Pityosporites* type; **15**, TEM of the whole grain in Figs 5 and 6 showing structured wall; although the pollen grain is compressed the wall appears to be composed of irregularly shaped, robust elements, ×2700; **16**, high-magnification TEM of the same grain in Figs 5, 6 and 15 showing the structured wall, ×4100; **17**, TEM of the whole grain in Figs 7 and 8 showing the sulcus region (S) (also see Fig. 7) and the homogeneous wall structure with what appear to areas of regularly placed lacunae (arrow); note that the wall structure becomes more homogeneous in the sulcus region, ×4000; **18**, TEM of the whole grain illustrated in Figs 11 and 12 showing the wall structure composed of cylindrical, branching elements; this pollen grain is similar to the one illustrated in Figs 5, 6, 15 and 16;

Continued on p. 63

tured layer (Figs 15–23, 38–40). Adjacent to the apertures this structured layer is composed of a thick, homogeneous layer that is variously lacunate (Figs 15–20, 23). In the region of the sacci the infrastructural layer is composed of anastomosing irregular shaped interconnecting elements (Figs 15–19, 21–22). The sacci are not formed by a separation of the nexine and sexine. The infrastructural layer is underlain by a homogeneous to lamellated basal layer that varies in thickness (Figs 20, 23)

***Inaperturopollenites* type**, Figs 33–34, 37, 55, 59–60

Pollen of this type is inaperturate (Figs 33–34), large, ranging in size from 26 to 80 μm. Exine sculpturing can be psilate, scabrate, or verrucate (Figs 33–34, 55).

Pollen wall structure is homogeneous (Fig. 37) to slightly lacunate (Figs 59–60). A homogeneous to lamellate basal layer is often distinguishable (Fig. 60).

DISCUSSION

The monosulcate aperture type occurs in a wide variety of fossil and extant groups. This pollen aperture type makes its first appearance in the Late Palaeozoic, and is distributed among the Palaeozoic and Mesozoic pteridosperms, gymnosperms and the dicots and monocots. The occurrence of this aperture type in a particular group, in and of itself, offers little insight into determining the taxonomic position, or evolutionary relationships of these groups. The association of this aperture type with other distinctive pollen features, however, may permit palynologists to estimate the time of origin, and to track the geographical distribution of various plant groups through time and space.

In this study three types of dispersed pollen from various localities and ages were investigated, a) monosulcate non-saccate pollen types, b) monosulcate saccate pollen types, and c) pollen with an indistinct monosulcate aperture, or inaperturate pollen. The monosulcate non-saccate pollen has been assigned to *Cycadopites* (Figs 1–4, 13–14), *Monosulcites* (Figs 24–28, 41–43, 46–47, 48–54, 56–58) and *Bennettiteaepollenites* (Figs 30–32, 35). Except for the configuration of the sulcus and/or the presence of exinal folds, all three taxa have a similar shape, range in size, sculpturing and wall structure, despite the fact that they are derived from localities widely separated in time and space. Previous studies on similar forms from the Triassic Chinle Formation, western United States (Zavada 1990), Cretaceous sediments of the United States (Zavada 1984), and the Upper Cretaceous Dakota Formation, central United States (Zavada & Dilcher 1988) exhibit the same narrow range in characteristics, i.e. pollen is oval to circular in shape, ranges in size from 18 to 45 μm and is monosulcate, the sculpturing is psilate to slightly scabrate to verrucate; the pollen wall is homogeneous to homogeneous lacunate; and the outer sexine is generally underlain by a homogeneous or lamellated basal layer (nexine). The outstanding feature of these pollen types is the lack of morphological diversity over a wide geographical area and long geological time compared to superficially similar forms in the angiosperms. This morphological monotony, however, is occasionally punctuated by Triassic and/or Jurassic monosulcate pollen that, although in size, shape and, in some cases, sculpturing, is superficially similar to the above taxa, has a pollen wall structure that is more similar to the pollen wall structure observed in the monosulcate pollen of the angiosperms (e.g. Figs 54, 55, 57, 58, 59, 60; Cornet 1989; Cornet & Habib 1992).

Saccate monosulcate pollen, much like the non-saccate monosulcate pollen, exhibits limited variation in shape, size and sculpturing. Sacci are generally described as bladder-like extensions of the exine that result from the separation of the sexine from the nexine. Ultrastructural studies of fossil and extant saccate pollen have shown that saccus formation is a result of a number of exinal modifications (Osborn & Taylor 1994, and references therein; Kurmann & Zavada 1994). The sacci in *Pityosporites* (Figs 5–12, 15–23, 29, 38–40, 44–45) are of the protosaccate type (*sensu* Scheuring 1974). Scheuring (1974) has considered protosacci to be fundamentally different from the formation of sacci in the conifers, i.e. coniferalean sacci are formed by a separation of the sexine and the nexine (eusaccate condition, *sensu* Scheuring 1974). Meyen (1987) suggested that the term protosaccate might imply a plesiomorphic condition, and suggested that the term quasi-saccate would be more accurate, because the evolutionary relationship of the protosaccate condition and the eusaccate condition (*sensu* Scheuring 1974) has not been established. Among the fossil saccate pollen investigated in this study, the sacci are formed by an elaboration of the infrastructural elements, i.e. anastomosing, irregularly shaped rods (Figs 18–22). In none of the taxa investigated in this study is there a clear separation of the sexine and the nexine. The variation in saccus number, morphology, and the mode of formation suggest that this pollen feature was derived independently in a number of taxonomic groups through time.

Two species of *Inaperturopollenites* were investigated (Figs 33–34, 37, 55, 59–60). These pollen types have exines that are more conspicuously sculptured than the exines observed in a number of monosulcate taxa (Figs 33–34, 55). The pollen wall of both types, however, are comparable to

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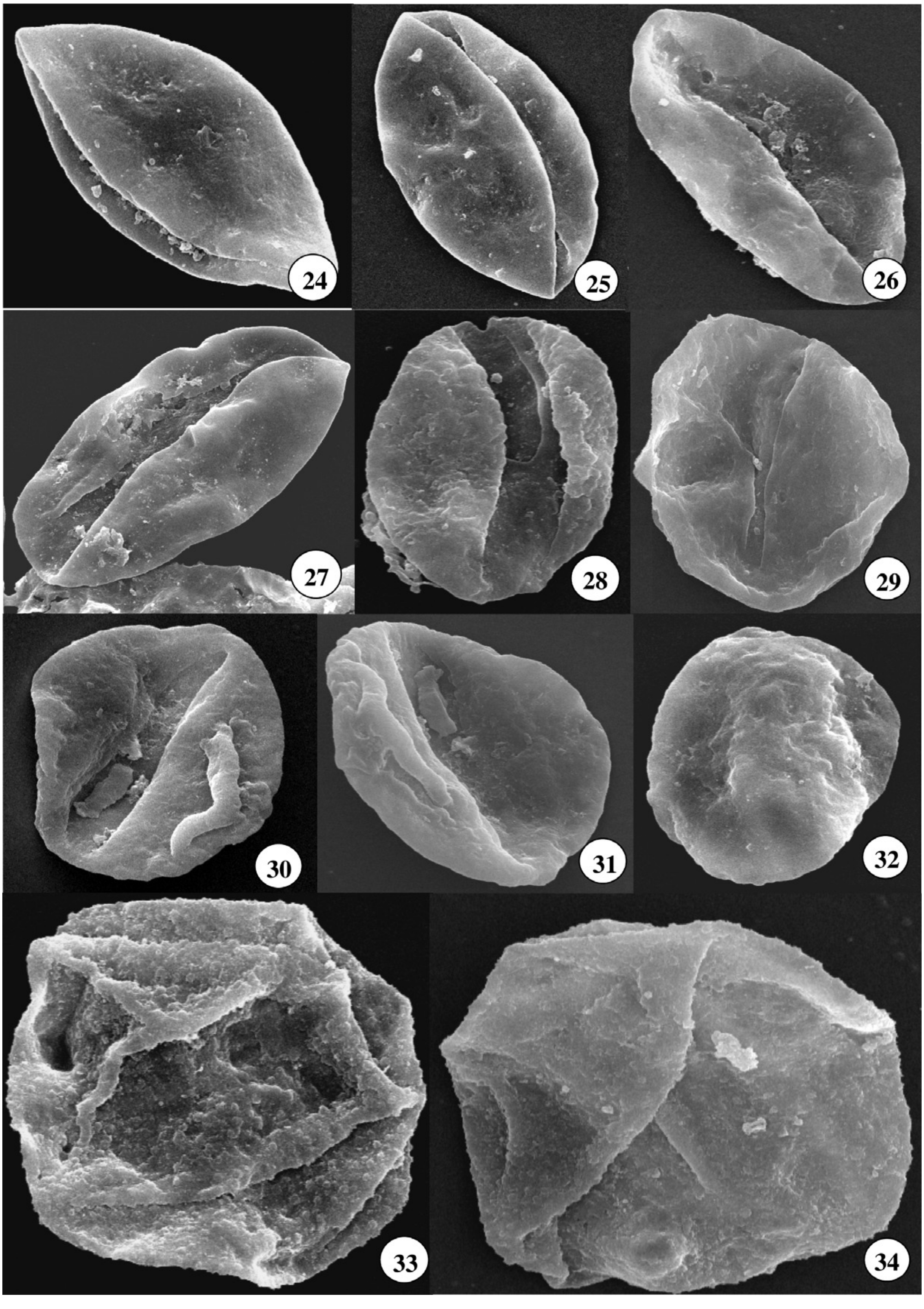
however, the pollen grain and the wall appear to less compressed, and more representative of the wall structure, the (S) indicates the sulcus region seen in the SEM of the same grain illustrated in Fig. 11, ×3400; **19**, TEM of the whole grain illustrated in Figs 9 and 10 showing the thin, homogenous wall structure adjacent to the aperture (S) that is occasionally interrupted by small lacunae; the portion of the pollen wall adjacent to the aperture grades into a marginal portion that is characterized by irregular, cylindrical elements that comprise a wall that is thicker and more elaborated than the wall adjacent to the aperture (*cf.* protosaccate), ×2800; **20**, high-magnification TEM of the same grain in Figs 11, 12 and 18 showing the lacunate (arrow) wall structure adjacent to the apertural region, ×15000; **21**, high-magnification TEM of the same grain in Figs 11, 12, 18 and 20 showing the irregularly shaped cylindrical infrastructural elements that comprise wall structure of the periphery of the pollen grain, ×11000; **22**, high-magnification of the peripheral pollen wall of the same grain in Figs 9, 10 and 19 showing the irregularly shaped cylindrical elements; this structure is similar to a protosaccus, ×4300. **23**, high magnification of the pollen wall in the vicinity of the apertural region of the same grain in Figs 9, 10, 19 and 22 showing the homogeneous wall structure, ×11200.



Figures 24–34. SEM of pollen from the Triassic locality Little Switzerland, Molteno Formation, South Africa. **24–28**: *Monosulcites* type; **24**, ×2700; **25**, ×2300; **26**, ×2000; **27**, ×1200; **28**, ×2700. **29**: *Pityosporites* type, ×1600. **30–32**: *Bennettiteaepollenites* type; **30**, distal view, ×1500; **31**, side view of the same grain in Fig. 30, ×1500; **32,** proximal view of the same grain in Figs 30 and 31, ×1500. **33–34**: *Inaperturopollenites* type; **33**, ×1,500; **34**, flip side of the same grain in Fig. 33, ×1500.

the pollen wall structure in monosulcate, non-saccate pollen types, i.e. the outer exine is homogeneous (Fig. 37) to lacunate (Figs 59–60) and is underlain by a homogeneous to lamellated basal layer. The type of sculpturing and wall structure fall within the range observed in the monosulcate non-saccate pollen types.

A majority of the monosulcate (and inaperturate) pollen types of the Upper Palaeozoic and the Triassic and Jurassic,

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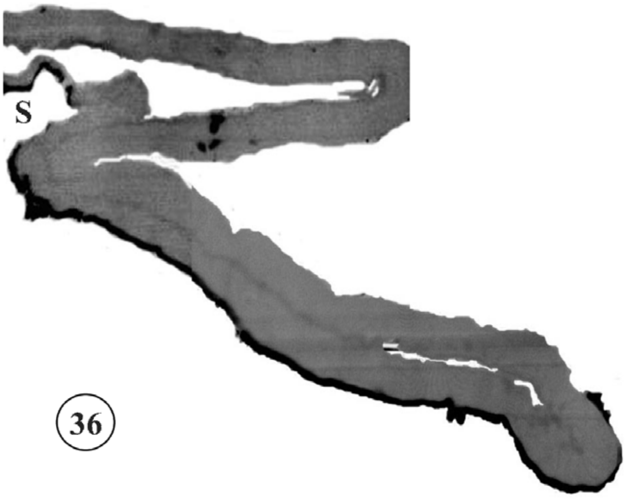

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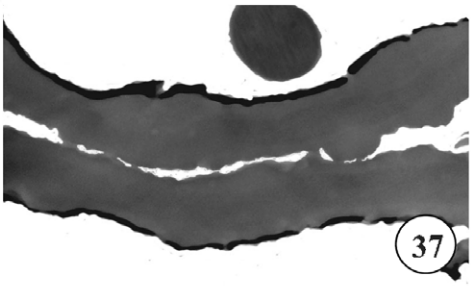

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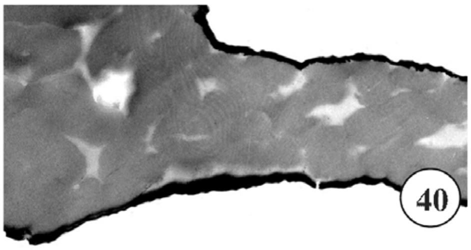

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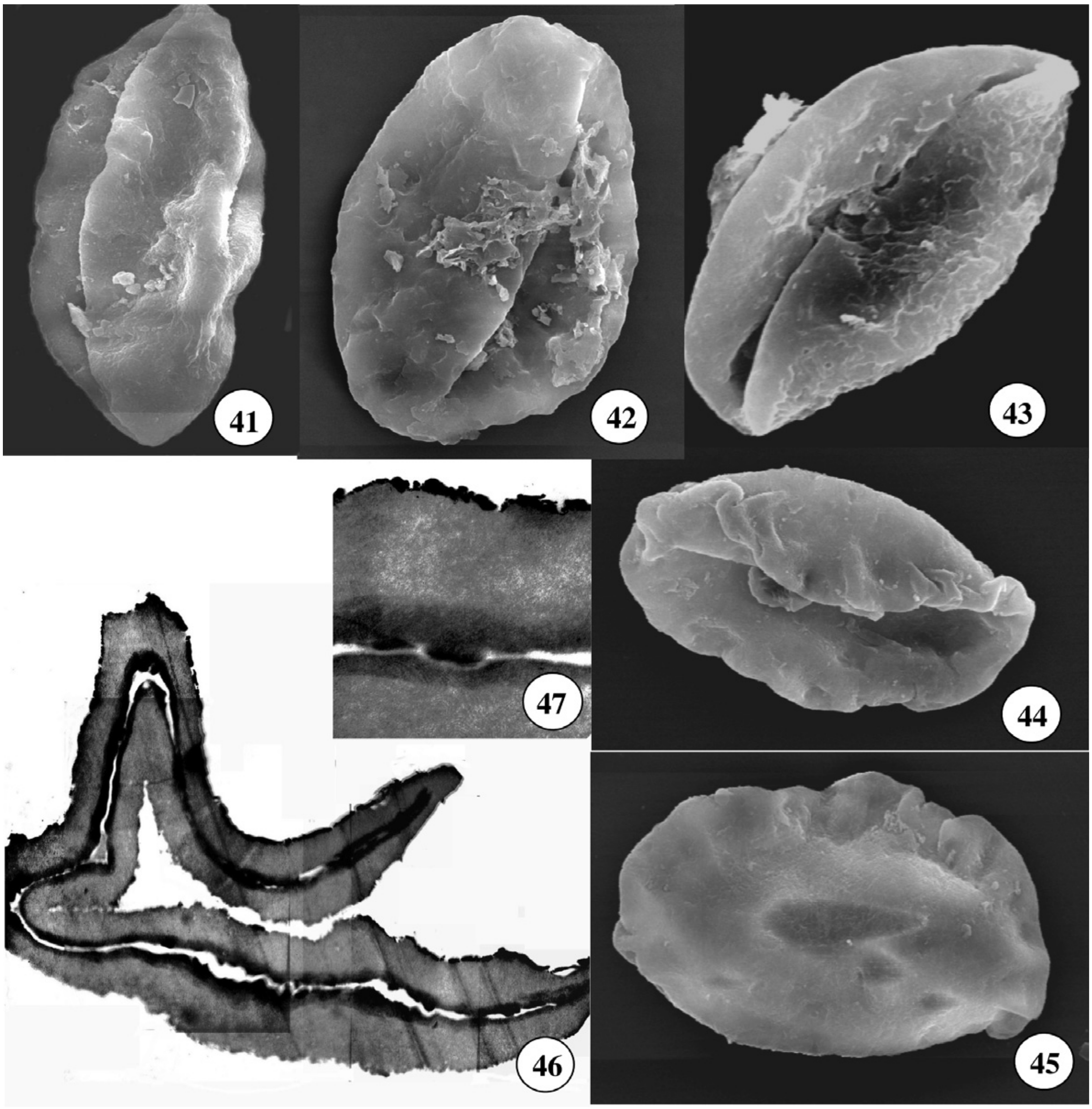
Figures 35–40. TEM of pollen from the Triassic locality Little Switzerland, Molteno Formation, South Africa. **35–36**: *Bennettiteaepollenites* type; **35**, TEM of the whole grain illustrated in Figs 30, 31 and 32 showing homogeneous wall structure and thin basal layer; note that the fold adjacent to the aperture in Fig. 30 which appears to be a vestigial saccus is actually a random fold of the exine due to post-depositional compression (arrow); the (S) indicates the apertural region, ×3300; **36**, TEM of the same grain in Fig. 26 showing homogeneous wall structure and thin basal layer, the (S) indicates the apertural region, ×12 800. **37**: *Inaperturopollenites* type; TEM of the pollen wall of the same grain in Figs 33 and 34 showing the homogeneous wall structure, and thin basal layer, ×12 500. **38–40**: *Pityosporites* type; **38**, TEM of the whole grain in equatorial region of the same grain in Fig. 29 showing the scattered lacunae in the wall, × 4000; **39**, TEM of the same grain in Figs 29 and 38 near the periphery of the grain showing the more open lacunate infrastructure; compare with pollen from the Permian in Figs 7, 8 and 17, and 11, 12 and 18, ×4000; **40**, high-magnification TEM of the pollen wall in the same grain in Figs 29, 38 and 39 showing the irregular, robust cylindrical elements which comprise the infrastructure, ×12 500.

although possessing an aperture type similar to primitive angiosperms, exhibits a narrow range in morphological diversity with regard to sculpturing and pollen wall structure, features that provide little insight into the relationships of pre-Cretaceous plant groups to the angiosperms. Among the morphological monotony of the Triassic and Jurassic monosulcate pollen are monosulcate pollen types that have a wall structure that is more similar to the pollen wall structure observed in angiosperm pollen, i.e. the pollen wall has a well-developed tectum, and an infrastructural layer composed of columella-like structures that are fused to a distinctive basal layer (e.g. Fig. 57). In addition, Cornet (1989), and Cornet & Habib (1992) have reported dispersed pollen from the Triassic of North America, and the Jurassic of France with reticulate exine sculpturing, a feature found only in angiosperms. These



Figures 41–47. SEM and TEM of pollen from the Lower Cretaceous locality Dunbrodie, Kirkwood Formation. **41–43**: *Monosulcites* type; **41**, SEM , ×1000; **42**, SEM, ×1500; **43**, SEM, ×2500. **44–45**: *Pityosporites* type; **44**, SEM, ×1500; **45**, SEM of the same grain in Fig. 44, note the marginal fringe that appears to be a vestigial saccus, ×1500. **46–47**: *Monosulcites* type; **46**, TEM of the whole grain in Fig. 42 showing thick homogeneous wall and thin basal layer; note the similarity of this wall structure type to that of the pollen in Figs 3, 4, 13, 14, and 30, 31, 32, 35, and 26, 36, ×3300; **47**, high-magnification TEM of the same grain in Figs 46 and 47 showing the homogeneous wall structure and differentially staining basal layer, ×13 300.

pollen types occur in low frequency, but may represent the occurrence of pre-Cretaceous angiosperms or an angiosperm stem group (also see Doyle & Hotton 1991; Doyle & Donoghue 1993; Dilcher 2001a,b).

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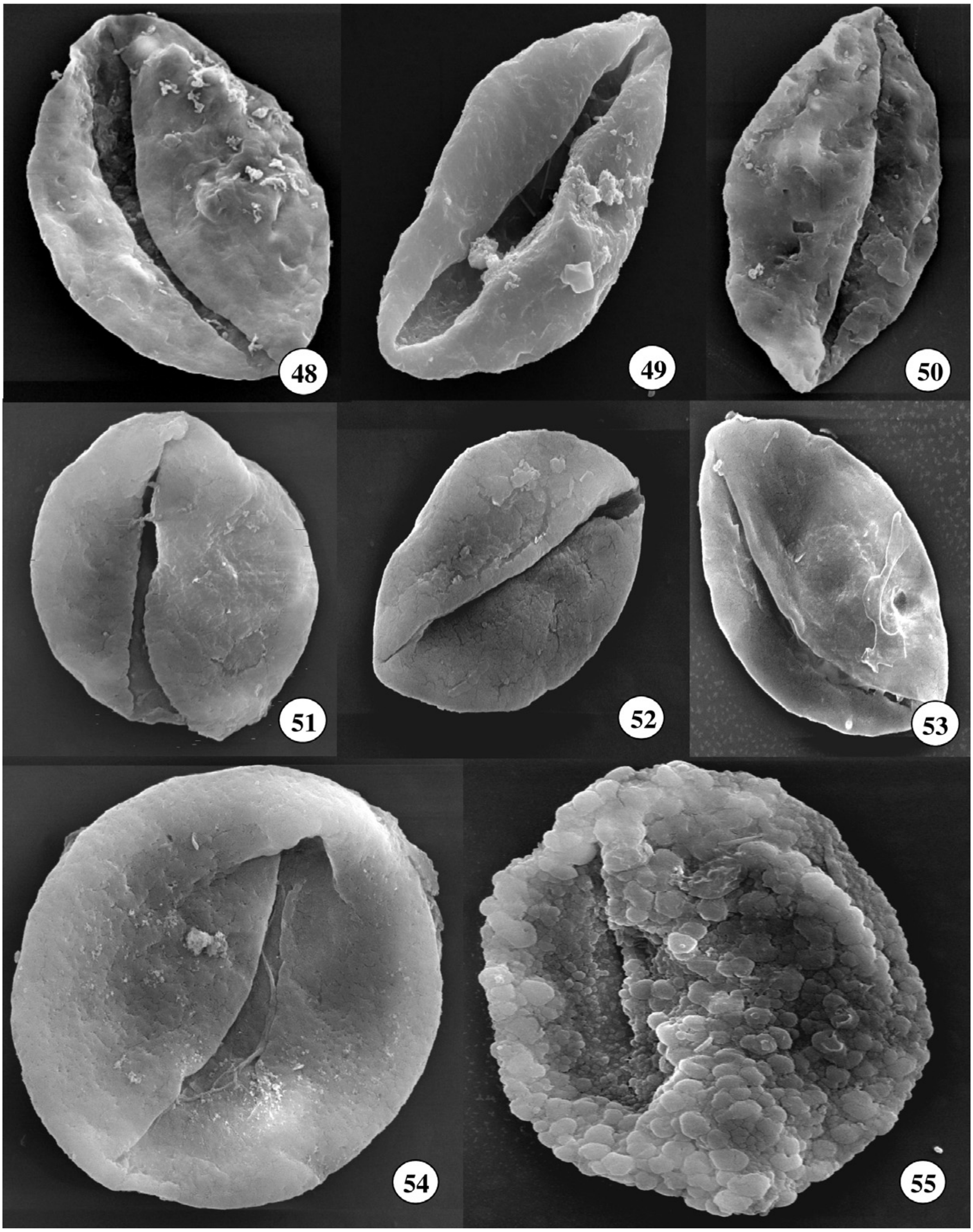

Figures 48–55. SEM of pollen from the Triassic (Norian) of Sichuan, China, Xujiahe Formation. **48–50**: *Monosulcites* type, **48**, ×2000; **49,** ×2000; **50**, ×1800. **51–55**: SEM of pollen from the undifferentiated Jurassic of Afghanistan; **51–54**: *Monosulcites* type; **51**, ×2500; **52**, ×2200; **53**, ×2600; **54**, ×3500. **55**: *Inaperturopollenites* type, SEM of pollen from the Triassic (Norian) of Sichuan, China, Xujiahe Formation, ×2100.

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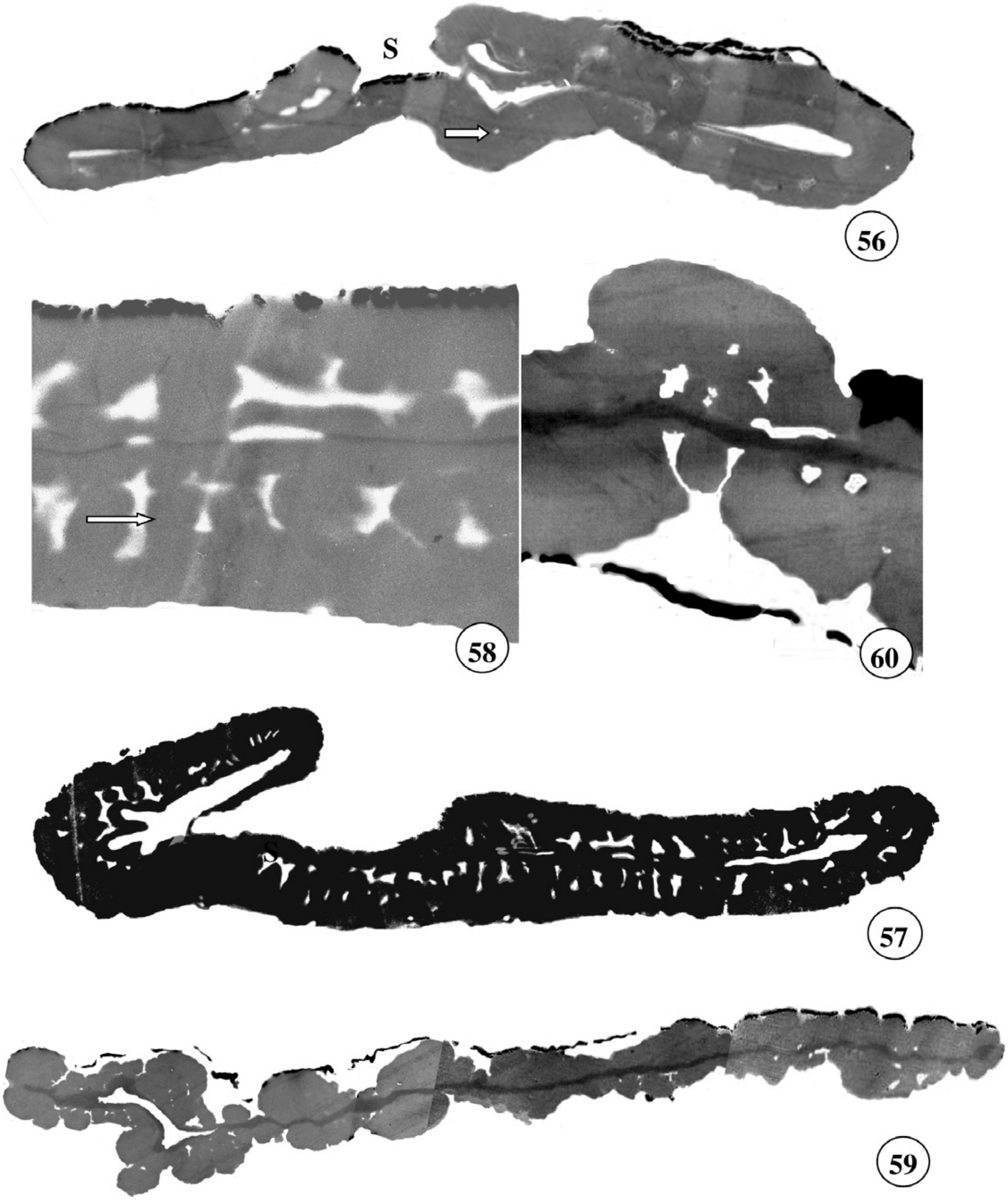

Figures 56–60. TEM of pollen from the undifferentiated Jurassic of Afghanistan. **56–58**: *Monosulcites* type; **56**, TEM of the whole grain illustrated in Fig. 51 showing the homogeneous wall structure with the occasional lacuna (arrow), and the thin basal layer, (S) indicates the apertural area; compare the wall structure of this taxon with the wall structure of pollen recovered from Africa in Figs 3, 4, 13, 14, and 30, 31, 32, 35, and 26, 36, ×5000; **57**, TEM of the whole grain illustrated in Fig. 54 showing the columellate-like elements of the infrastructure, the imperforate tectum and the thin basal layer; the (S) indicates the apertural area, ×6800; **58**, high-magnification TEM of the pollen wall of the same grain in Figs 54 and 57 showing the columellate-like structures (arrow) that are not fused to the thin basal layer; note that the tectum is imperforate, ×16 000. **59–60**: TEM of pollen from the Triassic (Norian) of Sichuan, China, Xujiahe Formation; **59**, TEM of the whole grain illustrated in Fig. 55 showing rugulate sculpturing, occasionally lacunate wall and thin basal layer, ×4500; **60**, high-magnification TEM of the non-apertural wall of the same grain in Figs 55 and 59 showing the rugulate sculpturing, the thin basal layer and the infrastructural lacunae, ×17 500.

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New skulls of *Kolpochoerus phacochoeroides* (Suidae: Mammalia) from the late Pliocene of Ahl al Oughlam, Morocco

Denis Geraads
UPR 2147 du CNRS, 44 rue de l'Amiral Mouchez, 75014 PARIS, France
E-mail: dgeraads@ivry.cnrs.fr

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The discovery of two male skulls of *Kolpochoerus phacochoeroides* from the late Pliocene of Ahl al Oughlam in Morocco, and the revision of the whole collection from this locality, allows us to extend the description of this North African form, to estimate its sexual dimorphism and the extent of individual variation in a large isochronous sample, to reveal some ontogenic changes, and to confirm its distinction as a species on its own, as its cranial proportions (large occipital, short snout) and tooth characters (lack of enamel on upper canines, reduced incisors and premolars, complicated third molars) set it clearly apart from the East and South African forms. A cladistic analysis shows that *K. phacochoeroides* and *Hylochoerus* are the terminal branches of the *Kolpochoerus* clade, which is the sister-group of *Potamochoerus.*

Keywords: Africa, Pliocene, Pleistocene, Suidae, Mammalia, *Kolpochoerus,* cladistics.

INTRODUCTION

The late Pliocene site of Ahl al Oughlam in Morocco has been excavated under the author's leadership, as part of the 'Programme Casablanca' of the Institut National des Sciences de l'Archéologie et du Patrimoine of Rabat. It is the richest fossil locality of the North African Neogene, with about 55 species of mammals (Raynal *et al.* 1990, 2001; Geraads 1993, 1995, 1996, 1997, 2002; Alemseged & Geraads 1998; Geraads & Amani 1998; Geraads *et al.* 1998; Geraads & Metz-Muller 1999). The formation of the site was probably instantaneous at the geological scale, and the whole collection is thus close to a single biocoenosis sample.

In 1993, I published a description of the material of *K. phacochoeroides* available at that time. The amount of fossils recovered from this site has greatly increased since then, and about 500 specimens (many of them fragmentary) have now been identified. In sharp contrast to East or South Africa, there is still no evidence of any other suid species. The best new specimens are two virtually complete male skulls: AaO-3655, in very good condition, and AaO-3656, which is crushed. Relationships of this species can now be much better evaluated by comparison with the living forms, especially *Potamochoerus* and *Hylochoerus,* that are usually recognized as belonging to the same clade, and with other species from various sites, mostly those from East Africa housed in the National museums of Ethiopia (NME), Kenya (KNM) and Tanzania (NMT). The material from Ahl al Oughlam is housed at the Institut National des Sciences de l'Archéologie et du Patrimoine, Rabat, Morocco.

Abbreviations: AaO: Ahl al Oughlam; ASB: Asbole (early Middle Pleistocene of Ethiopia: Geraads *et al.*, in press); MNHNP: Muséum National d'Histoire Naturelle, Paris.

SYSTEMATIC PALAEONTOLOGY

Genus *Kolpochoerus* van Hoepen & van Hoepen, 1932
Mesochoerus Shaw & Cooke, 1941
Omochoerus Arambourg, 1943
Promesochoerus Leakey, 1967
Ectopotamochoerus Leakey, 1967
Type-species: *K. sinuosus* van Hoepen & van Hoepen, 1932

Diagnosis. although *Kolpochoerus* is one of the most common and frequently described suids of the African Plio-Pleistocene, and although general agreement as to the content of the genus has more or less been reached, the available diagnoses of the genus vary widely. Many authors did not provide any diagnosis (Hendey & Cooke 1985; Geraads 1993; Pickford 1994; Brunet & White 2001). Others provided only very general primitive features that could apply to many suids (sexual dimorphism, brachyodont teeth, general resemblance to *Sus* and *Potamochoerus*), or are variable (especially those which apply only to the latest members of the group, such as hypsodonty, cement cover, length of talon/talonid). Only a few valid features are generally recognized, starting with the original diagnosis (van Hoepen & van Hoepen 1932: 59; my translation): 'Molars whose pillars have strongly folded enamel. The pillars of the middle row are quite simple. Between the first and second pair of pillars [of M3/m3] stands a median pillar, but between the second and third pairs stand two triangular pillars, opposed by their bases.'

Cooke (1978) provided a long list of features, of which the following are the most diagnostic: zygoma expanded and drooping, canines resembling those of *Hylochoerus,* upper premolars with protocone, molars with pillars higher and more distinct than in *Sus* and *Potamochoerus,* P4 complicated, mandible inflated.

The cladistic analysis (see below) suggests the following list of apomorphic features: broad forehead, concave cranial profile, zygomatic shelf deep and pneumatized, P2 well behind the root of the canine, P3 with an anterolingual cusp, a pair of central pillars between the second and third pairs on m3.

Currently recognized species

The description below is based upon the male skulls AaO-36555 and AaO-3656. They are compared with the female skull AaO-239 (Geraads 1993), with the living forms, and with the other *Kolpochoerus* species, namely:

- *K. paiceae* (Broom, 1931) from the Pleistocene of South Africa (Hendey & Cooke 1985);
- *K. majus* (Hopwood, 1934) from the Pleistocene of East Africa, represented by several skulls, only a few of which have been described (Gilbert *et al.* 2000; Geraads *et al.*, in press a);
- *K. heseloni* (Leakey, 1943), which includes *K. olduvaiensis,* a late and derived form, appears to be the correct name for the species often called *K. limnetes* (see Pickford 1994 and Cooke 1997), from the Plio-Pleistocene of East Africa;
- *K. maroccanus* (Ennouchi, 1953), a poorly known species from Morocco; the age of the type is unknown, but a referred M3 is of late early Pleistocene age (Geraads *et al.* 2004);
- *K. afarensis* Cooke, 1978, from the Pliocene of East Africa;
- *K. deheinzelini* Brunet & White, 2001, from the early Pliocene of Ethiopia and Chad;
- *K. cookei* Brunet & White, 2001, from the late Pliocene of Ethiopia.

Sexual dimorphism in *Potamochoerus*

Among the above-mentioned species, the best-known form is *K. heseloni,* followed by *K. afarensis, K. paiceae* and *K. majus,* while the remaining three species are known only by teeth. However, almost all known *K. heseloni* skulls are of male individuals, while *K. paiceae* is known only by female skulls. In order to limit the effects of this drawback on the comparisons, I have evaluated the sexual dimorphism in *Potamochoerus,* the only close relative of the fossil genus which could be illustrated by enough specimens (16 females and 18 males, all fully adult, from the MNHNP).

In *Potamochoerus,* males are slightly larger than females, for all skull measurements, but all of these overlap widely, and differences between both sexes amount to only a few percent (Table 1). This agrees with the findings of Made (1991). The most significant differences are in muzzle length, and bi-auditory and minimum orbital widths. Bi-zygomatic width of females falls entirely within the male range, although the narrower males are of rather young specimens.

Morphological features allowing sexual identification must be used with caution. The anterior border of the zygomatic arch is more transverse in males, and sloping more backwards in females. The zygoma is pneumatized in males, less so (and often not at all) in females. The same differences hold for *Hylochoerus* but in this genus, even the females have inflated arches.

Table 1. Measurements of modern *Potamochoerus* skulls.

	Mean ♀ $n = 16$	Mean ♂ $n = 18$	♀ in % ♂
Condylobasal length	298.9	314.8	94.9 **
Length from back of condyle to M3	95.2	97.0	98.1
Length from back of M3 to front of I1	198.8	205.5	96.7
Length from orbit to front of canine	153.8	167.3	91.9 **
Length from front of P2 to front of I1	92.7	102.3	90.6 **
Bizygomatic width	158.9	171.2	92.8 **
Maximum bi-orbital width	101.0	108.7	93.0 *
Minimum bi-orbital width	71.6	76.8	93.2 **
Minimum width between temporal lines	36.4	39.1	93.1
Width over occipital crest	78.4	85.4	91.8
Minimum occipital width	63.0	67.0	94.0
Width over external auditory meatus	118.5	129.9	91.2 **
Occipital height	82.1	89.5	91.8 *

* = significant difference; ** = highly significant difference.

The most conspicuous sexual difference lies in the supra-canine flange, which extends upwards in *Potamochoerus* males more than in any other suid genus, as a thin lamina of bone ending in a roughened thickening, sometimes reaching the level of the nasals, which are wide and rough in adult males. Females normally have almost no supra-canine flange, and smoother nasals, but one of the examined specimens (with no registered sex data), although female by most of its other features and measurements, has a strong canine flange, so that there is a doubt concerning the discriminant value of this feature.

Considering the fossil forms, the only well-preserved (unpublished) female skull of *Kolpochoerus heseloni* from Peninj (NMT; photographs of the specimen were also kindly provided by H.B.S. Cooke) displays similar sexual differences from the male ones. The supra-canine flange is weak, but skull dimensions (Hendey & Cooke 1985) are only slightly smaller than in males. The same holds for *K. phacochoeroides,* in which the main difference lies in canine size. There is, therefore, every reason to believe that sexual dimorphism was not particularly great in this group, and that the female skulls provide a good idea of what the male skulls were.

Kolpochoerus from Ahl al Oughlam

Kolpochoerus phacochoeroides (Thomas, 1884)

Sus phacochoeroides Thomas, 1884: 10

Holotype. Mandible fragment from the limestones of Aïn el Bey, Algeria (Thomas 1884: pl. 10, figs 1–2). MNHNP, No. AFN-1. Besides Ahl al Oughlam, it is not known from any other locality.

Diagnosis. Convex parietal profile, auditory duct very oblique, occipital high and broad, with condyles high above the tooth-row, drooping zygomatic arch, supra-canine flange and snout muscle scars usually weak, snout short and rounded in section, auditory bulla small, upper canine large, with trifoliate cross-section, enamel band vestigial or absent, lower canine of *verrucosus* type, I1 small, marked wear gradient on cheek-teeth, premolars reduced in size, P4 with a posterolingual fovea, M3/m3 with complex tubercles and numerous accessory pillars,

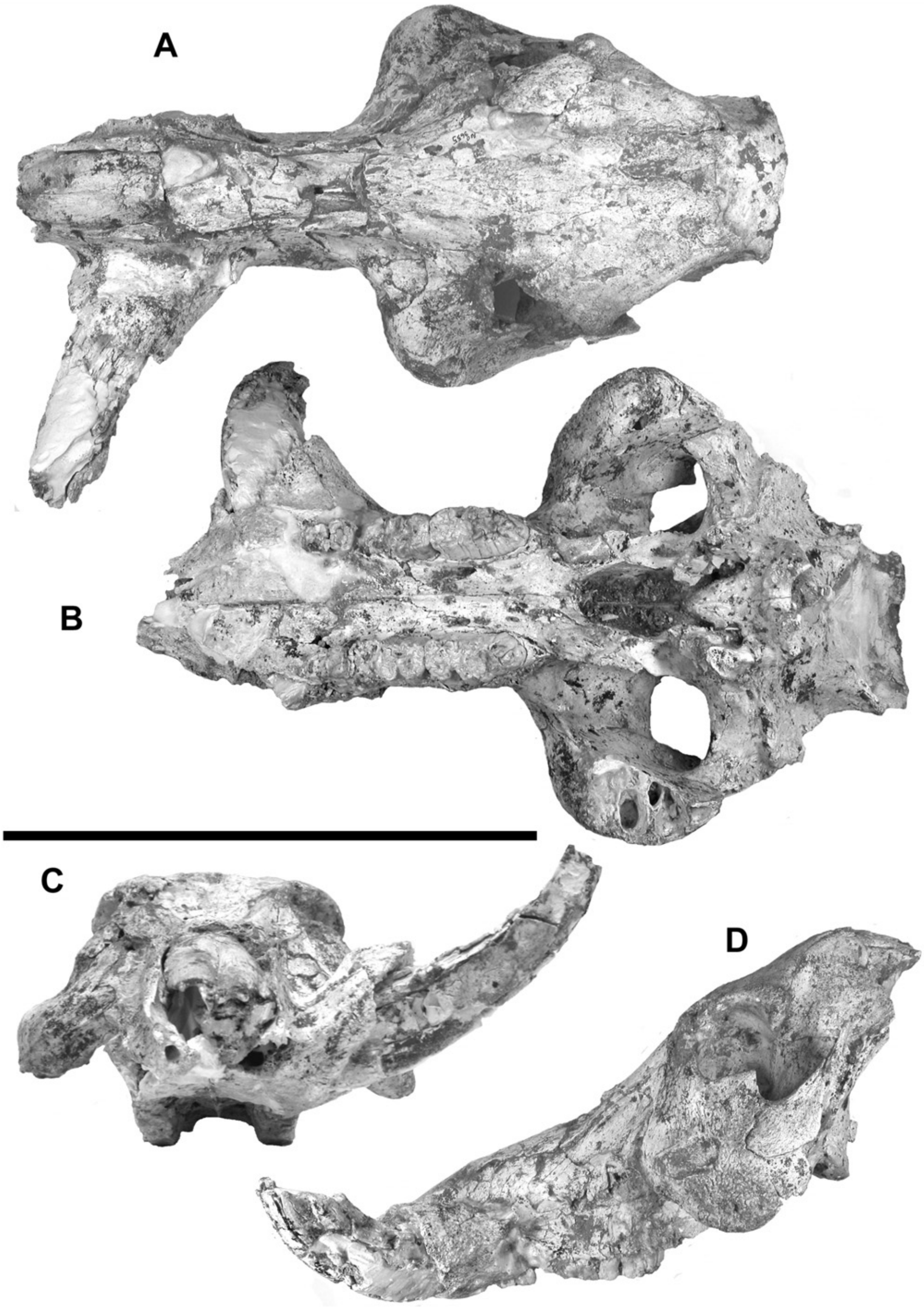

Figure 1. *Kolpochoerus phacochoeroides,* Ahl al Oughlam, AaO-3655. **A**, dorsal view; **B**, ventral view; **C**, anterior view; **D**, lateral view. Scale bar = 30 cm.

but normally with only one pillar between the second and third pairs of m3.

Material from Ahl al Oughlam. *K. phacochoeroides* is the only suid from Ahl al Oughlam. It is represented by two male skulls, a fragment of female skull, several mandibles and tooth-rows, and more than 200 complete isolated teeth, but very few postcranial elements.

Description and comparisons of the male skulls (Fig. 1). The sagittal profile of the skull is strongly convex above the temporal fossae, slightly convex along the forehead, then slightly convex again along the nasals. It was probably similar in the female (AaO-239; Geraads 1993: pl. 1, fig. 1) which is, however, somewhat crushed dorsoventrally. *K. heseloni* usually has a more concave profile in the naso-frontal area, although this is not true of KNM-ER-772 from the *M. compactus* zone of Koobi For a (Harris & White 1979: pl. 10, top). *K. afarensis* and *Potamochoerus* have no concavity at all, and the latter has a straight nasal profile. None of the living African suids has the strongly convex parietal profile of the fossil forms.

The forehead is slightly concave transversely between the orbits, in contrast to *Potamochoerus and K. afarensis,* where it is convex, and to *Hylochoerus,* where it is deeply concave and very broad between the temporal fossae. As in all other forms, except *Hylochoerus,* where they are more rostral, the supra-orbital channels arise at the level of the anterior orbital border.

The nasals are longitudinally and transversely domed, as in *Hylochoerus* and *Phacochoerus.* The lateral face of the latter is concave, although less so than in *Potamochoerus.*

The maxilla forms a long canine sheath along the tooth but this sheath is anteroposteriorly short, being little

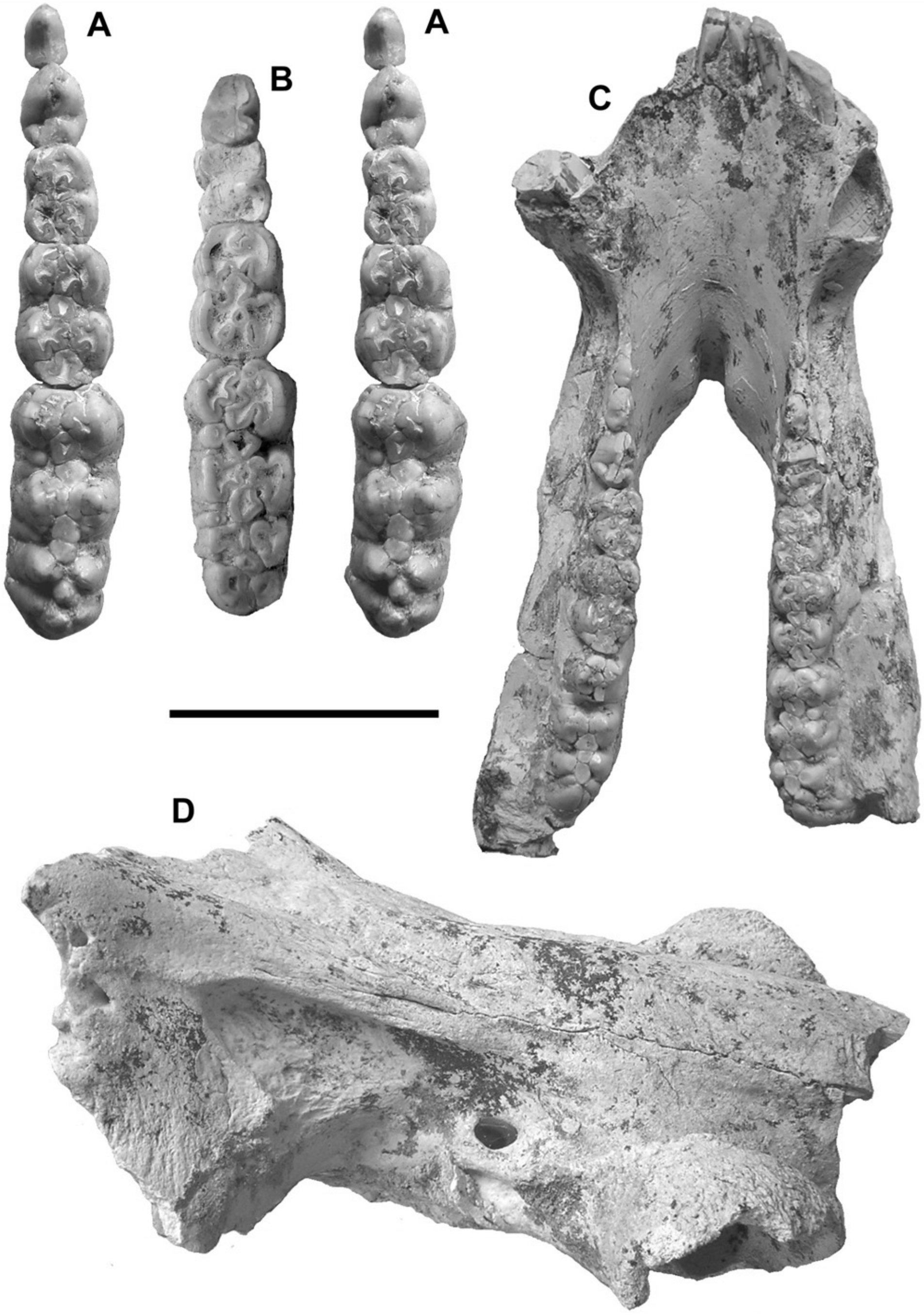

Figure 2. *Kolpochoerus phacochoeroides,* Ahl al Oughlam. **A**, AaO-141, p3–m3, occlusal view (stereo pair); **B**, AaO-2065, p4–m3, occlusal view; **C**, AaO-3478, dorsal view; **D**, AaO-4516, right antero-latero-dorsal view of muzzle. Scale bar = 5 cm for A, B; 7.5 cm for C, D.

expanded behind the alveolus. Along its dorsal part, the crest that limits laterally the supra-canine gutter is weak, as in *Hylochoerus,* and mostly restricted to the posterior part. In *K. heseloni,* this area is variable, but the supra-canine flange is always stronger in males, and the groove for the rhinarium tendons is often partly roofed over by a lateral thickening of the premaxilla/maxilla-nasal suture, as in *Potamochoerus.* However, this thickening disappears in later specimens (*K. olduvaiensis*) of this lineage (Harris 1983: 241, and skull Omo-H2). Sexual dimorphism is weak at Ahl al Oughlam, and mostly linked with the size of the canine.

Posteriorly, the area of insertion of the *m. levator rostri* is more excavated and extends slightly farther posteriorly than in *Hylochoerus,* but is usually much less marked than in *Potamochoerus,* where this rhinal musculature is extremely strong. Only AaO-4516 (Fig. 2D) has a well-marked muscle scar there; perhaps this difference is linked with the greater ontogenic age of this specimen, which is unfortunately toothless. Other *Kolpochoerus* are similar to *K. phacochoeroides,* except *K. afarensis,* which has a deep insertion for *m. levator rostri,* plus another conspicuous muscle scar above it, in front of the upper lachrymal foramen. This scar is also present on AaO-4516 and in *Sus,* but not in other African suids. Pickford (1988) found it in *Lopholistriodon,* and referred it to the *m. levator labialis lateralis.* There is no visible scar for *m. depressor rostri,* in contrast to both living African forms. All this suggests that the rhinarium was not more used for digging than in *Phacochoerus* or *Hylochoerus,* and much less than in

Potamochoerus or even *K. afarensis.*

The shortness of the muzzle is a significant feature of *K. phacochoeroides.* In all male and female specimens, the P2 reaches farther forward than the posterior border of the canine bony sheath. Only *K. majus* may have premolars in such an anterior position, and the premolar rows may also diverge anteriorly, so that the P2s are much wider apart than the P4s, while the tooth-rows are parallel in other species. In *K. heseloni* (Harris & White 1979: pl. 9, top; and on the Omo and Peninj specimens), as well as in *K. paiceae* (Hendey & Cooke 1985: fig. 2) and in the living forms, the premolar series remains far behind the canine alveolus, because the muzzle is much longer than in *K. phacochoeroides.*

As a consequence of the shortened snout, the infraorbital foramen is located above M2, whereas it is above M1 in *K. majus* (Asbole), *K. paiceae* (Hendey & Cooke 1985: fig. 2), late *K. heseloni* (Peninj), and in the living forms.

In the males from Ahl al Oughlam, although the morphology is that of their sex, the degree of inflation of the zygomatic arches is smaller than in the evolved form of *K. heseloni,* and even than on the female Peninj skull, being more similar to *Hylochoerus.* The maximum thickness of the zygomatic inflation is 86 mm in KNM-ER-788, but only 42 mm in AaO-4565, 41 mm in AaO-3655, and 46 mm in AaO-3656. As in the modern forms, the anterior borders of the zygomatic arches, when seen from above, are transverse, whereas they slant clearly posteriorly in the female, as in all females of *Kolpochoerus.* Lateral inflation is poor in all females, except in the Peninj skull, the only well-preserved female skull of *K. heseloni.*

In anterior view, the zygomatic arches are markedly drooping. Cooke & Wilkinson (1978) thought that they became more transverse through the evolution of *K. heseloni,* and in all known male specimens of the evolved form of this species, the arches are indeed transverse, but skull L193-109 from unit C8 of the Omo Shungura Fm, roughly contemporaneous with Ahl al Oughlam, also has transverse zygomas. KNM-ER-212 (Harris & White 1979: pl. 12, bottom left) has drooping arches, more like those of *K. phacochoeroides,* but its age is unknown.

In the males of *K. phacochoeroides,* the orbit is set far back in the skull, a feature which is associated with a very deep zygoma arising behind M3, and posterior pterygoids borders which are oblique posterodorsally, instead of more vertical (perpendicular to the tooth-row) in other species. The medial part of the zygoma, under the orbit, is very much deeper in *Phacochoerus* than in *Potamochoerus. K. phacochoeroides* is intermediate, as is *Hylochoerus,* but without the large lachrymal fossa which is characteristic of this genus.

The orbit is large, especially when compared to the zygomatic arches, and higher (posterodorsally to anteroventrally) than long. In other forms, except perhaps *Hylochoerus,* it is circular and smaller (especially in KNM-ER-788). The superior orbital rim and the temporal lines of AaO-3655 and AaO-3656 are slightly but distinctly inflated, as in some Omo skulls and some *Potamochoerus,* but none of them displays the extreme inflation of KNM-ER-788.

The occipital is broad at its top, as in the female skulls of *K. majus,* and in contrast to *K. heseloni* and *Potamochoerus,* but it is also higher, and broader at the level of auditory meatus, than all other species. On the whole, the occipital is both higher and broader than in other forms. Comparative measurements are given in Table 2.

The bulla is quite small, as in *Phacochoerus.* In other species it is seldom preserved, and is apparently unknown in *K. heseloni.* In *K. majus* it is also small but more elongated, with a rostro-ventral spine. In *K. afarensis,* it is very large, long and inflated, comparable to those of *Hylochoerus* and *Potamochoerus.*

About 20 petrosals of *Kolpochoerus* have been retrieved from Ahl al Oughlam. They are quite variable in size, but not so much in shape, being rather rectangular, almost always lacking the anterior or posterior spines of *Sus,* which are also often found in *Potamochoerus* and *Hylochoerus.* The promontorium is larger and more inflated medially than in the other African genera. The centrodorsal apex is prominent, as in other genera except *Phacochoerus.* The posteroventral process, which extends along the bulla, is variably developed, but always short, as in other African suids, and in contrast to *Sus,* where it is longer. The vestibular fenestra (*fenestra ovalis*) is much smaller than the cochlear fenestra (*fenestra rotunda*), as in *Potamochoerus,* and in contrast to *Phacochoerus,* where they are almost of the same size, the other genera being intermediate.

Mandible. The material from Ahl al Oughlam includes several mandibles, but the ascending ramus is not preserved in any of them. The occurrence of several specimens of various ages allows the recognition of the ontogenic changes that take place in the rostral area, and can be summarized as follows:

In the youngest specimens (AaO-5, AaO-4012), the canine is very close to p2; the symphysis may extend distally as far as p4, and the incisor series forms a deep arch in occlusal view. In the older specimens, it looks as if the canines had moved mesially: the diastema is longer, the distal border of the symphysis is more mesial, and the incisor arch is shallower. The symphysis looks broader because its maximum width is more anterior. Measurements are given in Table 3. *K. afarensis* and *K. heseloni* have a symphysis similar to those of the juvenile specimens of *K. phacochoeroides. Hylochoerus* and *K. majus,* instead, have very anteriorly placed canines, with a very shallow incisor curve between them, and the diastema is long (Leakey 1958: pl. 2, fig. 1). Ontogenic changes in the Moroccan species strongly suggest that this condition is derived.

Teeth: Of the upper incisors, as in other *Kolpochoerus* species, I1 is the largest, but it is still small compared to *Potamochoerus* or *K. heseloni* or even to *K. majus.* There is no lingual cingulum. A short diastema separates I1 from I2, itself separated from I3 by a longer diastema; this latter tooth is absent in AaO-4456. In other species (illustrated by KNM-ER-788 for *K. heseloni* and ASB-198 for *K. majus*), the diastemata between the incisors are shorter, while that between I3 and C is longer. Skull L6-10 of *K. majus* from Bodo, and *K. paiceae,* have no I3s. I2 and I3 are normally

Table 2. Comparative measurements in mm, of *Kolpochoerus* skulls. In part from Harris (1983) and Hendey & Cooke (1985).

	Bizyg. width	Min. bi-orbital width	Length from rear of M3 to front of I1	Condylo-basal length	Length from occipital condyle to back of M3	Bi-mastoid width	Max. width of nuchal crest	Occipital height	Length from orbit to front of canine	Length from front of P2 to front of I1
K. afarensis										
NME-AL 602-1	240–				152	160		145		
NME-AL 154	230									
K. majus										
NME-ASB 198-2			232	390	152	155	150	135	195	118
NME-Bodo L6-10			231	365	146	132	122	122	198	
K. heseloni										
NME-Omo L193-109	290			410	150	162	110	141	250+	
NME-Omo 75	310			450+	145?				260	
NME-Omo H2	320		300?		145?				260	
NME-Omo 74-7					145?	160	110			
NME-Omo 325-2093	330		330?	450	145?				270	165 ?
KNM-ER 212	278+	108		436				164		
KNM-ER 221	326	104						160		
KNM-ER 409	302	112						152 +		
KNM-ER 449	340									
KNM-ER 759						184		161		
KNM-ER 772	340	121				183	145	135		
KNM-ER 787		88					123	118		
KNM-ER 788	370	112		495		177	145	166	300?	180
KNM-ER 3463	293	101					128	156		
KNM-ER 3499	335	11					141	164		
KNM-ER 5117	336+	131					121+	155		
NMT-Peninj	318	125		465			150			160 ?
K. phacochoeroides										
AaO 3655	237	115	230 ?	360 ?	134	178	130 ?	138	235	105 ?
AaO-3656	232		240	375 ?	130 ?	178.5		135 ?	235	120
AaO-4516									230	
AaO-275			210							80
AaO-239			217						185?	97
K. paiceae										
Skurwerug PQ2166	260	104		375			112			
Potamochoerus, mean	164	74	203	307	96	124	82	85	161	98
Hylochoerus, mean	186	88	216	343	123	135	104	81	180	

Table 3. Measurements of the mandibular symphysis in *Kolpochoerus* (mm)

	Width over canine alveoli	Minimum width	Sagittal length
K. phacochoeroides			
AaO-5	116	85	123
AaO-37	111	84	
AaO-72	99+	86	100
AaO-134	74	60	96
AaO-296	72	63	86+
AaO-361		55	82
AaO-2065	115	93	105
AaO-2240	80	64	80
AaO-3478	110	80	102
K. afarensis			
AL-134	74	60	96
AL-296	72	63	86+
AL-361		55	82
K. majus			
ASB-37	111	84	
ASB-44	113	93	111
ASB-172	99+	86	100–
K. paiceae			
Elandsfontein 16675	102	86	106
Elandsfontein 20928	110	95	106
Skurwerug	93.5	73.5	101
K. heseloni			
KNM-ER-432	118	90	127
KNM-ER-433		78	115
KNM-ER-946	131	102	143
KNM-ER-1314	102	86	116
KNM-ER-2701	73	62	112
KNM-ER-4304	117	86	133
Olduvai FLK	92	73	115
Olduvai MMK	136	92	139
Omo K11-71-114	80	65	100
Omo L635-1	84++	65++	120 ?
Omo L64-5	112	85	114
Omo L895-2	95	74	
Omo O27-3-67	127 ?	97	145
Omo O75-69-4909	68	54	103
Omo O75N-71-127		69	95
Kolpochoerus sp.			
Ubeidiyeh		95	160?

absent in *Hylochoerus,* and I1 is often missing as well.

In all male (AaO-3655, AaO-3656, AaO-4456), female (AaO-239), and unsexed (AaO-275) specimens, the upper canine emerges mostly transversely, slightly forwards, and with a weak upward component from the very base. Only *Hylochoerus* may have a similar orientation. The female canine is directed downwards in *K. afarensis,* while those of *K. heseloni, K. majus* and *Potamochoerus* have a slight downward component at the base.

The canine has a trifoliate cross-section, with a shallow ventral groove, and two deeper anterodorsal and posterodorsal grooves, which delimit a small dorsal lobe. Other species of *Kolpochoerus,* and *Hylochoerus,* have a similar cross-section, but it is less clearly trifoliate in *Potamochoerus.* Enamel is normally absent, but thin anteroventral and posteroventral ribbons are present near the tip of juvenile specimens (especially AaO-239 and 275). The canines of *K. heseloni, K. majus,* and of *Potamochoerus* have a thick broad ventral band of wrinkled enamel, but it is very thin in *Hylochoerus.*

Table 4. Anteroposterior and dorsoventral diameters of *Kolpochoerus phacochoeroides* upper canines (mm).

		Anteroposterior	Dorsoventral
AaO-8	♀	33.5	26
AaO-9	♀	29.2	24
AaO-23	♀	34	25.5
AaO-239	♀	34	24
AaO-267	♂	58.5	39
AaO-2000	♀	28.2	25.5
AaO-3656	♂	*c.* 53	*c.* 40
AaO-4456	♂	61	40

Although the skulls are not larger than those of *K. heseloni* or *K. majus,* the male canines of *K. phacochoeroides* are even stouter (Table 4) than most specimens of these species (50 × 39 in KNM-ER 788 according to Hendey & Cooke 1985: 20; 36 × 33 in a male *K. majus* from Asbole); however, very large canines of *K. majus* are known from Daka (Gilbert 2000: fig. 7.2) and Garba IV at Melka Kunture (Geraads *et al.*, in press b). Thus, although the sexual dimorphism is weak, sexual bimodality is more marked than in *Potamochoerus, Hylochoerus,* and probably than in most other *Kolpochoerus* species.

As already noted (Geraads 1993), the wear gradient of the upper cheek teeth is variable, but I now believe that this is indeed a valid difference with other species, and especially with *Potamochoerus.* The most extreme case is AaO-239 (Geraads 1993: pl. 1, fig. 1B), where the premolars are worn almost to their roots, while the M3s have just erupted. Several other specimens, including the two male skulls, display a similar gradient. No such gradient exists in *K. heseloni,* where M3s in medium wear may be associated with only moderately worn P4s (Harris & White 1979: fig. 62; Harris 1983: pl. 6.12.K). Other species are not so well documented, but look more like *K.* heseloni. Functionally, *K. phacochoeroides* looks intermediate between *K. heseloni,* with normal functional premolars, and *Hylochoerus-Phacochoerus,* with premolars so reduced that they become spared by wear.

The premolars are remarkably reduced in size, much as in *K. paiceae,* but a small P1 was present (as shown by its alveolus or alveoli), at least on one side, in all specimens where this region is well preserved. Shedding of this tooth in adulthood was therefore uncommon, at most. This tooth is usually absent in *K. heseloni* and *K. paiceae,* but present in *K. majus.* In *Potamochoerus* it is usually absent, irrespective of age.

P2 is seldom preserved, but the alveoli show that it was a very reduced tooth (Fig. 3), comparable to that of *K. paiceae,* but relatively and absolutely much smaller than in *K. heseloni* (except in the Peninj cranium, which has no P2), *K. majus* or *Potamochoerus* (although it is variable in the latter).

P3 is similar to those of other species, except that, as in *K. afarensis* and *K. maroccanus,* but in contrast to *K. heseloni* (e.g. Harris & White 1979: figs 62, 64), the main labial tubercle is not well separated from the postero-labial one, which is low. All *Kolpochoerus,* except *K. deheinzelini,* differ from *Potamochoerus* by the presence of a strong mesio-

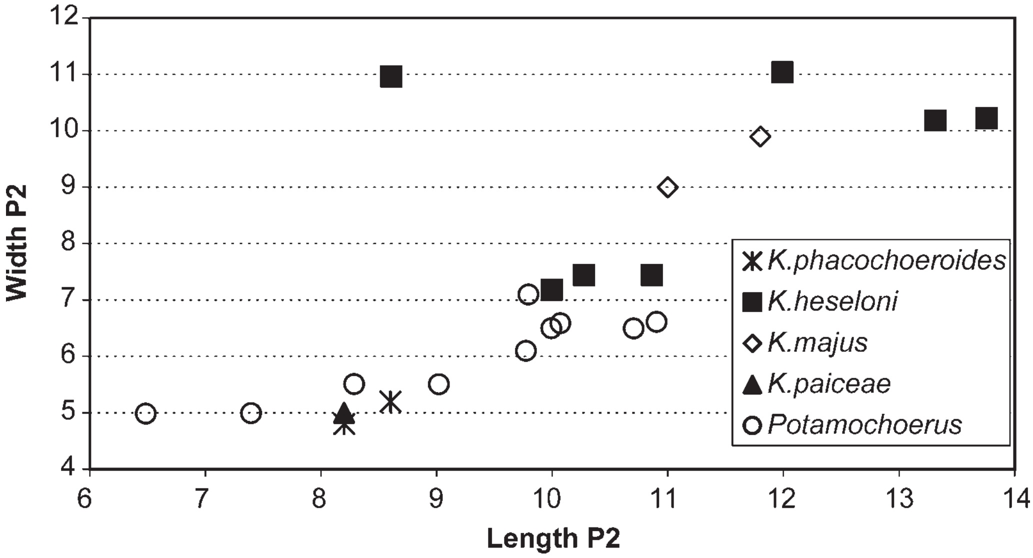

Figure 3. Plot of length *vs* width of *Kolpochoerus* upper second premolars. *Potamochoerus* from Fessaha (1999); *K. majus* from Geraads *et al.* (in press), *K. paiceae* and *K. heseloni* from Hendey & Cooke (1985).

lingual complex of cusps.

The P4 of *K. phacochoeroides* is variable in size, but not so much in morphology. Labially, the metacone is separated by a weak groove from the protocone, and smaller than it. Both tubercles send lingual expansions into the central fovea. These are often connected to each other (the 'sagittal cusplets' of Pickford 1988), but usually fail to reach the main lingual cusps, which form the highest peaks of a semi-circular ridge running more or less continuously from the parastyle to the metastyle. Lingually, a high cingular ridge forms the margin of a characteristic posterolingual fovea (Geraads 1993: fig. 5A), present in 22 P4s out of 26. In *K. afarensis,* the labial cusps are subequal in size and much better separated, as in *Potamochoerus,* but there may be an incipient lingual fovea, which is absent in *K. heseloni* and *K. majus.* The latter species has a simple P4, with a small lingual part and the paracone by far the largest cusp.

The M3s are variable in size, but the coefficient of variation (s = 8.1 for M3 length) is smaller than, e.g. for *K. heseloni* of the *M. andrewsi* zone of Koobi Fora (s = 11.9; Harris 1983: tab. 6.18), which does not sample a long time-period. They are larger than those of *K. afarensis,* or than those of *K. heseloni* from Omo member B. They are slightly smaller, on the average, than those from Omo-D-E-F, clearly smaller than those of Omo-G, Upper Burgi, Olduvai bed I, and much smaller than those of the KBS and Okote members, or *K. paiceae* from Elandsfontein. Most M3s of *K. majus,* and those of *K. maroccanus,* are close to the upper limit of the *K. phacochoeroides* range.

The morphology of M3 is homogeneous, the smallest and largest teeth differing mostly in the number of talon pillars. They are rather hypsodont, more so than those of *K. heseloni* from Omo member G, and more like those of the KBS member of Koobi Fora. The enamel is never as thick as in some Omo-G specimens, and is certainly thinner on the average. The main and secondary pillars have the same general pattern as in *K. heseloni* (Harris & White 1979: 39–40), but are better isolated in their apical portion. This combination of thin enamel and isolated pillars prevents the formation of flat areas of the occlusal surface consisting only of enamel, as found in slightly worn teeth of *K. heseloni.* An accessory pillar usually blocks the lingual valley between the first and second pairs of pillars, but the corresponding labial valley is wide. There is a marked tendency for the accessory pillars of the talon to subdivide above the base, so that they are hard to count objectively. The shortest and most simple tooth (AaO-906) has but about six pillars distal to the second pair, but this number may reach almost 20 in the longest M3 (AaO-3521) which can be compared, in size and morphology, to advanced members of the *K. heseloni* lineage (e.g. KNM-ER-788: Harris & White 1979: figs 65–66).

As described by Harris & White (1979: 40–41), the M3s of *K. majus* have a main lingual talon pillar. In the simplest teeth of this species (female skulls ASB-198-2 from Asbole;

Table 5. Measurements of *Kolpochoerus phacochoeroides* upper tooth series (mm).

	P2 ap	P2 tr	P3 ap	P3 tr	P4 ap	P4 tr	M1 ap	M1 tr	M2 ap	M2 tr	M3 ap	M3 tr
AaO-2			12.8	10.8	12.6	13.7		15.7	22.9	21.2	41.8	22
AaO-3932					12.1	13.6		15.5	22.8	21.1	42.2	23.8
AaO-3656			12.2	11.4	12.2	15.2	15.3	16.3	21.9	21.5	42.7	24.7
AaO-3			13	12.1	13.5	15			24.3	21	42.8	23
AaO-275	8.2	4.8	11.6	9.8	12.5	14.4	16.6	15.5	23.5	20.6	43.5	21
AaO-3655					12.6	16.3			22.8	22.5	43.7	25.3
AaO-239	8.6	5.2	11.3	11.6	11.5	14.6	15	15	23.7	19.5	46.5	22.5
AaO-4			12.5	12.1	12.7	14.2			24.4	20.7		22.4

Table 6. Measurements of *Kolpochoerus phacochoeroides* upper cheek teeth (mm).

	P3			M1			M2			P4			M3	
	A-P	TR		A-P	TR		A-P	TR		A-P	TR		A-P	TR
AaO-348*	11.3	10.2	AaO-4094	15.8	16	AaO-4353	20.5	20	AaO-1382	10.5	13.1	AaO-906	37.6	23
AaO-3511	11.3	10.8	AaO-3578	16	14	AaO-4092	21.3	20.5	AaO-3152	11	12	AaO-3589	37.8	21.2
AaO-4369	11.3	11.3	AaO-3504	16.1	15	AaO-1489	21.5	21.8	AaO-3560	11.2	14.2	AaO-1462	38.5	24.9
AaO-4355	11.5	11.2	AaO-4364	16.3	15.9	AaO-4093	21.7	20.7	AaO-3562	11.2	13.4	AaO-3502	40	22.1
AaO-3563	11.8	11.1	AaO-3577	16.6	14.3	AaO-2592	21.8	17.5	AaO-1484	11.3	14	AaO-4400	40	22.1
AaO-2594	16.5	13.1	AaO-3561	16.7	13.5	AaO-3481	22	21.1	AaO-4351	11.4	13.2	AaO-3583	40	23.1
AaO-1381	12	11.5	AaO-3567	16.7	15.1	AaO-4343	22	21.1	AaO-4358	11.4	13.6	AaO-4087	41.5	21.3
AaO-4409	12.2	11.4	AaO-924	16.9	15	AaO-2590	22.3	20	AaO-4097	11.6	13.8	AaO-1479	41.5	25
AaO-919	12.3	12.8	AaO-2089	16.9	15.8	AaO-2591	22.3	18.2	AaO-4346	11.7	13.5	AaO-1388	41.7	23.5
AaO-4096	12.3	11.4	AaO-928	17.1	15	AaO-4401	22.8	21.8	AaO-1490	12	14.2	AaO-4088	41.8	23.2
AaO-4347	12.3	11.3	AaO-42	17.2	16	AaO-40	23.1	21.3	AaO-4403	12.1	14.8	AaO-3586	42.2	21.6
AaO-4350	12.3	11.7	AaO-26	17.5	14.8	AaO-2589	24	21.8	AaO-4356	12.2	14.3	AaO-1478	43.1	23.5
AaO-3513	12.4	11.6	AaO-2054	17.8	15.7				AaO-1380	12.4	15	AaO-4090	44.2	23
AaO-3512	12.5	11							AaO-918	12.6	15.4	AaO-3519	45	23.1
AaO-3564	12.5	11.7							AaO-55	12.7	14.7	AaO-3480	45.8	24.2
AaO-350	12.6	10.6							AaO-53	12.8	14.4	AaO-2587	46	23.1
AaO-349	12.7	11							AaO-56	12.8	14.8	AaO-4341	46.4	24.5
AaO-1493	12.7	11.3							AaO-57	12.8	13.8	AaO-3581	46.8	24.5
AaO-3149	12.7	13							AaO-2599	12.8	14.3	AaO-2586	47.4	25
AaO-4406	12.9	12.5							AaO-54	12.9	15.2	AaO-1411	47.6	25.4
AaO-58	13	11.6							AaO-1482	13	16.7	AaO-2585	48.5	24.6
AaO-1494	13	14							AaO-4407	13	16.8	AaO-3580	49.5	27.7
AaO-2600	13	13							AaO-2598	13.1	15	AaO-3521	52.5	25.7
AaO-351	13.3	10.3							AaO-3565	13.2	16.7			
									AaO-3558	14.3	17			
									AaO-3147	14.5	16.1			

*Isolated teeth.

L6-10 from Bodo), only two or three more labial pillars are added labially to build up the talon, but more complex examples, such as ASB-169 and ASB-200 from Asbole, have many more secondary pillars, some of them circling lingually the main talon pillar. In every case, the furrows on the main trigon pillars are shallow, so that these pillars have a more rounded outline than in *K. phacochoeroides* and *K. heseloni,* where they are usually more X- or H-shaped. Still, distinction of isolated teeth is certainly not straightforward.

Kolpochoerus maroccanus has simple M3s similar to those of *K. majus,* or to the most simple examples from AaO, but they are more brachyodont, the enamel is thick, at least in the type-specimen, and the pairs of pillars are well separated.

Like the upper ones, the lower incisors are small, i2 being the largest, followed by i3. The central pairs are more parallel in *K. heseloni* and *Potamochoerus*; *Sus* and all living African suids have small i3s, but on the whole, lower incisors display much less inter-specific variation than upper ones.

The lower canine is always of *verrucosus* type, with a lingual side not much broader than the mesio-labial one. It is of *scrofa* type in *K. afarensis* (*contra* Cooke 1978). All other *Kolpochoerus* also have a lower canine of *verrucosus* type, like *Hylochoerus, Metridiochoerus* and *Phacochoerus,* but the section is closer to that of *S. scrofa* in *Potamochoerus,* although the mesio-labial face is not so short. The dimensions of the three faces are given in Table 7. They clearly fall into two size groups, doubtless reflecting sexual dimorphism, because these differences cannot be due to ontogeny (the dimensions do not significantly increase towards the base).

Table 7. Measurements of *Kolpochoerus phacochoeroides* lower canines (mm).

		Lingual	Mesio-labial	Disto-labial
AaO-5	♂	23	21.5	19
AaO-7	♂	20.8	19.5	15
AaO-278	♀	13.3	13.4	9.8
AaO-912	♀	16.5	14	11
AaO-926	♀	16.7	15.5	11.3
AaO-2617	♂	20.8	18.3	15
AaO-3478	♂	21	19	15.5
AaO-4012	♀	17.5	15.2	12

The lower premolars are very characteristic, being rounded rather than rectangular, and with a strong size gradient. The p2 is a minute tooth, definitely shed in some old specimens. The p3 has a thick ovoid outline and no central constriction (in contrast to all other species of *Kolpochoerus*). It is clearly smaller, relative to the width of m2 used as a proxy for overall size, than in *K. heseloni* (Fig. 4). There may be a weak anterior accessory cusp. The p4 has the same thick rounded ovoid outline as p3, with a maximum width at talonid level. The talonid is short, and its components, even in early wear, are transversely set, mainly because of a strong lingual buttress, which often becomes an isolated pillar. Distally, a strong labial buttress also supports the central talonid pillar. The main cusp is conical, but may also be buttressed on either the labial or

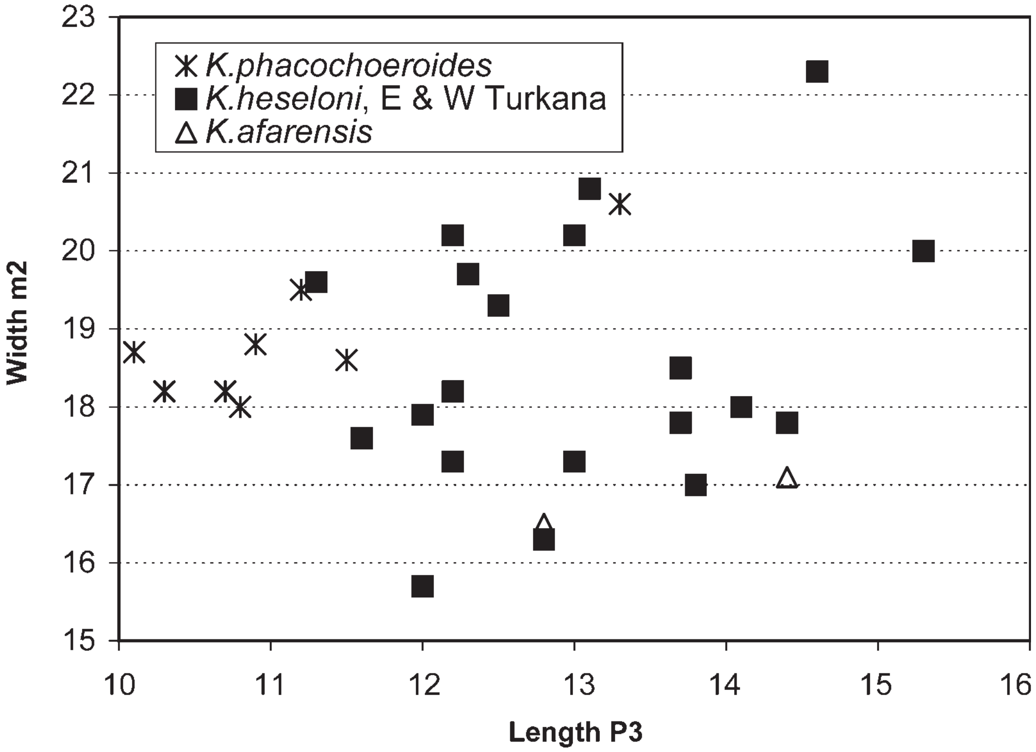

Figure 4. Plot of p3 length *vs* width of m2 (taken as a proxy for overall size) in *Kolpochoerus. K. afarensis* from Cooke (1978); *K. heseloni* from Harris (1983) and Harris *et al.* (1988).

lingual sides. Mesially, it quickly narrows, usually without any anterior accessory cusp. In any case, as in *K. afarensis,* this mesial part is never expanded transversely, in sharp contrast to *K. heseloni* and especially *K. majus,* where this tooth is much more rectangular.

On m3, the double median pillars between the second main pair and the 'talonid', which is a characteristic feature of other species of *Kolpochoerus,* is seldom seen here, and is usually replaced by a single flattened median pillar. It is normally followed by a third pair, where symmetry is preserved, then by one or two median pillars, and by a complex of pillars where symmetry is lost. Comparative measurements are shown in Fig. 5.

Postcranial elements. They are rare at Ahl al Oughlam, and no long bone is complete. I interpret as sexual dimorphism the differences in size in the right associated Mt III and IV AaO-3820, of large size, and the smaller unassociated Mt III AaO-2977 and Mt IV AaO-2223, of smaller size (Table 10). Other bones suggest a sexual dimorphism of similar amplitude, much weaker than on the upper canines.

Conclusion

K. phacochoeroides as a distinct species. Some authors (e.g. Pickford 1994; Sahnouni *et al.* 2004) do not recognize the North African *K. phacochoeroides* as distinct from contemporaneous East African *K. heseloni.* Still, the above comparisons leave no doubt about this distinctiveness. The short snout, lack of enamel on upper canines, reduced canine flanges, high and broad occiput, are quite unlike *K. heseloni.* Only teeth were available to the above-mentioned authors, but even these can be distinguished: the disto-lingual fovea of P4 is not found in East Africa, and the same is true of the single median pillar between the second and third lobes of m3 (e.g. the tooth figured by Pickford, 1994: pl. 6, fig. 6, as *K. phacochoeroides,* has the double pillars of *K. heseloni*).

Table 8. Measurements of *Kolpochoerus phacochoeroides* lower tooth series (mm).

	p2 ap	p2 tr	p3 ap	p3 tr	p4 ap	p4 tr	m1 ap	m1 tr	m2 ap	m2 tr	m3 ap	m3 tr
AaO-2065					14	10.4				15.4	42.5	19
AaO-926	5.5	4.7	10.1	8	14.2	10.8		13.6		18.7	44.1	20.3
AaO-3479			11.2	8	14.5	12.3			26.8	19.5	46.1	19.8
AaO-7					16.6	12			24	19.1	47.4	21.7
AaO-141			11.5	7.9	15.2	12.1	16.8	13.6	25.1	18.6	49.6	21.3
AaO-3478	8	4.9	10.7	7.7	13.7	12	16.4	14	23.4	18.2	50.7	20.8
AaO-5			13.3	8.4	17	12	16.3	13.9	24.2	20.6	51.5	19.5
AaO-2617	5.5	5.8	10.9	8.4	15	12.4	18.3	14	27.3	18.8		23
AaO-4012			10.3	8	13.9	12	17.2	14.2	25	18.2		
AaO-907			10.8	7.7	13.8	11.2		13.6	24.5	18		
AaO-901	7.6	4	11.5	8.1	13.4	11.2						
AaO-278				7.5	15.1	10.9			24.6	18.1		
AaO-3534			10.7	8.5	14	11.7						

Table 9. Measurements of *Kolpochoerus phacochoeroides* lower cheek teeth (mm).

	p3			p4			m1			m2			m3	
	A-P	TR		A-P	TR		A-P	TR		A-P	TR		A-P	TR
AaO-3510*	10.3	7.9	AaO-2610	13.2	10.5	AaO-314	15.5		AaO-3570	22	18.3	AaO-352	42.2	18.9
AaO-3503	10.6	7.8	AaO-4098	13.2	11.1	AaO-3566	15.6	12.7	AaO-3582	22	18.1	AaO-3584	42.3	18
AaO-1483	10.8	9.2	AaO-2595	13.3	11.3	AaO-922	15.9	12.5	AaO-3568	22.	16.8	AaO-3509	42.4	19.2
AaO-1414	10.9	8.4	AaO-1495	13.5	11.3	AaO-4348	15.9	13	AaO-353	23	16.9	AaO-3516	42.8	19.5
AaO-3532	11.3	8.5	AaO-2596	14	11.2	AaO-908	16	12.8	AaO-913	23.5	19.5	AaO-3588	42.9	17.9
AaO-3161	14	11.9	AaO-3577	14.1	11.5	AaO-1492	16.3	12.6	AaO-3505	23.7	17.8	AaO-1461	44.9	19.7
AaO-4359	15	11.4	AaO-106	14.3	9	AaO-3523	16.6	12.4	AaO-3571	24.5	19.6	AaO-1404	45	21.1
			AaO-2597	14.3	12.2	AaO-25	16.7	12.5	AaO-4402	24.5	18.1	AaO-2588	45.2	21.6
			AaO-1481	14.5	12.3	AaO-1486	16.9	13.3	AaO-914	25.1	19.1	AaO-904	45.5	19.8
			AaO-3569	14.6	11.7	AaO-920	17	13.4	AaO-4352	25.2	18	AaO-3587	45.7	21.3
			AaO-3522	14.7	11.4	AaO-4344	17.3	13.9	AaO-1491	25.5	20.2	AaO-4404	45.7	20.5
			AaO-3160	15.8	13.5	AaO-4354	17.8	13.9				AaO-4405	46.8	19.3
												AaO-1488	47.4	19.5
												AaO-903	48.4	20.7
												AaO-1465	49.5	21.7
												AaO-1463	50	21.8
												AaO-3585	50	21
												AaO-4086	59.4	25.4

*Isolated teeth.

Phylogeny of *Kolpochoerus*

Although several recent papers deal with Plio-Pleistocene African suids, the question of the inter-relationships of the various fossil (*Nyanzachoerus, Notochoerus, Kolpochoerus, Metridiochoerus*) and living (*Potamochoerus, Hylochoerus, Phacochoerus*) genera has seldom been addressed in detail. It is generally agreed that *Nyanzachoerus* gave rise to *Notochoerus, Metridiochoerus* to *Phacochoerus*, and that *Potamochoerus, Hylochoerus* and *Kolpochoerus* are closely related, but the consensus ends up here. Leaving aside the former two genera, which belong to the Tetraconodontinae, a group of African Suidae remains. *Metridiochoerus,* which should include *Phacochoerus* to form a natural group (but with the latter name having priority), appears in the fossil

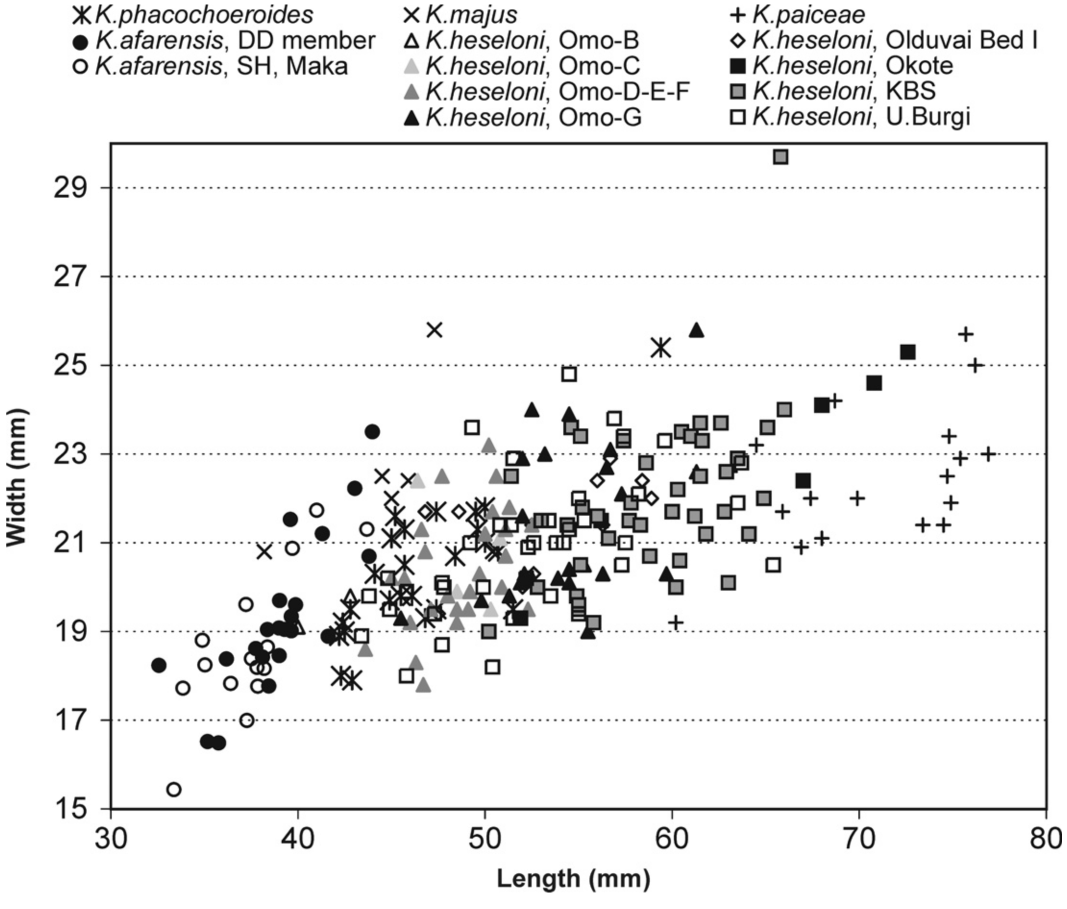

Figure 5. Plot of length *vs* width of *Kolpochoerus* lower third molars. *K. afarensis* from Hadar DD and SH members, *K. heseloni* from Omo Shungura members B-G, Olduvai, and Koobi Fora Formation members. Origin of data as for Figs 3 and 4, plus Cooke (1976) for Omo.

Table 10. Measurements of *Kolpochoerus phacochoeroides* metapodials (mm).

			Max. length	Width of shaft	Distal width	Distal A–P max.
AaO-3820a	Mt III	♂	98	18	23.5	22.5
AaO-3820b	Mt IV	♂	99.5	19	24	22
AaO-2977	Mt III	♂	81.5	15.7	19	18.7
AaO-2923	Mt IV	♂	84	16.6	20.7	20.2

record soon after the earliest definite member of the *Kolpochoerus* group, *K. afarensis* (Harris & White 1979; Harris 1983). It is therefore likely that it belongs to a different clade (Pickford 1993: fig. 13) and *Metridiochoerus* will not be considered here, as a detailed phylogeny of all African suids is beyond the scope of this paper. I shall only briefly discuss further down the cladogram of Bender (1992). Recent molecular analyses (Gongora *et al.* 2004), unfortunately, did not consider *Hylochoerus,* and therefore shed no new light on the interrelationships of the African forms.

The earliest members of the *Kolpochoerus* clade could be the two new species recently named and briefly described by Brunet & White (2001), *K. cookei* from Ethiopia and *K. deheinzelini* from Ethiopia and Chad. The former, known by two last molars only, is mainly characterized by its very small size, and further differs from *K. afarensis* by the presence of a single median pillar between the second pair and the last median tubercle, but more material is needed to confirm the generic attribution of this species.

Kolpochoerus deheinzelini is better known, but by teeth only. It is smaller than *K. afarensis,* although the size ranges slightly overlap. The p4 has a more bulbous appearance, but is not broader, and has no Innenhügel, like *K. afarensis,* but also like *Potamochoerus,* to which it is similar. The m3 is almost identical to those of *K. afarensis,* except that there is only one tubercle between the second pair and the hypoconulid. Brunet & White (2001) mentioned that the lower premolars are large, but a p4 from KB7 (Chad) is not longer, relative to m3, than in *K. afarensis,* and the P4 from KB3 is small relative to the molars.

The relationships of the various species of *Kolpochoerus* were assessed through a parsimonious phylogenetic analysis performed (with Hennig86) on the character matrix given in Tables 11 & 12. *K. deheinzelini,* being known only by teeth, has not been shown here, but branches at the third branch of a trichotomy, together with *Potamochoerus* and *Kolpochoerus* s.str. Within *K. heseloni,* I have recognized two OTUs, an early form (exemplified by e.g. skull L-193-109 from Omo-C8), and a derived one (from Omo member G upwards, with skull KNM-ER 788 from the *M. compactus* zone at Koobi Fora as a typical example).

Quantitative characters were rather easily converted

Table 11. Character list and states used in the cladistic analysis.

0	Cranial profile	Straight	Concave		
1	Parietal profile	Straight	Convex		
2	Forehead	Narrow	Broad	Very broad	
3	Forehead transverse profile	Convex	Slightly concave	Deeply concave	
4	Position of orbit	Middle of M3	Back of M3		
5	Level of zygomatic arch	M1	M3		
6	Zygomatic shelf	Low	Deep		
7	Orientation of zygomatic arch	Transverse	Slightly drooping	Drooping	
8	Pneumatization	Weak	Strong	Very strong	
9	Snout muscle scars	Well-marked	Reduced		
10	Ante-canine part	Short	Medium	Long	
11	Position of P2 relative to C	Behind	Much behind	Far behind	
12	Supra-C flange	Almost absent	Weak	Strong	Very strong
13	Snout section	Rounded	Squarish	Square	
14	Auditory bulla	Large	Small		
15	Auditory duct	Horizontal	Oblique	Very oblique	
16	Width of occipital crest	Narrow	Broad		
17	Position of condyle above tooth-row	Low	High	Very high	
18	Height of occipital	Low	High	Very high	
19	Upper canine section	Trifoliate	Other		
20	Enamel on upper canine	Present	Absent		
21	I1	Large	Small	Very small	
22	Lingual cingulum on I1-I2	Absent	Present		
23	I3	Present	Much reduced or absent		
24	P/p1	Normal	Reduced		
25	P/p2	Normal	Reduced		
26	P3 antero-lingual cusp	Absent	Weak		
27	Section of lower canine	Verrucose	Intermediate	Scrofic	
28	p3-p4	Long	Shortened		
29	Size of upper canine	Small	Medium	Large	
30	Length of m3/M3	Short	Medium	Long	Very long
31	Shape of tubercles	Simple	More complex	Very complex	
32	Between 2nd and 3rd pairs of m3	One pillar	Two pillars		

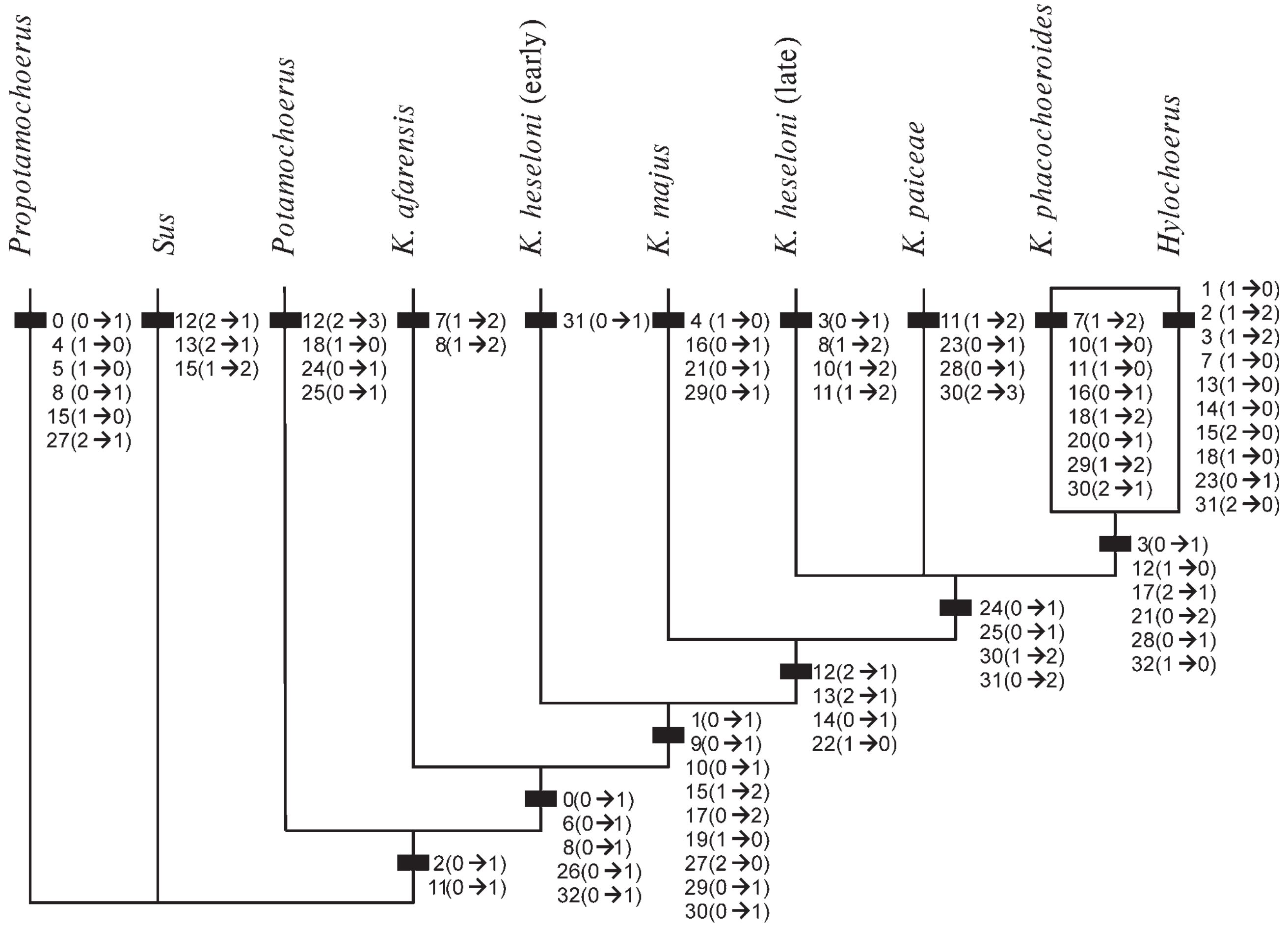

Figure 6. Cladogram of *Kolpochoerus* and related forms.

into discrete ones using gaps in the value ranges (characters 3, 16 and 18 being expressed as a function of condylo-basal length). Still, the matrix involves a good deal of subjectivity. There is no *a priori* character polarity. The modern genus *Sus* and the relatively well-known *Propotamochoerus* from the Miocene of Europe and India (Pickford 1988), were used as outgroups. The former is probably close to the ancestry of the African forms, while the latter might be the sister group of *Sus* + non-tetraconodont African genera (e.g. Pickford 1993: fig. 12). If they are taken as sister-groups of the African forms, the consensus tree (Fig. 6) has a length of 82 steps, a consistency index of 62, and a retention index of 59.

This cladogram incorporates more features and more taxa than a previous version (Geraads 1993). Some of the characters used in 1993 have not been retained in the present analysis, mainly because a better evaluation of intra-specific variability prevented clear distinction of character states. The main difference in the resulting cladogram is that *K. afarensis,* which appeared as close to *Potamochoerus* (as also accepted by Cooke 1997), now returns to *Kolpochoerus.* The main reason for the former placement was the ventrally directed upper canine; I have not retained this character because it is known on a single female specimen.

These African taxa are defined by a broader forehead and a more anterior canine relative to the cheek-teeth. These characters, of course, are unknown in *K. deheinzelini.* I take *Potamochoerus* as the sister taxon of a large group including all other species of *Kolpochoerus* and *Hylochoerus.* This large group can be called *Kolpochoerus*; no synapomorphy supports the inclusion of *K. deheinzelini* in it (and none was put forward by Brunet & White 2001). *Kolpochoerus,* as here understood, is defined by a concave cranial profile, a deep zygomatic shelf, a more extensive pneumatization (as in *Propotamochoerus*), a mesio-lingual cusp on P3, and two pillars between the second and third lobes of m3. *Kolpochoerus afarensis* arises at the base of this group, but these features bar it from the ancestry of the bush pig. More derived *Kolpochoerus* have a convex parietal profile, a more oblique auditory duct, the occipital condyles higher above the tooth-row, a longer antecanine part, reduced snout muscle scars, a verrucose lower canine, a larger upper canine with a trifoliate section, and longer third molars. In agreement with the

Table 12. Matrix used in the cladistic analysis.

	0 9	10 19	20 29	30 32
K. phacochoeroides	1111111211	0001121120	1200111012	120
K. majus	1110011111	1111121210	0100001002	101
K. heseloni (early)	1110111111	1122?20210	0??0??1001	111
K. heseloni (late)	1111111121	2211?20210	00?0?11001	221
K. paiceae	111011????	12?11202?0	00?111101?	321
K. afarensis	1?101?1220	?1?20??0??	0??00?1200	001
Potamochoerus	0010110100	0132010001	0010110200	000
Hylochoerus	1022111011	1100000100	02?111?011	200
Propotamochoerus	1000000110	0022?00011	0010000100	000
Sus	0000110100	0011020011	0010000?00	000

chronology of the fossil record, the early version of *K. heseloni* branches next, but is followed by *K. majus,* the earliest record of which is only at Konso-Gardula (Asfaw *et al.* 1992). The reduction of the supra-canine flange marks a further step in the loss of fossorial habits. The late version of *K. heseloni, K. paiceae,* and *K. phacochoeroides* + *Hylochoerus* form an unresolved trichotomy; they all have reduced anterior premolars, longer M3/m3s, and more complex tubercles. The latter grouping is somewhat unexpected, but is defined by a reduced supra-canine flange, an occipital condyle not so high above the tooth-row, reduced upper central incisors, short premolars, and only one pillar between the second and third lobes of m3. *Hylochoerus* is mostly defined by a large number of reversals.

This cladogram can be compared with that of Bender (1992), who made a valuable attempt to propose a cladogram of African non-tetraconodont suids. He suggested that *Metridiochoerus-Phacochoerus* are the sister-group of *Hylochoerus-Kolpochoerus,* this clade of four taxa being the sister-group of *Potamochoerus-Potamochoeroides.* However, as this cladogram was not calculated by parsimonious analysis, the features defining each node may not be true synapomorphies. Those defining the *Hylochoerus-Kolpochoerus* clade are roughly the same as I have accepted here. On the other hand, those defining the *Potamochoerus-Potamochoeroides* clade are either primitive (Bender's character 1), or shared by many other African suids (2–5). Of the characters said to define its sister-group of four taxa, I recognize only the size of the upper canine as valid. I do not see any major difference in the direction of the upper canine or shape of the lower one, and the others are valid only for the most derived members of this group. Still, his cladogram has the merit of incorporating all non-tetraconodont genera, including those of the *Metridiochoerus* group that I have not considered here.

The agreement between the cladogram proposed here and the known chronological range of the taxa is far from satisfactory, but cladograms with branching order following chronology are significantly longer and more homoplasic. There are some reports of fossil *Potamochoerus,* but none is based upon cranial elements large enough to support the identification. If the cladogram is correct, one may propose the *ad hoc* explanation that its ancestors remained elusive because they lived in forested areas. *Kolpochoerus majus* appears later in the fossil record than evolved *K. heseloni,* but might easily have remained unrecognized, as its early members were certainly quite similar to the latter species. *K. phacochoeroides* is also higher on the cladogram than expected, as it branched at least 3 Ma ago. The features that link it to *Hylochoerus* are unusual for *Kolpochoerus.* Some of them, as well as the increase in number of accessory pillars, are also found in the *Metridiochoerus-Phacochoerus* group, which is poorly represented in North Africa: its first occurrence is at Aïn Boucherit, close to the Plio-Pleistocene boundary (a mandible wrongly assigned to '*Omochoerus*' by Arambourg 1979), but only from the early middle Pleistocene (Tighenif) onwards is it becoming common. Thus, it is most likely that it is the virtual absence of warthog-like suids during the Pliocene and early Pleistocene that led North African *Kolpochoerus* to acquire convergent features, mostly linked with increased grazing adaptations. The great adaptability of this genus is also shown by its wide geographical range: of the well-known Plio-Pleistocene East African suids, it is the only genus known from both ends of the African continent at this time-period, second only to the earlier *Nyanzachoerus* in terms of realm extent. It is even known in Israel (Geraads *et al.* 1986), together with a few other African elements.

However, besides Ahl al Oughlam, it has a very sparse record in North Africa. Only its type locality, Aïn el Bey in Algeria, has also yielded *K. phacochoeroides.* Scrappy remains (Ennouchi 1953; Sahnouni *et al.* 2002; Geraads *et al.* 2004) document one or more other species, but the North African Plio-Pleistocene is still poorly documented.

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A new species of *Plesiogulo* (Mustelidae: Carnivora) from the Late Miocene of Africa

Yohannes Haile-Selassie[1]**, Leslea J. Hlusko**[2*] **& F. Clark Howell**[3]

[1]*Cleveland Museum of Natural History, 1 Wade Oval Drive, Cleveland, OH 44106, U.S.A.*

[2]*Department of Integrative Biology, University of California, Berkeley, CA 94720, U.S.A.*

[3] *Laboratory for Human Evolutionary Studies, Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, U.S.A.*

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A new species of *Plesiogulo* (*Plesiogulo botori* sp. nov.) is described from 5.5–6.0 Ma deposits in East Africa. This new fossil material comes from two localities: Lemudong'o in southern Kenya, and Adu Dora, in the Afar Depression of Ethiopia. The new mustelid species is larger than all known Old World *Plesiogulo* species and extends the temporal and spatial range of the genus in Africa. *Plesiogulo botori* sp. nov. documents the earliest occurrence of the genus in Africa in general and the first evidence of its occurrence in late Miocene deposits of eastern Africa. Associated mammalian fauna at both localities where the species has been found indicate a closed/wooded habitat for the genus. This and other occurrences of the genus across Europe, Asia, and the New World indicate that the genus *Plesiogulo* was geographically widely dispersed during the upper Tertiary.

Keywords: Late Miocene, Carnivora, Mustelidae, Kenya, Ethiopia.

INTRODUCTION

The large mustelid *Plesiogulo* (Zdansky, 1924) was first described from the late Miocene or early Pliocene of China (Schlosser 1903). Species of this genus have since been identified from late Miocene and early Pliocene deposits in Asia, Europe, North America and South Africa, and was clearly geographically widespread. Five species are well characterized (Harrison 1981). Though there are distinct morphological differences between these taxa, in terms of size alone three are small (*P. crassa, P. praecocidens,* and *P. marshalli*) and two are large (*P. lindsayi* and *P. monspessulanus*). The exact relationship between *Plesiogulo* and the living wolverine *Gulo* is uncertain (Kurten 1970; Harrison 1981).

From the Chinese fossil record, Schlosser (1903) described '*Lutra*' *brachygnathus* from an unknown locality. Zdansky (1924) assigned a number of cranial and mandibular specimens to *Plesiogulo brachygnathus.* This is a very small form of *Plesiogulo.* The type specimen is a mandible with p3–m1 (Schlosser 1903). The other specimens come from a total of seven localities in Shansi, China.

Teilhard de Chardin (1945) reassigned most of Zdansky's (1924) *P. brachygnathus* to *P. b. crassa.* He used Licent Collection 10.261 (snout and mandible with teeth) from Yushe, Shansi, as the type specimen and referred Lagrelius Coll. Nos. 1–4, and 6–12, AMNH-26376 (ex-Lagrelius No. 9), AMNH-26377 (ex-Lagelius No. 3), and Yale YPM 13816 (mandible fragment with teeth, Kurtén 1970) from the Dhok Pathan of India (per G.E. Lewis 1934) to this subspecies. Teilhard de Chardin (1945) also assigned a cranium and associated mandible (Licent Coll. No. 553) from K'ingyang, Kansu, to *P. b. minor.* Kurtén (1970) then elevated Teilhard de Chardin's (1945) subspecies to species rank, although he noted there were no tangible morphological differences to distinguish *P. crassa* from *P. minor.* He differentiated *P. crassa* and *P. minor* by size, as he found specimens of *P. minor* to be considerably smaller than those of *P. crassa.* However, Harrison (1981) has since reported that *P. crassa* falls within the range of variation observed in *P. minor. Plesiogulo crassa* has also been identified from Cherevichnoe, near Odessa on the Black Sea in the Ukraine. Korotkevich & Semenov (1975) referred 45-3106 (snout with teeth), 45-3271 and 45-3272 (associated crania, mandible and teeth), and 45-3107 (right and left mandible with dentition) from the MN-12 of Cherevichnoe to *P.* cf. *crassa.* These specimens are housed at the Ukrainian Academy of Sciences, Kiev. *P. crassa* is also known from cranial and jaw remains from Paveodar (Irtysh River, west Siberia). The remains were originally attributed by Orlov (1941) to *P. brachygnathus,* and subsequently assigned to *P. crassa* by Kurtén (1970). They are housed in the collections of the Paleontological Institute of the Russian Academy of Sciences (Moscow).

Another small Chinese species, *Plesiogulo praecocidens,* was named by Kurtén (1970) for specimens from Locality 49 of Baote, Shansi, previously assigned by Zdansky (1924) to *P. brachygnathus.* The type specimen is a left mandible with p3 and m1 (Loc. 49 No. 13; no UPI number) and the hypodigm includes a maxillary fragment with P4-M1 from the same locality (Loc. 49 No. 5; UPI No. M 19). *Plesiogulo praecocidens* has a more expanded M1 than other species of *Plesiogulo* and it also lacks M1 mid-constriction (Kurtén 1970).

In Europe, *Plesiogulo monspessulanus* was named by Viret (1939) for a right mandible fragment with p3–m1. This was the only specimen recovered from the Montpellier red sands but the species has since been recognized from a geographically wide range of sites. Teilhard de Chardin (1945) referred a Yushé mandible from China (Licent Collection 14.046) to a new taxon, *P. b. major.* Kurtén (1970) elevated this subspecies to full species rank and argued that *P. major* is differentiated from *P. monspessulanus* by its retention of the m1 metaconid (although he did question the taxonomic significance of this trait). Hendey (1978) and Alcala *et al.* (1994) also noted the similarities between

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*Author for correspondence. E-mail: hlusko@socrates.berkeley.edu these two species and suggested that *P. major* is synonymous with *P. monspessulanus.* Hendey (1978) referred three dental specimens from Langebaanweg, South Africa, to *P. monspessulanus,* presenting the first evidence for *Plesiogulo* in Africa. Alcalá *et al.* (1994) referred three isolated teeth from the upper MN-13 locality of Las Casiones (Teruel Basin, Spain) to *P. monspessulanus.* From another site in Spain, the MN-13 locality of Venta del Moro, Morales (1984) identified an isolated P4 fragment as being large and like *P. monspessulanus.* This species has a large geographic range covering China, Europe, and South Africa.

From North America, *P. marshalli* (Hibbard 1934) is represented by a number of craniodental and postcranial remains from ten late Hemphillian sites (see Harrison 1981). Other specimens of *Plesiogulo* from four late Hemphillian North American localities have been referred to a new species, *P. lindsayi,* a species the size of *P. monspessulanus* (Harrison 1981).

Plesiogulo was previously unknown in eastern Africa. The new fossil material presented here comes from two late Miocene eastern African localities: Lemudong'o in southern Kenya (Ambrose *et al.* 2003), and Adu Dora, in the Afar Depression of Ethiopia (WoldeGabriel *et al.* 2001). This is the earliest occurrence of *Plesiogulo* in Africa, and the first evidence of this genus in eastern Africa, although *Plesiogulo praecocidens* has been preliminarily reported to be present in late Miocene deposits in the Tugen Hills of Kenya (Morales *et al.* 2004, abstract). The two sites that have yielded remains of the new *Plesiogulo* species are more than 1000 km apart demonstrating a fairly wide geographic range for this taxon. The faunal assemblages associated with *Plesiogulo botori* sp. nov. suggest a closed/woodland habitat at both sites (Ambrose *et al.* 2003; WoldeGabriel *et al.* 2001). This is unlike the habitats of the Chinese species, which are believed to have lived in open country (Kurtén 1970).

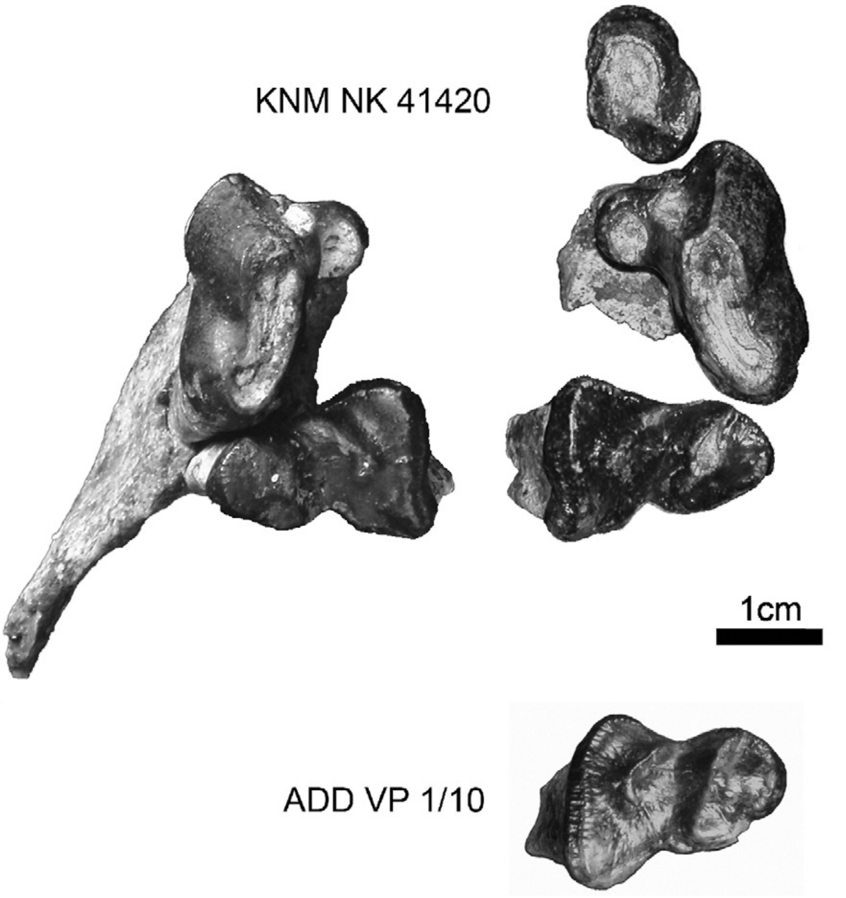

Figure 1. Specimens assigned to *Plesiogulo botori* sp. nov. Anterior is to the top. **A**, Occlusal view of KNM-NK 41420 (the holotype); **B**, occlusal view of ADD-VP-1/10.

Institutional abbreviations: KNM-NK, Kenyan National Museum, Narok specimens; ADD-VP, Adu Dora vertebrate paleontology specimen, National Museum of Ethiopia.

SYSTEMATICS

Carnivora Bowdich, 1821
Mustelidae Fischer, 1817
Mellivorinae Gill, 1872
Gulonini Webb, 1969
Plesiogulo Zdansky, 1924

***Plesiogulo botori* sp. nov.,** Fig. 1

Holotype. KNM-NK 41420, an associated partial maxillary dentition including left P3–M1, right P4–M1, partial right zygomatic process and fragment of right temporal bone preserving the glenoid cavity recovered from the Narok locality, Lemudong'o, Kenya (Fig. 1a; all measurements are given in Table 1) housed in the National Museums of Kenya, Nairobi.

Paratype. ADD-VP-1/10, left M1 (Fig. 1b), from the Adu Dora locality of the Middle Awash, Afar Depression, Ethiopia.

Horizon. All the specimens referred to *Plesiogulo botori* were collected from deposits radiometrically dated to between 5.54 ± 0.17 and 6 Ma.

Etymology. 'botor' means 'old' in the Masai language, spoken by the people living near Lemudong'o, Kenya, where the type specimen was found.

Diagnosis. A species possibly larger than all known species of *Plesiogulo* and at the higher end of the range of variation seen in *P. lindsayi* from North America. The P3 and P4 are longer and wider compared to *P. monspessulanus* and the M1 is longer.

Plesiogulo botori differs from *P. lindsayi* in the lack of an anterior cingulum on P4. The M1 internal lobe of *P. botori* is expanded relative to the external lobe, compared to the condition in *P. monspessulanus* and *P. lindsayi.* The M1 protocone of *P. botori* is tall compared to that of *P. monspessulanus,* and the lingual cingulum is not continuous but rather interrupted mesially.

Comparative description

KNM-NK 41420 comprises associated left P3, right and left P4, M1, partial right zygomatic process and fragment

Table 1. Comparison of upper dental dimensions.[1]

	P. botori sp. nov.	*P. monspessulanus* (= *major*)	*P. brachygnathus* (ex-*Lutra brachygnatha*)	*P. crassa* (= *minor*)	*P. praecocidens*	*P. marshalli*	*P. lindsayi*	*G. gulo*
P3								
Length	14.6	13.9	No data	11	No data	11.6	13.0	10.4
Width	10.2	9	No data	6.9	No data	8	9.3	6.3
Length/width	1.43	1.54	No data	1.59	No data	1.45	1.39	1.65
P4								
Length	24.5	23.2	17.1–20.5	18.3–20.8	17.2	20.1	23.5	19.75
Width	16.7	15.6	11.1–14.0	12.9	10.9	13.9	17.3	11.9
Length/width	1.47	1.49		1.51	No data	1.45	1.36	1.66
M1								
Width	21.2	18.6	13.8–19.4	15.8–17.8	13.8	18.2	20.0–21.5	13.9
Lingual lobe length	15.9	15.4	12.0–16.3	13.2	12.4	15.1	13.3–15.5	8.3
Minimum length	10.1	No data	8.4–11.7	8.4	7.8	9.1	9.7	No data
Max length/min length	1.57	1.54e		1.57	1.59	1.67	1.51	1.34e
Width/lingual lobe length	1.33	1.21		1.28	1.11	1.21	1.41	1.68
P3/P4 length	0.59	0.59	No data	0.57	No data	0.58	0.55	0.53
P3/P4 width	0.61	0.58	No data	0.54	No data	0.57	0.53	0.53

[1] Data for *P. monpessulanus, P. brachygnathus* and *P. crassa* are from Hendy (1978) and Alcalá *et al.* (1994), Zdansky (1924) and Kurtén (1970), respectively. Dimensions of *P. marshalli* and *P. lindsayi* are from Harrison (1981). Measurements of *Gulo gulo* are from Kurtén & Rausch (1959); e = estimated from published images, all reported measurements are in mm.

of right temporal bone. The occlusal morphology and overall crown shape of the P3 is similar to all other species of *Plesiogulo.* However, it is longer and broader than all known P3s of Eurasian *Plesiogulo* and thus similar to the North American *P. lindsayi.* The lingual bulge seen in the P3 of *P. botori* is shared with *P. lindsayi,* but is not present in the Langebaanweg specimen, L40042 (Hendey 1978). The P4 is relatively broad at the protocone level, being comparable to *P. crassa* (= *P. minor*), *P. marshalli,* and *P. monspessulanus* (= *P. major*?). *Plesiogulo lindsayi* has a relatively low length/breadth ratio of the P4. Even though the presence or absence of labial cingulum on the P4 has not been recorded for most species of *Plesiogulo, P. lindsayi* is reported to have labial cingulum (Harrison 1981), which *P. botori* lacks. This cingulum is also present in L40042, which has approximately the same length/width ratio (1.47 *vs* 1.49) as *P. botori.* The P4 protocone is a distinct cusp in almost all *Plesiogulo* species although there seems to be intra- and interspecific variation in its placement relative to the rest of the carnassial.

The protocone height of the M1 in both specimens of *P. botori* is more elevated than is seen in the Langebaanweg specimen. Additionally, neither of the three M1s of *P. botori* has the continual cingulum seen in the Las Casiones specimen from Spain, the sole reported M1 of *P. monspessulanus* from the site (Alcalá *et al.* 1994). The lingual and buccal lobes of the M1 are more equal in mesiodistal length in the Las Casiones specimen than is seen in either of the M1s of *P. botori.* M1 lingual lobe of *P. botori* tends to be proportionately more expanded than in M1s of both *P. monspessulanus* and *P. lindsayi* but less expanded than *P. marshalli.* The median constriction between the two lobes of the M1 is pronounced in almost all specimens of *Plesiogulo,* except that of *P. praecocidens,* which tends to have a more triangular occlusal crown shape. ADD-VP-1/10 is similar to the M1s of KNM-NK 41420 in almost all morphological and metric variables.

The associated right zygomatic process and right glenoid cavity of KNM NK 41420 preserve typical Mustelidae morphology but are not taxonomically informative at the species level.

DISCUSSION

Plesiogulo botori was compared to the five commonly recognized species of *Plesiogulo* with upper dentition. The three relatively smaller species (*P. crassa, P. praecocidens,* and *P. marshalli*) are distinct from *P. botori* primarily in size though numerous other characters also differentiate them. These species have similar overall M1 crown morphology, in that the buccal lobe is not expanded, giving the M1 a more triangular occlusal appearance. The M1 of *P. botori* is also more triangular in overall shape than the other larger *Plesiogulo* species (*P. monspessulanus* and *P. lindsayi*) in that the buccal lobe is relatively more reduced in mesiodistal length relative to the expanded lingual lobe. The lingual and buccal lobes of the M1 of *P. lindsayi,* for example, are sub-equal, giving the molar a more rectangular appearance to this tooth rather than a more triangular appearance as in *P. botori.*

Plesiogulo crassa has a relatively narrower P3, even though the P4 is of approximately the same relative length/width ratio as *P. botori. Plesiogulo marshalli* has approximately the same length/breadth ratio as *P. botori* but lacks the lingual bulge on P3 and has a less distinct P4 protocone. The M1 internal lobe of *P. marshalli* is also more expanded (internal lobe length/minimum length) than that of the M1 of *P. botori* or any of the other species of *Plesiogulo. Plesiogulo praecocidens* lacks a median constriction completely, even though its buccal lobe, relative to the lingual lobe, is considerably more narrow than in *P. botori* or any of the other species of *Plesiogulo.*

Plesiogulo botori is dated to between 5.54 ± 0.17 myr (Adu Dora, Ethiopia, WoldeGabriel *et al.* 2001) and 6.04 ± 0.019 myr (Lemudong'o, Kenya, Ambrose *et al.* 2003). This species is associated with mammalian taxa with more closed/wooded habitat preferences. The mammalian fauna from the late Miocene of the Middle Awash, Ethiopia, is largely dominated by tragelaphines, cercopithecines, colobines, and reduncines (WoldeGabriel *et al.* 2001). The Lemudong'o faunal assemblage consists of large birds of prey, colobines, and other indicators of a possibly closed habitat (Ambrose *et al.* 2003). This indicates a wider habitat preference for *Plesiogulo* contrary to what has been documented from China, where the genus is associated with open habitat.

A number of mustelid species have been reported from the Lothagam Formation in Kenya. However, no specimens of *Plesiogulo* have been documented from either the Upper or Lower Nawata Members of the Formation (Werdelin 2003). The paleoenvironment of the 6 million year old Upper Nawata Member has been reconstructed to have been a fairly dry and open environment (Leakey & Harris 2003). The absence of *Plesiogulo* from these deposits may indicate that the genus was limited to a closed habitat at least in late Miocene East Africa.

Plesiogulo praecocidens has been reported for the 6.1–5.7 myr Tugen Hills site of Lukeino in Kenya (Morales *et al.* 2004). These specimens have not yet been fully published, but the preliminary report indicates that there may have been two species of *Plesiogulo* in eastern Africa during the late Miocene.

The *Plesiogulo* from South Africa and associated fauna are biochronologically attributed to a wide temporal range between 3.5–7 myr (Hendey 1978), but probably closer to 5 myr (Haile-Selassie 2001). Most species of *Plesiogulo* are known from China. However, the genus has also been documented from some European Turolian (and perhaps older) localities, as well as many North American late Hemphillian ones, indicating a wide geographic distribution for this genus. Its African record was thus far limited to Langebaanweg, South Africa. The discovery of *P. botori* from deposits as old as 6 Ma extends the temporal and spatial range of the genus in Africa. This and further (still unpublished) occurrences of the genus indicate an even greater diversity within the upper Tertiary.

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Damaliscus niro horns from Wonderwerk Cave and other Pleistocene sites: morphological and chronological considerations

J.F. Thackeray[1*] & J.S. Brink[2‡]

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

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

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Wonderwerk Cave, situated near Kuruman in the Northern Cape Province of South Africa, has yielded well-preserved horns of many antelope, including three horn fragments of *Damaliscus niro.* These specimens were discovered in the course of guano-mining operations in the 1940s. Remarkably, they retain a keratinous sheath. Dimensions of *Pleistocene* horn cores from Sterkfontein, Olduvai, Cornelia-Uitzoek, Florisbad and Maselspoort are used to assess the Wonderwerk specimens. Assuming that morphological variability can be used to assess relative chronology, we suggest that the Wonderwerk specimens date to the Middle Pleistocene, intermediate in age between specimens from Florisbad (between 400 000 and 100 000 years BP) and Cornelia-Uitzoek (*c.* 800 000 years BP). One of the Wonderwerk specimens has a radiocarbon date of close to the limit of the method. We interpret this to reflect an indefinite age of greater than 40 000 years ago. This is not in conflict with the suggested Middle Pleistocene age of the specimens. The horns are of further interest in that the keratin sheaths have carbon-nitrogen ratios that suggest the presence of protein suitable for ancient-DNA analysis.

Keywords: morphological variability, chronology, early Florisian.

INTRODUCTION

Wonderwerk Cave is a dolomitic solution cavity, extending almost 140 metres into a hill on the eastern side of the Kuruman hills, in the Ghaap Plateau Dolomite Formation in the Northern Cape Province (Fig. 1). Malan & Cooke (1941) gave a preliminary account of faunal remains, which had been discarded by guano-diggers at the site. Subsequently, Malan & Wells (1943) gave a more detailed report of these fossil collections. These assemblages have a Florisian character, comparable to those from the Florisbad springs (Brink 1978, 1988, in prep.)

Systematic excavations at Wonderwerk have been undertaken since the late 1970s (Beaumont 1979, 1990; Thackeray *et al.* 1981; Thackeray 1984a,b; Humphreys & Thackeray 1983), under the aegis of the McGregor Museum. The preservation of fauna is good in the cave where even keratinous sheaths of horn cores have been recovered (Malan & Wells 1943; Beaumont 1990). Two *Damaliscus niro* horns from the guano-digging operations (Figs 2 & 3) are here designated WH1 and WH2, respectively the larger and smaller of two fragments, which evidently belonged to one individual. A third horn fragment (WH3) from the same collections, representing the same species, has recently been recognized.

Although these horns are now assigned to the alcelaphine species *D. niro,* initially they had been identified as those of *Capra ibex.* Robert Broom had gone so far as to suggest that the horns had been carried in prehistory from Ethiopia, where ibex occur at present (Malan & Wells 1943). E.C.N. van Hoepen of the National Museum in Bloemfontein had examined the horns and had said 'to our astonishment it really is an ibex' (translation by J.F.T. from Afrikaans, Archaeological Survey manuscript, State Archives file B20/1/1, Pretoria; Thackeray 1987). The Abbe Breuil, who was familiar with ibex from Palaeolithic contexts in France, supported this view. Wells (1965) recognized WH1 and WH2 as horns of *D. niro* (Thackeray 1987, 1989, 1990), which are characterized by long, curved horns, similar to those of *Hippotragus equinus* (roan) and *Hippotragus niger* (sable). In fact, horns of *D. niro* were once regarded as *Hippotragus niro,* but Leakey (1965) recognized that '*Hippotragus niro*' was an alcelaphine rather than a hippotragine, a view supported by others (Gentry 1965; Gentry & Gentry 1978).

Damaliscus niro is represented in Early Pleistocene contexts at Sterkfontein (Member 5), Olduvai (Beds I and II) (Gentry & Gentry 1978; Vrba 1976) and in terminal Early Pleistocene faunal assemblages from Cornelia-Uitzoek. The fossil assemblages from Cornelia-Uitzoek

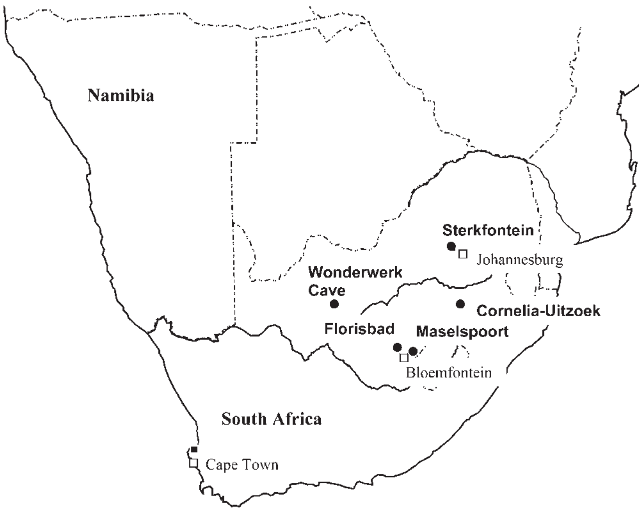

Figure 1. Map showing the localities of Wonderwerk, Florisbad, Maselspoort, Cornelia-Uitzoek and Sterkfontein, where horns of *Damaliscus niro* have been found.

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*Author for correspondence. E-mail: thack@nfi.co.za

‡E-mail: jbrink@nasmus.co.za

are the type materials of the Cornelian Land Mammal Age (LMA), estimated to date to *c.* 800 000 years BP (Brink & Rossouw 2000; Brink, in press). *D. niro* is also found in Middle and Late Pleistocene deposits at Florisbad and Maselspoort (Brink 1987, 1988; Fig. 1). The Florisbad spring assemblage is the type of the Florisian LMA and is dated by Electron Spin Resonance to between 400 000 and 100 000 years ago (Brink 1987, submitted; Grün *et al.* 1996). It was noted that the horn cores of *D. niro* become more rounded with decreasing geological age and that this is reflected by changes in the relationship between anterior–posterior length (APL) and mediolateral breadth (MLB) as measured at the nodes and internodes of the horn cores. Thackeray *et al.* (1996) quantified morphological variability in the shape of *D. niro* horn cores.

OBJECTIVES

The objectives of this analysis were firstly to try to obtain a radiocarbon date for the Wonderwerk horn specimen WH1, because it has no stratigraphic context, and to test the prospects of extracting ancient DNA from the specimens. Secondly, we compared dimensions of WH1 and WH3 with those of other specimens attributed to the same species, from Early, Middle and Late Pleistocene contexts, in order to assess the relative chronology of the *D. niro* horn cores from Wonderwerk. It has been demonstrated for the black wildebeest that morphological variability reflects geological age (Brink 1993, submitted). Therefore, it is assumed that horn core variability in *D. niro* may be used to indicate relative chronology, but not necessarily absolute chronology. The data presented in Thackeray *et al.* (1996) are used here as reference.

RESULTS

Radiocarbon and isotopic analyses

A small sample of keratin (<1 g) selected from a previously damaged portion of WH1 was submitted to the Radiocarbon Accelerator Unit at Oxford University. A date of 39 800 ± 1600 BP (OxA-2333) was obtained. Although this is an absolute date, just within the range of the radiocarbon dating technique, it is 'more realistic to regard the date as equal to or older than 40 000 B.P.' (R.E.M. Hedges, pers. comm to J.F.T.).

Keratin samples were analysed for stable carbon isotope ratios (^{13}C: ^{12}C), using facilities at Oxford University and at the University of Cape Town. Delta ^{13}C values of –7.2 per mil (<2 mg microsample UCT 3257, from WH1), and –9.3 per mil (from the same sample as that which provided a radiocarbon date, OxA-2333) indicate that *D. niro* was a grazer feeding on C_4 grassland (Thackeray 1990).

A carbon:nitrogen ratio of 3.6 obtained from microsample UCT 3257 (<2 mg) from WH1 is similar to the ratio which might be expected for modern keratin. This is remarkable for keratin from a horn core, which is older than 40 000 years, and suggests that it would be possible to extract ancient DNA from these specimens. The excellent preservation of the keratinous horn sheath of WH1 is attributable in part to dry conditions in the recesses of Wonderwerk Cave (Thackeray 1990).

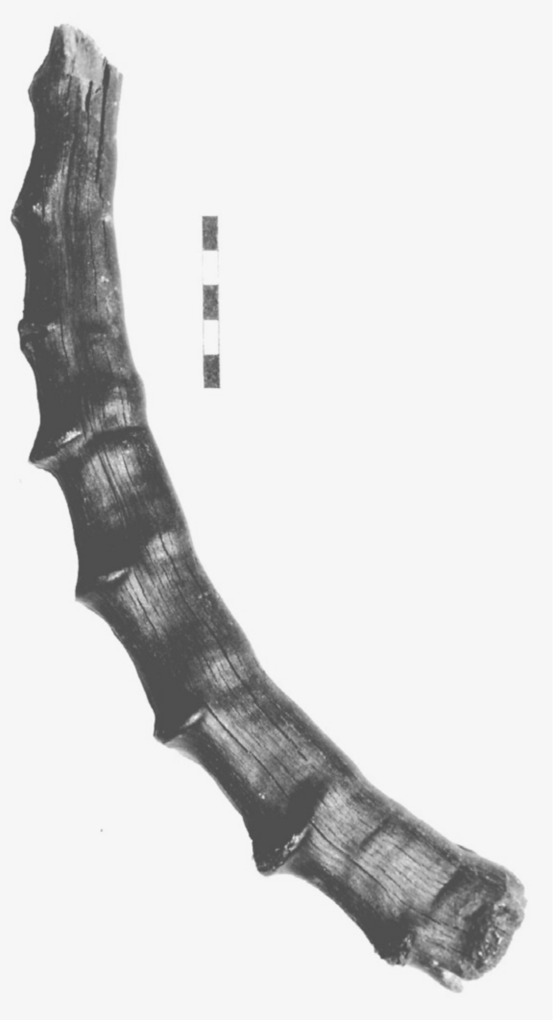

Figure. 2. Photograph of the horn of *Damaliscus niro* (WH1) recovered by guano miners at Wonderwerk Cave *circa* 1940. The horn retains a keratinous sheath. Scale in centimetres.

Figure 3. Photograph of Wonderwerk horn WH2 (left) and X-ray image (right).

Morphological analysis

Anterior–posterior length (APL) and mediolateral breadth (MLB) dimensions of the horn core of WH1 have been determined from CT scans, taken at intervals along the length of the horn. CT sections were taken non-destructively at nodes and internodes. Conventional X-ray images were obtained from WH3, a fragment which lacks the bony core but which has a well-preserved keratinous sheath, the inner margins of which reflect APL and MLD dimensions of the missing core.

By means of least-squares linear regression analysis, relationships between log-transformed APL values (x-axis) and log-transformed MLB values (y-axis) can be determined, using the general form of the regression equation $y = mx + c$, where the m-coefficient refers to the slope of a regression line, based on measurements of APL and MLB in millimetre units.

The following equation was obtained from log-transformed APL and MLB values of Wonderwerk horns WH1 and WH3:

$$y = 1.440x - 0.915 \ (r = 0.984,\ n = 11 \text{ measurements}) \quad (1)$$

(standard error of m-coefficient: 0.162)

Regression analyses were undertaken in the same way on horn cores from Early, Middle and Late Pleistocene contexts (Thackeray *et al.* 1996). The following results were obtained:

Early Pleistocene horn cores
(Olduvai Beds I and II; Sterkfontein Member 5)

$$y = 1.047x - 0.202 \ (r = 0.98,\ n = 47 \text{ measurements}) \quad (2)$$

(standard error of m-coefficient: 0.027)

Terminal Early Pleistocene horn cores
(Cornelia-Uitzoek)

$$y = 1.195x - 0.517 \ (r = 0.97,\ n = 22 \text{ measurements}) \quad (3)$$

(standard error of m-coefficient: 0.070)

Middle & Late Pleistocene horn cores
(Florisbad and Maselspoort)

$$y = 2.105x - 1.935 \ (r = 0.87,\ n = 50 \text{ measurements}) \quad (4)$$

(standard error of m-coefficient: 0.171)

The curvature of WH1 and that of a horn core of *D. niro* from Cornelia-Uitzoek (C770.1) are both associated with a radius of *c.* 230 mm. Fig. 4 serves to reconstruct a mid-Pleistocene horn of *D. niro,* from the juxtaposition of specimen C770.1 (including the base of a large horn) and Wonderwerk specimen WH1 (closer to the tip of a horn).

DISCUSSION

The m-coefficients associated with equations 2, 3 and 4 reflect temporal changes in breadth relative to anterior–posterior length at the nodes of Pleistocene *D. niro* horn cores. The slope for the end-Early Pleistocene horn cores from Cornelia-Uitzoek is 1.195, associated with a standard error of only 0.070. The coefficient obtained from analysis of the Early Pleistocene cores (1.047) is significantly lower ($P = 0.05$) than that associated with the Cornelia-Uitzoek specimens. By contrast, the coefficient of 2.105 obtained from Middle and Late Pleistocene specimens from Florisbad and Maselspoort is significantly higher ($P = 0.05$) than that obtained from analysis of the Cornelia-Uitzoek specimens. The coefficient for the Wonderwerk specimen (WH1) is 1.440, intermediate between values obtained from analyses of Cornelia-Uitzoek and Florisbad specimens, but closest to the value obtained from end-Early-Pleistocene horn cores of Cornelian age.

Table 1. Anterior–posterior length (APL) and mediolateral breadth (MLB) dimensions (mm) of the bony core of Wonderwerk horn core fragment WH1, determined from non-destructive CT scans through nodes and inter-nodes of the horn sheath; CT scans taken at approximately 90° to the tangent of the curvature of this horn. Dimensions obtained from WH3 were taken from X-ray analyses of the well-preserved keratinous sheath, the inner margins of which can be used to infer APL and MLB dimensions of the bony core (missing from this specimen). If WH1 and WH3 represent one individual, WH1 would be part of the horn near the tip, whereas WH3 would be closer to the base of the horn.

	APL	MLB
WH1 (adjacent internode)	8.2	2.8
WH1 (adjacent node)	8.8	2.7
WH1 (adjacent node)	11.0	3.6
WH1 (adjacent node)	15.0	5.
WH3 (adjacent internode)	35.0	20.0
WH3 (adjacent node)	36.5	21.0
WH3 (adjacent internode)	37.0	21.0
WH3 (adjacent internode)	37.5	22.0
WH3 (adjacent internode)	37.0	22.5
WH3 (adjacent node)	38	23
WH3 (adjacent internode)	39	26.5

The approximate date for the Cornelia-Uitzoek samples (associated with a m-coefficient value of 1.195) is *c.* 800 000 BP, or somewhat older (Brink & Rossouw 2000; Brink, submitted), while the age for the Florisbad samples (associated with a m-coefficient of 2.105) is *c.* 400 000 to 100 000 B.P. (Grün *et al.* 1996). Given the infinite radiocarbon age of the Wonderwerk horn core specimen, we would place the Wonderwerk horns (associated with an intermediate m-coefficient of 1.44) in an intermediate period within the Middle Pleistocene.

It should be noted that the degree of intraspecific variation and sexual dimorphism of the horn cores in the various temporal assemblages of *D. niro* appear not to be different from that of the living blesbok/bontebok (*Damaliscus pygargus*), which is a close relative of *D. niro.* Furthermore, the relationship between mediolateral and antero–posterior diameter of the nodes and internodes of the *D. niro* horn core appears not to be affected by intra-population variability as seen in the fossil assemblages (Thackeray *et al.* 1996). There is at present no evidence for geographic variability in the horn cores of *D. niro.*

CONCLUSIONS

We conclude that Wonderwerk horns WH1, WH2 and WH3 are outside the range of the conventional radiocarbon dating technique. By comparison with specimens of Early, Middle and Late Pleistocene age we suggest that the Wonderwerk specimens are closest in age to the terminal-Early Pleistocene samples from Cornelia-Uitzoek. This suggests an early Florisian faunal age, which in absolute terms may approach 800 000 years ago, which is the assumed upper limit of the Florisian LMA (Brink, submitted). The remarkable preservation of the Wonderwerk specimens, and the associated C:N ratio of 3.6 for a keratinous horn sheath, indicate the potential opportunity for DNA analysis. Preliminary analyses undertaken on part of the horn drilled by T.J. Robinson (University of Pretoria) and Williamson (1996) were inconclusive, but indicated the presence of DNA in a degraded form. This discovery is remarkable in that it possibly represents the oldest ancient DNA known thus far.

We thank R.E.M. Hedges for assistance with radiocarbon dating of a small sample (<1 mg) of keratin obtained from WH1; F.W. Zonneveld for assisting with CT scanning of specimen WH1; A. Morris and E. Vrba for assistance in relocating WH1 which was temporarily lost in the Anatomy Department of the Medical School of the University of Cape Town, where it had been studied by the late L.H. Wells; R. Liversidge of the McGregor Museum, and staff of the Kimberley hospital, for assistance with X-ray analysis of WH2 when the specimen was in Kimberley, before being returned to the University of the Witwatersrand where collections formerly associated with the Archaeological Research Unit were curated (unfortunately WH2 is now missing); T. Huffman of the University of the Witwatersrand for efforts to retrace WH2; P. Beaumont for access to WH3, and staff of the Jacaranda Clinic in Pretoria for X-ray analysis of WH3. The carbon-isotope analysis of a microsample of WH1 was approved by permit Per/4/187 granted through J. Deacon by the National Monuments Council. Specimens WH1 and WH3 are now curated by the McGregor Museum, Kimberley. This project was supported by the National Research Foundation (GUN 2065329) South Africa.

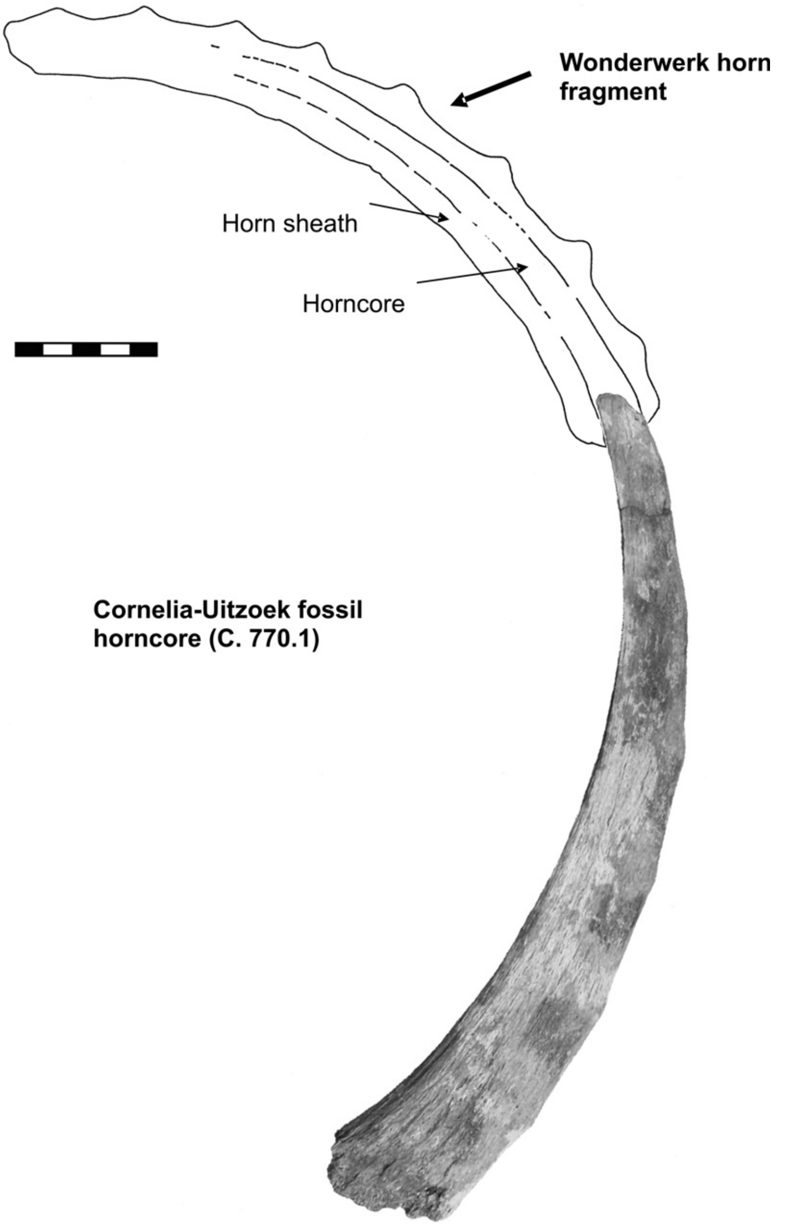

Figure. 4. Reconstruction of a mid-Pleistocene horn of *Damaliscus niro,* based partly on Cornelia horn core C770.1 (near the base of a large specimen), and partly on Wonderwerk horn WH1 (with keratinous sheath, nearer the tip of the horn). Both horn fragments are associated with curvatures with a radius of *c.* 230 mm.

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The first use of bone tools: a reappraisal of the evidence from Olduvai Gorge, Tanzania

Lucinda R. Backwell[1*] **& Francesco d'Errico**[2]
[1]*Institute for Human Evolution, School of Geosciences, University of the Witwatersrand, Private Bag 3, Wits, 2050, Johannesburg, South Africa*
[2]*UMR 5199 du CNRS, Institut de Préhistoire et de Géologie du Quaternaire, Avenue des Facultés, 33405, Talence, France, and Department of Anthropology, The George Washington University, 2110 G Street NW, Washington D.C. 20052, U.S.A.*

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Purported early hominid bone tools from Olduvai Gorge are studied for microscopic traces of use-wear, and evidence of intentional flaking by knapping. Comparative microscopic analyses of the edges of the purported tools, and areas far from the potential functional zone, as well as edges of bone pieces from the remainder of the assemblage, show that possible modifications due to utilization are not distinguishable from features attributed to post-depositional abrasion. Taphonomic analysis of the bone tool collection, a control sample of bone shaft fragments from the remainder of the Olduvai assemblage, and experimentally broken elephant long bones, identifies significant differences in the size and type of mammals represented. The bone tool collection records an abundance of large to very large mammals, while the control sample comprises mostly medium-size bovids. Puncture and cut-marks occur on one third of the bone tool collection, and on only a few pieces in the control sample, suggesting hominids were the agent responsible for the breakage of most of the bones previously described as tools. Analysis of the number, location and length of flake scars in the three assemblages, reveals that a reduced proportion of purported bone tools bear invasive, contiguous, often bifacially arranged removals, not seen in the control or experimental collections. This makes these specimens good candidates for having been shaped and used by early hominids. Complete bones with tool-generated puncture-marks, previously interpreted as anvils, are interpreted here as hammers used on intermediate stone tools.

Keywords: Olduvai Gorge, early hominid, bone tools.

INTRODUCTION

Many bone, antler, and ivory tools are reported from Lower and Middle Palaeolithic sites in Africa and Europe (Schmidtgen 1929; Bastin 1932; Breuil 1932, 1938; Koby 1943; Dart 1957; Kitching 1963; Breuil & Barral 1955; Bonifay 1974, 1986; Freeman 1978, 1983; Cahen *et al.* 1979; Howell & Freeman 1983; Howell *et al.* 1995; Gaudzinski 1999); for a review of the evidence see Henshilwood & Sealy (1997), Villa & d'Errico (1998, 2001), Henshilwood *et al.* (2002) and d'Errico & Backwell (2003). These claims have, however, been repeatedly called into question. Studies demonstrating that a number of natural processes occurring during the life of an animal or after its death can produce pseudo-tools that have been, or may be, misidentified as intentionally modified or used bones. Pre-mortem phenomena that produce pseudo-tools or pseudo-anthropic use-wear include the remodelling of the bone structure (d'Errico 1996), vascular grooves (Shipman & Rose 1984; d'Errico & Villa 1997), teeth use-wear (Gautier 1986), breakage and wear of deer antler (Olsen 1989) and elephant tusk tips (Haynes 1991; Villa & d'Errico 2001). Post-mortem processes are more numerous and include gnawing or digestion by carnivores, rodents and herbivores (Pei 1938; Sutcliffe 1970, 1973, 1977; Binford 1981; Haynes 1983; Villa & Bartram 1996), fracture for marrow consumption by hominids and carnivores (Bunn 1981; Gifford-Gonzalez 1989, 1991), trampling (d'Errico *et al.* 1984; Haynes 1988, 1991) root etching (Binford 1981; Andrews 1990), weathering (Brain 1967) and the action of different sedimentary environments (Brain 1981; Lyman 1984, 1994). As suggested by these and other authors (Shipman 1988; Shipman & Rose 1988; Bonnichsen & Sorg 1989; Villa *et al.* 1999), in order to distinguish between pseudo-tools and true tools, it is necessary to adopt an interdisciplinary approach, combining taphonomic analysis of the associated fossil assemblages, microscopic studies of possible traces of manufacture and use, and the experimental replication of the purported tools. It is by applying this approach, for example, that Dart's (1957) theory for an early hominid 'Osteodontokeratic' culture has strongly been challenged and largely refuted (Klein 1975; Shipman & Phillips 1976; Maguire *et al.* 1980; Brain 1981). Dart's hypothesis created the conditions for a receptive environment, one in which potentially used or manufactured bone could be recognized and its designation as an artefact tested, using more reliable frames of inference.

The South African evidence

Building on this premise, Robinson and Brain in South Africa, and Mary Leakey in East Africa, proposed again that early hominids used bone tools. In 1959 Robinson published a single bone tool from Sterkfontein Member 5 West (*c.* 1.7–1.4 Mya) consisting of a pointed metapodial shaft fragment with evidence of use on the tip. In the course of 24 years of excavation at Swartkrans, Brain (Brain *et al.* 1988; Brain 1989; Brain & Shipman 1993) identified 68 bones, bovid horn cores and one equid mandible from Members 1–3 (*c.* 1.8–1 Mya) bearing similar modifications. Comparative microscopic analysis of the wear pattern on the smoothed tips of these bones, and on modern shaft fragments used experimentally to dig up tubers and work skins, suggested to Brain and Shipman

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[*] Author for correspondence. E-mail: backwell@science.pg.wits.ac.za

that the surface modifications were not natural, and that the activities they tested experimentally were indeed those in which the Swartkrans tools were involved.

A recent reappraisal of this material confirmed the anthropic origin of the use-wear (Backwell 2000; Backwell & d'Errico 2001; d'Errico *et al.* 2001). Comparison between the Swartkrans tool wear pattern and that on bones from 35 reference collections, consisting of fauna modified by 10 non-human agents, identified no natural counterpart for the Swartkrans modifications. These authors also showed that the wear on the bone tools does not represent an extreme in variation of a taphonomic process affecting to a lesser degree the rest of the assemblage. In addition, analysis of the breakage patterns and size of the bone tools from this site, compared with the remainder of the faunal remains, indicated that early hominids selected heavily weathered, elongated and robust bone fragments for use as tools.

Quantification of striation width and orientation comprising the wear pattern suggested that these tools were not used to extract tubers or work skins. The wear pattern more closely fits that created experimentally when bone is used to excavate in a fine-grained sedimentary environment, such as that found in the pre-sorted sediment constituting termite mounds present in the Sterkfontein area. This led them to propose that the main, if not exclusive function, of the Sterkfontein and Swartkrans bone tools, and of the similar 23 undescribed specimens from Drimolen (*c.* 2–1.5 Mya) (Keyser 2000), was that of extracting termites. In another paper, Backwell & d'Errico (2003) report 16 additional bone tools from Swartkrans and show that there are no significant differences between Members in the type and size of the bone fragments used as tools, as well as in the length and type of the wear pattern, indicating that no major changes occurred through time in the subsistence strategy for which the tools were used. Previously unrecognized evidence of intentional shaping through grinding is also identified by d'Errico & Backwell (2003) on the tips of six horn cores and an ulna, indicating that southern African early hominids had the cognitive abilities to modify the functional area of bone implements with a technique specific to bone material, in order to achieve optimal efficiency in digging activities. No firm evidence exists on who used these bone tools. Brain (Brain *et al.* 1988: 835) and Susman (1991, 1994) suggest they were used by both early humans and robust australopithecines. Backwell & d'Errico (2003) consider instead the robust australopithecines as the more probable modifiers and users of these tools. The reasons they put forward in support of this scenario are the absence of *Homo* remains in Swartkrans Member 3 – where *Paranthropus (Australopithecus) robustus* fossils occur in association with relatively few stone and many bone tools, together with the virtual absence of diagnostic stone tools at Drimolen – a site dominated by robust australopithecine remains, and a substantial collection of similar bone tools. In addition, no such bone tools are found at South African sites postdating 1 Mya, the time of the robust australopithecine extinction.

The East African evidence

Mary Leakey (1971) reports 125 artificially modified bones and teeth from Olduvai Beds I and II bearing evidence of intentional flaking, battering and abrasion. These specimens derive from massive elephant, giraffe and *Libytherium* limb bones, and to a lesser extent from equids and bovids, as well as from hippopotamus and suid canines. In a comprehensive reappraisal of this material, Shipman (1989) correctly points out that Leakey's identification of Olduvai bone tools was not based on explicit criteria, and lacked analogies that would allow the ruling out of alternative interpretations.

In her reappraisal of the Olduvai material, Shipman (1984, 1989) uses a control sample consisting of scanning electron microscope-analysed resin replicas of bones submitted to a number of natural phenomena (e.g. weathering, chewing, licking, digestion, wind), and experimental or ethnographic bone tools used for butchering, digging, grinding, and hide and meat processing.

Microscopic analysis of these collections provided criteria (Shipman & Phillips-Conroy 1977; Shipman *et al.* 1984; Shipman & Rose 1988) to identify the material on which bone tools were used (hide, meat, soft vegetables), the kinesis and function (digging, bark-working, grinding hard grains, butchering), and the duration (brief, moderate, extensive) for which they were used. Shipman's ability to distinguish between unused and used bones, and to identify their main function, was verified through blind tests. The control sample also includes experimental reproduction of wind abrasion through the use of an abrasion gun driven by pressurized air. Sedimentary abrasion was mimicked using a tumbling barrel with different types of sediments, with and without the addition of water. According to Shipman (Table 1), utilization produces differential wear between functional and non-functional zones of the tool, and at a microscopic scale, between more exposed and recessed/concave areas, while aeolian and sedimentary abrasion with no water creates a pitted or pebbly texture, homogeneously altering the entire surface. Pits caused by striking harder particles may occur on areas worn by utilization, but they are irregularly spaced and sized. Also, experimental abrasion only rarely creates scratches, while utilization on mixed substances produces a glassy polish crossed by striations. Shipman stresses, however, that these criteria are provisional and that further experimental studies of abrasion are needed to firmly identify distinctive features.

Application of these criteria to 116 of the 125 pieces described by Leakey – teeth were excluded from Shipman's analysis – led her to conclude that 41 were utilized by hominids and the remainder bore ambiguous traces, or evidence of abrasion by sediment. Four of the tools bearing punctures – a patella, astragalus, femoral condyle and magnum – are interpreted as anvils due to the triangular or diamond shape of the impressions, which are different from those produced by carnivores; the absence of counter-bites; large size of the bones difficult to bite; location of the marks consistent with their proposed use, and their apparent antiquity. Shipman, following Leakey, proposes that the marks on these tools

Table 1. Summary of the criteria proposed by Shipman and Rose (1988) and Shipman (1989) to distinguish natural abrasion from utilization and identify the task for which bone tools were used.

	Utilization							Experimental abrasion		
	Soft		Mixed and hard substances					Aeolian	Sediment flow	Hydraulic
Task	Hide working	Cutting meat	Vegetable processing	Digging soil	Bark-working	Grinding hard grains	Butchery	Abrasion gun	Tumbling barrel with sediment (from loess to gravel)	Tumbling barrel with sediment (from loess to gravel) and water
Location	Edge	Raised areas of the edge	Raised areas of the edge	Raised areas of the edge	Raised areas of the edge	Raised areas of the edge	Raised areas of the edge	All over	All over	All over
Edge shape	Round and smooth	Round and smooth	Round and smooth	Round and smooth	Round and smooth	Round and smooth	Round and smooth	Round and smooth	Round and smooth	Round and smooth
Polish	Fine glassy polish	Polish	Fine glassy polish	Fine glassy polish	Fine glassy polish	Fine glassy polish	Fine glassy polish	Absent	Absent	Absent
Striations	Few or none	Few or none	Fine and coarse striations	Fine and coarse striations	Fine and coarse striations	Fine and coarse striations	Fine and coarse striations	Absent	Few	Few or none
Pitting	Few or none	Few or none	Irregularly spaced and sized pits	Irregularly spaced and sized pits	Irregularly spaced and sized pits	Irregularly spaced and sized pits	Irregularly spaced and sized pits	Evenly pitted surface	Evenly and heavily pitted surface	Absent

may have been produced by stone awls, found at the same localities, used to pierce leather/hide.

Among the remaining 37 specimens diagnosed as implements, 35 are described as bones broken and shaped by flaking prior to use. Twenty-six are interpreted as light-duty implements used on soft substances (hide-working), and the remaining 11 described as heavy-duty tools utilized on mixed substances, perhaps in butchering or digging activities. According to Shipman, wear patterns cannot be confused with sedimentary abrasion or weathering, since bone tools show, with the exception of three cases, a low degree of natural alteration. Variables such as taxon, body part, breakage (location, orientation, type and number) and type of surface alteration (weathering, abrasion) were recorded by Shipman on the 41 tools and on 350 randomly selected bones from Olduvai and a few other sites. Comparison of these parameters indicated that the bone tools had a significantly higher occurrence of flaked fractures, flake scars and punctures, and a lower presence of stepped, jagged, or smooth fractures, suggesting that the bone tools were broken shortly after the death of the animal. It also showed that humeri, scapulae and femora, particularly from giraffids and elephants – relatively rare taxa at Olduvai – are over-represented among the bone tools.

Objectives

In sum, South and East African early hominid sites dated to between 1.8–1 Mya have yielded what appear to be very different types of bone tools. The former are characterized by long bone shaft fragments and horn cores of medium- to large-sized bovids, collected after weathering, and possibly used in specialized digging activities. Marginal shaping by grinding occasionally involves robust horn core tips. Those from East Africa mainly consist of freshly broken or, more rarely, complete irregular bones from very large mammals, used as such, or modified by flaking. Irregular bones or epiphyses appear to have been used as hammers, while the others were apparently involved in a variety of light- and heavy-duty activities. What are the reasons for such differences? Were these bones used by the same or by different hominid species, if not taxa? If the first applies, do they reflect different cultural traditions? One may expect, if this is the case, to find additional differences between these two regions in other aspects of material culture and adaptation. Although the Oldowan is associated with sites from both regions, this lithic technology appears to occur in East Africa at least more than half a million years earlier than in South Africa (Kibunjia 1994; Kuman 1994, 2003; Semaw *et al.* 1997; Kuman & Clarke 2000). This gap may be due to a time lag in the diffusion of this behaviour, staggered independent invention, or a scarcity of late Pliocene deposits in South Africa. Since few studies (Petraglia & Korisettar 1998) have tried to address this question by a detailed comparative technological analysis of contemporaneous lithic assemblages, as currently conducted by Roche's team on East African sites (Roche *et al.* 1999), it is difficult at present to know whether what is generally called Oldowan in these two regions corresponds to a single cultural tradition, or the expression of distinct regional trends. In addition, exactly who was responsible for the Oldowan technology is still a matter of debate. Since the identification of *Homo habilis* (Leakey *et al.* 1964; Tobias 1965), it has fallen into common usage to consider this species as the more probable maker of the Oldowan tools. The hypothesis of a robust australopithecine authorship, though marginal, has not been abandoned (Brain 1993; Susman 1994). A date of 2.6 Mya for the oldest occurrence of stone tools in the Afar, Ethiopia, slightly predating the oldest evidence for early *Homo* in East Africa (2.4–2.3 Mya) (Suwa *et al.* 1996; Deino & Hill 2002 in Semaw *et al.* 2003) brings new interest to the subject, with *Australopithecus garhi* proposed as the best candidate for the first user of stone tools in this region. An attribution to *Australopithecus* is further suggested by the relatively sophisticated stone tool technology and raw material procurement strategies recorded at the Gona sites. One may assume that to reach the advanced stage of technical and gestural competence recorded at Gona, the makers of the stone tool assemblages had already established a history of stone working. This may already have been in place by 2.9 and 2.7 Mya, a period poorly represented in the sections exposed at Gona, and for which no evidence of early *Homo* exists.

In this ongoing debate, bone tools have not received the attention they deserve. Variability in bone tool manufacture and use may provide a means independent of lithic technology to address crucial issues such as the characterization of early hominid cultural traditions. However, the artefactual nature of Lower Palaeolithic bone tools and the reality of the associated behaviours identified must be verified before we use this evidence to create scenarios of early hominid cultural evolution and adaptation. In this respect, the evidence for bone tool use is quite different from these two regions. Bone tools from South Africa are documented at a number of cave sites and may now be regarded as unquestionably utilized, if not modified, by hominids. Those from East Africa are attested only at Olduvai Gorge Beds I–II, in spite of the numerous sites excavated in the region, and their identification is based on results that may be preliminary. There are various reasons for this uncertainty. The first problem stems from the frame of inferences used by Shipman to assess the artefactual nature of the Olduvai bone tools. Although criteria are provided to distinguish between experimentally-used and abraded bone, it is uncertain whether such experiments successfully reproduce the entire range of post-depositional phenomena that may have affected the Olduvai bone assemblage, and whether the actual site formation processes that occurred there produced modifications that may closely mimic experimental traces of use, and be the source of misinterpretation. This is more so, considering that other studies postdating Shipman's research on Olduvai, including her own work (Olsen & Shipman 1988), have expanded our knowledge of natural modifications (e.g. Marshall 1989; Haynes 1991, Dechant Boaz 1994, Backwell 2000) and produced results that in some instances challenge her criteria. It has been shown, for example, that tumbling individual bones or bone objects with sand in leather bags produces a fairly large number of striations (d'Errico 1993a). The absence of striations on the bones tumbled by Shipman is most likely due to the presence of water during the experiment. However, no proof exists that water was a constant feature during the deposition of Beds I and II faunal assemblages (Potts 1988). Therefore, the presence of striations associated with polish on the edges of the purported bone tools does not necessarily result from use. In contrast to Shipman's proposition that digging produces a fine glassy polish, experimental reproduction of this task has produced a wear pattern dominated by individual striations (Backwell & d'Errico 2001) associated with a smoothing of the active zone, but not producing a glassy polish. While scanning electron microscopy (SEM) provides a useful means to study microscopic bone surface modification, intimate use of this tool shows that strong lateral variations often occur on adjacent areas, making a true documentation of the entire appearance of the inspected surface a challenging endeavour. This may be overcome by quantifying the surface features (e.g. Backwell & d'Errico 1999, 2001; see González-Urquijo & Ibáñez-Estévez 2003) on bone tools and/or increasing the number of micrographs presented to illustrate the variability of the surface features. To date, the microscopic evidence that documents the use-wear on the 41 bone tools from Olduvai consists of only 3 SEM micrographs. No documentation is presented on the appearance of the surface of the bone tools away from the area interpreted as utilized, nor on bones from the remainder of the Olduvai assemblage from where the bone tools derive, which prevents control comparison between clearly natural and purportedly anthropic modifications. Recognition of tools on the basis of use-wear alone may be misleading because tools may have been shaped for a number of reasons, and subsequently not, or only marginally, used. Identification of tools based on use-wear alone may thus result in the discarding of a number of true tools. Use-wear results should therefore be crossed with analyses of possible evidence of intentional shaping. Also problematic is the relationship between specific tools and the tasks Shipman assigns to them. Perhaps because of the preliminary nature of the work she published on the Olduvai material, Shipman only provides percentages of tools used for different functions and duration, without specifying which tool was used for what. Correlating tools with tasks is crucial to evaluating whether tools of particular morphology, weight, degree of shaping, and size, i.e particular types, were used for specific tasks. This would also enable comparison between knapped bone and stone tools, and the evaluation of degrees of gestural competence in the working of different raw materials.

Although tools are identified on the basis of their wear and not on evidence of manufacture, all but two are described as clearly broken and shaped prior to use. However, criteria to identify bone tools shaped by flaking are unclear. Experimental flaking of large- and medium-sized mammal bones, either to produce blanks, or to shape core tools, has shown this technique may be used with some success on bone, though it is conditioned by the unisotropic nature of this material (Bonnichsen 1979; Bonnichsen & Will 1980; Stanford *et al.* 1981; Walker 1999). The use of this technique at Lower Palaeolithic sites is demonstrated by the discovery of bone hand axes made of *Elephas antiquus* limb bones at three Italian sites (Biddittu *et al.* 1979; Biddittu & Segre 1982a, b; Biddittu & Bruni 1987). However, pseudo flaked bone tools may be produced by anthropic processes, such as bone breakage for marrow extraction (Peretto *et al.* 1996), or non-human modification, such as tramping by animals (Haynes 1988; 1991) and gnawing by large carnivores (Binford 1981; Villa & Bartram 1996). In spite of valuable work conducted in the last decade to identify firm criteria for distinguishing between individual percussion marks and carnivore notches (Blumenschine & Selvaggio 1988; Capaldo & Blumenschine 1994; Blumenschine 1995; Blumenschine *et al.* 1996; Capaldo 1998; Selvaggio 1998), the identification of bone tools shaped by flaking, especially those bearing a low level of modification and no compelling tool morphology, remains a matter of debate. This uncertainty affects a number of Lower and Middle Palaeolithic sites from Europe such as Morin (Freeman 1978, 1983) La Polledrara (Villa *et al.* 1999), Casal dei Pazzi (Anzidei *et al.* 1999), Castel di Guido (Campetti *et al.* 1989; Radmilli & Boschian 1996), Vaufrey (Vincent 1993), Torralba (Aguirre 1986), Bilzingsleben (Mania & Weber 1986; Mania 1990, 1995), Rhede (Tromnau 1983), Kulna (Mania 1990) and the Vallonnet (d'Errico 1988a). It also applies to Palaeo-Indian sites, such as Lange-Ferguson (Hannus 1990, 1997), where mammoth epiphiseal fragments and bone flakes have been interpreted, based on studies of traces of knapping and use-wear conducted by Shipman, as tools used by Clovis hunters to butcher mammoth carcasses.

In addition, Leakey and Shipman do not provide a complete list of the bones identified by the former as tools, nor give a complete representation of the bones interpreted as tools. A photograph of one aspect is given for some specimens, while others are represented by line-drawings. This prevents independent evaluation of the basic features characterizing these objects.

In this paper we provide a complete photographic record of this collection and reassess both Leakey's and Shipman's arguments for these being tools, using a multiple approach study based on data provided by microscopic, taphonomic, and morphometric analysis of the purported bone tools, faunal material from Olduvai, and experimentally and naturally modified bone.

MATERIALS AND METHODS

Contextual information

Olduvai Gorge is probably the most famous ensemble of Palaeolithic sites in the world and certainly the area which provides the most continuous record of human presence during the past two thousand millennia. Located in the eastern Serengeti Plains of northern Tanzania over an area that measures about 30 miles in length (Fig. 1) , the sites within the Gorge date from 2.1 My to 15 kya. Geologically, the formation is divided into seven main beds or levels (Hay 1976; Potts 1988): Bed I (about 2.1–1.7 My), Bed II (1.7–1.15 My), Bed III (1.15–0.8 My), Bed IV (0.8–0.6 My), the Masek Beds (0.6–0.4 My), the Ndutu Beds (0.4–32 ky), and the Naisiusiu Beds (22–15 ky). Radiometric dating of the tuff layers has clarified the age of the various levels within each bed. Comprehensive geological and palaeoenvironmental analyses (Hay 1976; Bonnefille & Riollet 1984; Cerling 1986; Kappelman 1984) have helped greatly in reconstructing the geomorphological, taphonomic and palaeoclimatic history of the Gorge. Table 2 summarizes available data on the location, stratigraphic provenance, age, associated hominid remains, stone tools, taphonomy, site function and number of faunal remains at sites yielding purported bone tools according to Leakey (1971), Hay (1976) Shipman (1989) and this study.

Mary Leakey defined three industries at Olduvai. She called these the 'Oldowan', 'Developed Oldowan' and 'Early Acheulean'. The Developed Oldowan was further subdivided into Developed Oldowan A, and Developed Oldowan B.

Stone tools from Bed I and the base of Bed II, attributed to the Oldowan, include side, end, two-edged, pointed, and chisel-edged choppers, polyhedrons, discoids, scrapers, a few subspheroids and burins. Hammers, utilized cobbles and flakes, some of them retouched, probably used in light-duty functions are also present. The Developed Oldowan A, found at sites from lower Bed II, differs from the Oldowan for an increase in spheroids and subspheroids, interpreted as the introduction of missiles as hunting weapons; light-duty tools are more varied. The Developed Oldowan B, from Middle and Upper Bed II contains very few bifaces. Although bifaces are absent in Bed I, 'proto-bifaces' appear in upper Bed I and Lower Bed II, picks are discovered above the base of Bed II.

Crude choppers and scrapers occur throughout Beds I and II, and spheroids and sub-spheroids, modified and battered nodules and blocks increase in frequency in Bed II. This corresponds to a rise in the number of artefacts relative to fauna in middle-upper Bed II. This may be due to better tool-making abilities and accessibility of raw materials, or to large mammals being common at these sites. Fewer large animals are needed to subsist, and fewer bones are recorded at sites if meat is transported (Leakey 1971).

The beginning of the Acheulean is marked by the appearance of bifaces with cleavers and hand axes, which appeared in Bed II. Compared to the Acheulean, the Developed Oldowan tools evidence greater variability and seem to differ technologically from the more recent tradition. Indications are that these two traditions coexisted. Discovery of human remains attributed to *Homo erectus* in association with hand axes in Bed II suggested to Mary Leakey that this human type and early forms of *Homo sapiens* were the makers of the Acheulean.

Early hominid behaviour at Olduvai

Olduvai assemblages have represented for the last four decades an arena that has challenged hypotheses on early hominid behaviour and subsistence strategies. Dense concentrations of animal bones and stone tools from Bed I

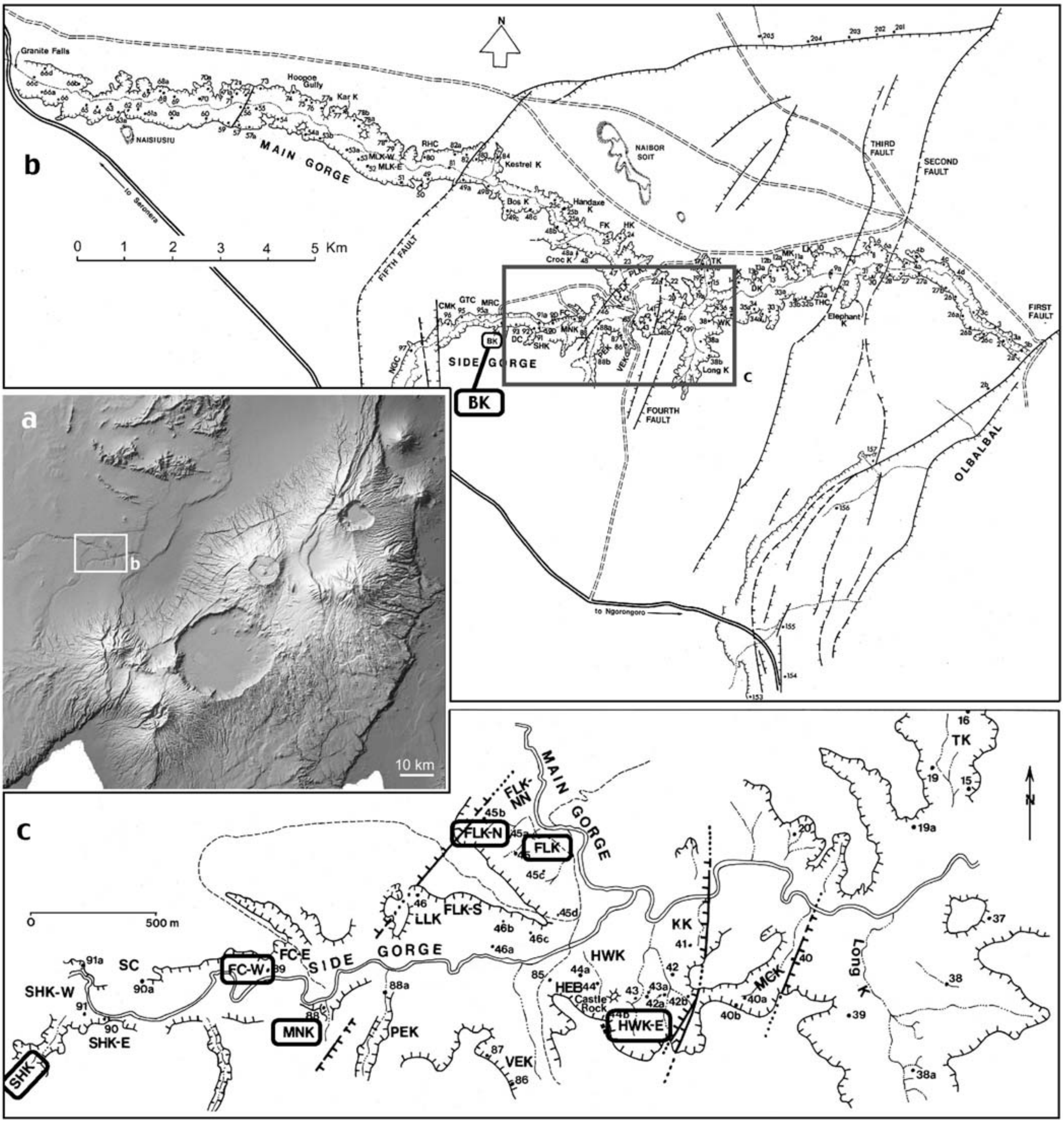

Figure 1. **a**, Regional topographic map of northern Tanzania, showing extent of Olduvai area in (b). **b**, Outline map of Olduvai Main and Side gorges showing faults, topographic features and localities. Faults are shown as heavy hachures. Roads are shown as dashed lines. **c**, Map showing localities near the junction of the Main and Side gorges (modified after Hay 1976). Encircled are sites that have yielded bone tools according to Leakey (1971).

and II sites were in the early phases of Olduvai investigations interpreted as living sites, home bases or central foraging places, where hominids processed the meat of animals using stone tools (Leakey 1971; Isaac 1971, 1978, 1983). In the late 1970s the campsite interpretation, based on analogy with behaviours recorded among modern hunter-gatherers, became the object of thorough scrutiny. Binford (1981) proposed that sites from Beds I and II simply represented zones where dead animals were scavenged by carnivores and hominids. Analysis of six levels from Bed I (FLK North Level 6, FLK *Zinjanthropus,* FLKNN Levels 2 and 3, DK Levels 2 and 3) led Potts (1988) to reject Binford's interpretation and propose that although the attraction of carnivores to these sites prohibited their use by hominids as home bases, bone remains from these sites should be interpreted as hominid accumulations of carcasses obtained by scavenging/hunting, and stone tools as 'stone caches' repeatedly used to process carcasses and possibly for other activities. Hunting is discarded by Shipman (1986a) based on her study of the occurrence and location of cut-marks on 2700 specimens from 10 Bed I contexts (DK I, FLK *Zinj.* and other levels, FLKN 1–6, FLKNN, PDK) and comparison with modern butchery sites from Kenya.

Table 2. Contextual information on Olduvai sites that have yielded important archeological features and putative bone tools. Data after Leakey (1971), Hay (1976) and Potts (1988).

Locality		Age range	Hominids	Loc.	Cultural attribution	Stone tools																Bone tools			Cut-marks	Site function	No. stone tools	No. faunal remains
Bed	Site					ch	pb	bf	pl	ds	sp	no	sh	sl	bu	aw	oe	an	ha	fl	co	L.	S.	This study				
II upper	BK	1.7–1.15	*H. erectus* *A. boisei*	rw	Dev. Oldowan B, Acheulean	101	0	38	8	33	199	512	18	105	23	45	37	4	18	5343	627	46	11	14	?	?	6801	2957
II middle	FC West	1.7–1.15	sp. indet.	cw	Dev. Oldowan B	49	0	5	4	4	48	53	11	9	1	2	0	7	23	748	159	5	2	1	?	Occupation site	1184	127
II middle	MNK	1.65–1.53	sp. indet. *Homo* sp. *H. habilis* cf. *H. erectus*	cw	Oldowan, Dev. Oldowan B, Acheulean	96	0	9	9	19	159	72	24	59	0	7	0	24	64	3269	449	42	15	17	Medium t overy large mammals	Occupation site	4399	1723
II middle	SHK	1.7–1.15		cw	Dev. Oldowan B	293	0	68	21	62	318	115	131	86	11	12	3	26	0	577	27	9	5	1	?	Occupation site	185	?
II lower	HWK East	1.7–1.15	sp. indet. *H. habilis* *A. boisei*	cw	Oldowan Dev. Oldowan A	41	1	0	0	3	1	14	4	0	2	0	0	0	21	24	0	6	3	1	?	Occupation site level 1	154	425
I upper	FLK North Levels 1–5	2.1–1.7	sp. indet. *Austr.* sp. *H. habilis* *A. boisei* *H. erectus*	cw	Oldowan Dev. Oldowan A & B	143	7	0	14	16	18	90	18	18	0	0	0	21	103	1126	118	0	0	0	Small mammals	FLKN 1–5 interpreted as occupation floor, home bases or central foraging sites	1594	7687
I upper	FLK North 6	2.1–1.7	*H. habilis*	cw	Oldowan Dev. Oldowan A & B	4	1	0	0	1	0	2	0	0	0	0	0	6	4	85	6	0	0	0	Large mammals	Butchering site with artefacts and elephant embedded in clay	130	2 258
I middle	FLK NN 3	2.1–1.7	sp. indet. *H. habilis*	cw	Oldowan	2	0	0	1	0	0	19	1	0	0	0	0	0	1	30	8	1	0	0	Rare, only on small mammals	Occupation site	72	2261
I middle	FLK levels 21, 17, 16, 15, 13, 12, 11, 10, 7	2.1–1.7	*H. habilis* *A. boisei*	?	Dev. Oldowan B	2	0	0	1	0	0	4	0	0	0	0	0	2	0	0	2	0	0	0	?	?	11	187
I middle	FLK *Zinj.* level 22	2.1–1.7	sp. indet. *Austr.* sp. *H. habilis* *A. boisei*	cw	Oldowan Acheulean	17	0	0	9	3	1	40	9	18	4	0	0	5	13	2193	155	6	3	0	Large & small mammals	Living floor, home base or central foraging site	2647	40 172
I lower	MK	2.1–1.7	*H. habilis*	?	Oldowan	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	?	?	?	?
I lower	DK	2.1–1.7	*Homo* sp. *H. habilis*	cw	Oldowan	47	1	0	32	27	7	79	10	20	3	1	0	3	48	776	118	2	2	1	Large & small mammals	Occupation site. Stone circle in level 3	1163	7855
? ?	FCKII	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	5	0	1	?	?	?	?

?: data fragmentary or absent.
Loc.: Location
rw: reworked stream chanel deposit; cw: close to water (lake shore/river/stream).
ch: choppers; pb: proto-bifaces; bf: bifaces; pl: polyhedrons; ds: discoids; sp: speroids/sub-speroids; no: nodules & blocks; sh: scrapers, heavy duty; sl: scrapers, light duty; bu: burins; aw: awls; oe: outils ecailles; lt: laterally trimmed flakes; an: anvils; ha: hammerstones; fl: flake; co: core.
Zinj.: *Zinjanthropus*.
L.: Leakey; S.: Shipman

Focusing on skeletal part frequency and cut-mark data on 60 000 bone specimens from the FLK *Zinjanthropus* site (middle Bed I), Bunn & Kroll (1986) found a high limb to low axial skeleton representation, with cut-marks located in places consistent with butchering practices. These data are interpreted as evidence of hominids transporting selected portions of carcasses to favoured localities in the landscape (Bunn 1986). In addition, a high proportion of prime adult mammal remains suggests to these authors that hominids aggressively scavenged and may even have hunted large animals. Bunn & Kroll (1986) note that sharp-edged stone flakes are among the best-known cutting tools, and numerically constitute the bulk of the Oldowan assemblages from Olduvai. The meat-cutting function of the flakes is supported by microwear studies (Keeley & Toth 1981) demonstrating that unmodified flakes from Koobi Fora were used to cut meat.

Using a landscape archaeology approach, Blumenschine & Masao (1991) sampled the spatial distribution, density and character of archaeological occurrences in a 1 km^2 area of the HWKE site, lower Bed II. A high percentage of core tools and long bone specimens preserving fractures or percussion marks indicative of hammerstone breakage, suggests to them an association with marrow extraction. Trenches near the lake shore preserve a greater proportion of large mammal long bones showing evidence of hammerstone breakage. This pattern is consistent with modern observations of lower levels of competition among carnivores for bovid carcasses in the near-lake environs surrounding Lake Ndutu in the Serengeti (Blumenschine 1987). It suggests hominids had better opportunities to gain access to whole marrow bones near the shore of palaeo-Lake Olduvai. Blumenschine & Masao (1991) argue that the apparent continuous distribution of artefacts and associated bones away from purported occupation sites show that repeated visits to particular loci cannot be proved for Bed II times. A lack of trees in the palaeo-lake margin zone meant no refuge from predators while processing carcass parts, which they propose were most frequently procured through scavenging of predator kills. Stone tools were transported to the butchering sites, and the variability in density of bones and artefacts suggests that hominids at times concentrated carcass parts for processing, attracted perhaps to isolated patches of shade or stone caches. The hypothesized paucity of trees suggests hominid visits were brief, and that their subsistence and social activities were focused elsewhere in the Olduvai Basin.

To test the various hypotheses concerning the timing and nature of hominid and carnivore activities in Plio-Pleistocene bone assemblages from Olduvai (Bunn 1986; Bunn & Kroll 1986; Leakey 1971; Binford 1981), Blumenschine (1995) focused his attention on the bone assemblage from the FLK *Zinjanthropus* site. Frequencies of percussion and tooth marks reject the hypothesis that carnivores had first access to long bone marrow. This contradicts Binford's interpretation of hominids as marginalized scavengers of already heavily ravaged carcasses. A high proportion of tooth-marked long bone mid-shaft fragments also rejects the alternative hypothesis, that carnivore access was secondary to butchery and marrow extraction by hominids (Leakey 1971; Bunn 1986). Blumenschine (1995) proposes that the sequence of carnivore and hominid access to long bones and their marrow is consistent with scavenging by hominids.

The Olduvai bone tool collection

The Olduvai bone tool collection housed in the Department of Archaeology at the National Museums of Kenya in Nairobi consists of 125 specimens that were analysed by us in October 2001. These include some pieces that were not designated as tools by Leakey (1971), since seven specimens interpreted as tools by her and later by Shipman (1989: 323), could not be located in the museum (HWKEII 368; HWKEII 886; MNKII 23369; MNKII 1099; BKII 2494; BKII 068-6688; BKII 3240). Annotated line-drawings, comprising two to four aspects of each specimen were made. These recorded the location of macro- and microscopic modifications such as original or post-depositional breakage, flake removals, punctures, carnivore traces, cut-marks, trampling and polish. Recorded variables also included taxon, body part, bone region involved, dimensions of each specimen, the weathering stage according to Behrensmeyer (1978), and location, number, association and length of flake scars according to fracture axis. While some of these variables have already been recorded by Shipman, others such as the number, location on the bone flake, occurrence on the periosteal *versus* medullar face, and dimension of removals, possibly due to intentional shaping, were recorded in the framework of the present study for the first time. The term 'flake' is used here to describe pieces detached from long bones, and may be taken to encompass fragments. Long bone ends or shaft pieces are described as such, or referred to as 'pieces'.

The same variables were recorded on a control sample of 86 randomly-selected limb bone shaft fragments from the FLKI, FLKNI, FLKII, BKII, MNKII and DKI Olduvai sites. This was to establish whether the modifications recorded on the purported bone tools did not represent an extreme in variation, affecting to a lesser degree the remainder of the Olduvai assemblage. Colour slides and digital images of two to four aspects of each piece were also taken in order to document the collection.

Using high-resolution dental impression material (Coltene President), 76 replicas were made from different areas of the purported tools and the control sample, which consisted of shaft fragments from the FLKI, FLKII and MNKII Olduvai sites. Cast areas included the edges of the tools, whether described by Shipman as utilized or not, regions located away from the purported functional zones, and similar areas on the control specimens. All puncture marks and some cut-marks were also moulded. Transparent replicas made with RBS resin (T2L Chimie, France) were cast from these moulds. All were examined in transmitted light using an optical microscope (Wild M3C) equipped with a digital camera, and 300 digital micrographs were captured. Forty-one replicas were analysed with a scanning electron microscope (840A Jeol) (Bromage 1987; d'Errico 1988b) and 380 SEM micrographs

Table 3. Elephant bone breakage and flake use experiments

Skeletal element	Bone No.	Weight (kg)	Preservation	Breakage technique	Gender of breakers	Tasks: Flaying	Working fresh hide	Working dry hide	Digging soil	Removing bark
Femur	1	19	Semi fresh	Struck against rock	m	2	2	1	2	1
Femur	2	22	Semi fresh	Rock on bone bridge	f	–	3	1	–	–
Ulna	3	11	Semi fresh	Struck against rock	f	–	–	–	–	–
Ulna	4	11	Semi fresh	Thrown against a rock	f	–	–	1	–	–
Femur	5	13	Weathered	Rock thrown on bone	m	3	2	–	1	2
Humerus	6	9	Semi fresh	Struck against rock	m	–	–	–	–	–
Humerus	7	22	Semi fresh	Struck against rock	m	1	–	–	–	–
Tibia	8	9	Semi fresh	Rock on bone bridge	m	–	–	–	–	–
Humerus	9	12	Semi fresh	Thrown against a rock	m	–	–	1	–	–
Total						6	7	4	3	3

were taken at ×15 to ×350 magnification. The presence of striations (either single or multiple, parallel or intersecting) and evidence of smoothing, polishing, pitting, and possible residues was recorded.

Comparative collections

Thirty-five non-human reference collections of known taphonomic history were examined and studied using the same microscopic techniques described above (Backwell 2000; Backwell & d'Errico 2001). These represent nine damage categories derived from both modern and fossil contexts, including animals (hyaena, dog, leopard, cheetah, porcupine) and geological processes (river gravel, spring, flood plain, wind, trampling).

Experimental material

Nine modern elephant limb bones (Table 3) were experimentally broken by 26 university students of mixed gender. Ranging between nine and 22 kg each in weight, eight of the bones originated from a young adult *c.* 20 years old that had died five months before the experiment. Only one bone originated from a teenage individual and was weathered. The experiment was conducted at Plovers Lake in the Sterkfontein Valley, South Africa. The students were asked to work in groups of three to five in order to break the bones and produce flakes, employing only resources available in the environment. Knapping of bone flakes was attempted by one of us (F.D.) using elongated pebbles to replicate the flake removals recorded on the Olduvai purported bone tool collection. Un-retouched flakes were used for flaying and cutting the fresh meat from an adult male eland, working fresh hides with the addition of sand, dry hides with the addition of salt, and digging in soil to extract tubers and grubs, as well as removing bark from trees.

RESULTS

Microscopic analysis

Olduvai

Edges or tips of the bone specimens described by Shipman as probable tools, show at microscopic scale a great deal of variation in their appearance (Table 4). The large majority are characterized by smoothing associated with or without either parallel or intersecting single or multiple striations (Fig. 2a–i).

This pattern is more pronounced on some pieces or areas of a single specimen, where it may in places completely obliterate the anatomical structure of the bone (Fig. 2b–c). The smoothing often decreases from the edge toward the inside of the object and in one case (Fig. 2d), a clear worn band of 1 mm wide appears on the edge. A minority of these bones present edges covered by a more-or-less glossy polish associated with no or very few striations (Fig. 2j–l). Although features that appear as micro-pits are common on most pieces (Fig. 2b,o), it is often difficult to distinguish between concavities produced by impact or pressure of sedimentary particles, and damaged bone structures such as vascular openings and Haversian canals (Fig. 2m,l).

Interpreting these wear patterns as evidence of tool use is problematic. Comparable wear is identified on areas of the purported tools located a considerable distance from the worn edge unsuitable for use (Fig. 2m–n). Microscopic analysis of the edges of the specimens described by Leakey as tools, but rejected by Shipman, also cautions against an anthropic interpretation, since a number of them (e.g. BK 3122, BK 201, MNKII 848) record wear that falls within the three categories described above on the Shipman tools (Fig. 2o–r). Examination of the control sample also reveals the same range of surface features seen on Shipman's and Leakey's tools (Fig. 3a–f), and consists of randomly selected shaft fragments from Olduvai Beds I–II, bearing no apparent traces of anthropic modification.

In addition to these observations, we have found on three specimens (two purported tools and one bone from the control sample) micro-crystals of calcite growing predominantly on vascular openings and cracks (Fig. 4). These crystals were probably created by the slow dehydration of bone containing water rich in calcium carbonate. The excellent state of preservation of the crystals and the fact that they clearly overlie the traces of abrasion, suggest that they appeared only after the abrasion process took place and that their growth represents the final taphonomic event that affected part of the bone assemblage. These crystals are easily affected by mechanical and chemical alteration and would not have survived in such a good condition if the bone had undergone even to a small degree (e.g. simple re-hydration) one of these processes.

Table 4. Summary of surface modifications recognized by microscopic analysis on specimens described as bone tools by Leakey and by Shipman, and on a control sample from Olduvai Bed I–II.

Site	Specimen and replica *	Previous studies		Present study										
		Tools **	Modification ****	Location			Surface modifications							
				Tip	Edge	Body	Smoothed	Polished	Randomly oriented single striations	Sets of parallel striations intersecting	Sets of parallel striations	Shallow grooves	Pitting	Cut-mark
DKI	067/4259	1, 2	Wear	–	■	–	■	–	–	■	■	–	■	–
FLKII	884a	1, 2	Punctures	–	–	■	■	–	■	■	■	–	■	–
FLKII	884b	1, 2	Punctures	–	–	■	–	–	–	–	■	–	–	–
FLKII	884c	1, 2	Punctures	–	–	■	–	–	■	–	–	–	–	–
FLKII	884d	1, 2	Punctures	–	–	■	■	–	■	–	–	–	–	■ (x)
FLKII	884e	1, 2	Punctures	–	–	■	–	–	■	–	–	–	–	–
FLKII	884f	1, 2	Punctures	–	–	■	–	–	■	–	■	–	■	■ (x)
FLKII	884g	1, 2	Punctures	–	–	■	–	–	■	–	■	–	–	–
FLKII	884h	1, 2	Punctures	–	–	■	–	–	–	–	■	–	–	–
FLKII	884i	1, 2	Punctures	–	–	■	–	–	–	–	■	–	■	–
FLKII	spit 5+a	1, 2	Wear	–	■	–	■	–	■	■	■	–	■	–
FLKII	spit 5+b	1, 2	Wear	–	■	–	■	–	■	–	■	–	■	–
FLKII	spit 5+c	1, 2	Wear	–	■	–	■	–	■	–	■	–	■	–
HWKEII	068/6690	1, 2	Wear	■	–	–	■	–	■	■	■	–	■	–
HWKEII	/3 (head)	1	Wear	■	–	–	■	■	■	■	■	■	■	–
FCII	068–6679	1,2	Wear	■	–	–	■	■	■	■	■	–	■	–
MNKII	475	1, 2	Wear	■	–	–	■	–	■	■	■	–	■	–
MNKII	068/6676	1, 2	Wear	–	■	–	■	–	■	–	■	–	■	–
MNKII	848	1	Wear	■	–	–	■	–	■	■	■	–	■	–
MNKII	925	1	Cut-mark	–	–	■	■	–	–	–	–	–	–	■
MNKII	1051a	1	Wear	–	■	–	■	–	–	–	–	–	–	–
MNKII	1051b	1	Punctures	–	–	■	■	–	■	–	■	–	■	–
MNKII	2889a	1, 2	Wear	–	■	–	■	–	–	■	–	–	■	–
MNKII	2889b	1, 2	Wear	■	–	–	■	–	–	■	–	–	■	–
MNKII	2474a	1, 2	Wear	–	■	–	■	–	■	■	■	■	■	–
MNKII	2474b	1, 2	Wear	■	–	–	■	–	■	■	■	–	■	■
MNKII	738	1, 2	Wear	–	■	–	■	–	–	–	■	–	■	–
MNKII	1731a	1, 2	Wear	–	■	–	■	■	■	■	–	–	–	–
MNKII	1731b	1, 2	Wear	–	■	–	■	–	■	■	■	–	■	–
MNKII	2903a	1, 2	Wear	–	■	–	■	–	■	■	■	–	■	–
MNKII	2903b	1, 2	Wear	–	■	–	■	–	■	■	■	–	■	–
MNKII	1046a	1, 2	Cut-mark	–	–	■	■	–	–	■	■	–	■	■
MNKII	1046b	1, 2	Cut-mark	–	–	■	■	–	■	■	■	–	–	■
MNKII	1741a	1, 2	Wear	–	■	–	■	–	–	–	■	–	■	–
MNKII	1741b	1, 2	Wear	–	■	–	■	–	–	–	–	–	–	–
MNKII	1741c	1, 2	Wear	–	■	–	■	–	–	–	■	–	■	–
MNKII	471a	1	Wear	■	–	–	■	–	■	■	■	–	■	–
MNKII	471b	1	Wear	–	■	–	■	–	■	■	■	–	■	–
MNKII	744	1	Wear	–	■	–	■	–	–	–	–	–	–	–
MNKII	1116	1	Wear	–	■	–	■	–	–	–	–	–	–	–
SHKII	068/6684	1, 2	Wear	■	–	–	■	–	–	–	–	–	–	–
SHKII	068/6688	1, 2	Wear	–	■	–	■	■	■	–	–	–	■	–

Continued on p. 105

Table 4 (*continued*)

Site	Specimen and replica *	Previous studies		Present study										
		Tools **	Modification ****	Location			Surface modifications							
				Tip	Edge	Body	Smoothed	Polished	Randomly oriented single striations	Sets of parallel striations intersecting	Sets of parallel striations	Shallow grooves	Pitting	Cut-mark
SHKII	068/6687	1, 2	Wear	–	■	–	■	–	■	■	–	–	■	–
SHK–EII	068/6681	1	Wear	–	–	■	■	–	■	■	■	–	■	–
SHKII	068/6685	1	Wear	■	–	–	■	–	–	–	–	–	■	–
BKII	3122a	1	Wear	■	–	–	■	–	–	–	–	–	–	–
BKII	3122b	1	Wear	■	–	–	■	■	■	■	■	–	■	–
BKII	068/6680a	1	Cut-mark	–	–	■	■	–	■	–	–	–	–	■
BKII	068/6680b	1	Cut-mark	–	–	■	■	–	■	–	–	–	–	■
BKII	1938a	1, 2	Wear	–	■	–	■	–	■	■	■	–	■	–
BKII	1938b	1, 2	Wear	–	■	–	■	–	■	–	–	–	■	–
BKII	1938c	1, 2	Wear	–	–	■	■	–	■	■	■	–	–	–
BKII	53–9 ex 1953a	1	Wear	■	–	–	■	–	■	■	■	–	■	–
BKII	53–9 ex 1953b	1	Wear	–	–	■	■	■	■	■	■	–	■	–
BKII	53–9 ex 1953c	1	Wear	–	■	–	■	–	–	■	■	–	■	–
BKII	201	1	Wear	■	–	–	■	–	■	■	■	–	■	–
BKII	2933a	1, 2	Punctures	–	–	■	■	–	–	–	■	–	■	–
BKII	2933b	1, 2	Punctures	–	–	■	■	–	–	–	■	–	–	–
BKII	2933c	1, 2	Punctures	–	–	■	■	–	■	–	■	–	–	–
BKII	068/6678	1, 2	Wear	■	–	–	■	–	■	■	■	–	■	–
BKII	068/6666	1	Wear	■	–	–	■	–	■	■	■	–	■	–
BKII	068/6670	1	Wear	–	■	–	■	–	■	■	–	■	–	–
BKII	933	1	Wear	■	–	–	■	–	–	–	–	–	–	–
BKII	187a	1	Cut-mark	–	–	■	■	–	–	–	–	–	–	■
BKII	187b	1	Cut-mark	–	–	■	■	–	–	–	■	–	–	■
BKII	187c	1	Cut-mark	–	–	■	■	–	■	■	■	–	■	■
BKII	068/6668	1	Wear	■	–	–	■	–	■	■	■	–	■	–
FCKII	068/6682z	1	Wear	–	■	–	■	–	–	■	–	–	–	–
FLKI	340a	***	***	–	–	■	■	–	–	–	■	–	–	■
FLKI	340b	***	***	–	–	■	■	–	–	■	■	–	■	■
FLKI	112	***	***	–	■	–	■	–	–	–	–	–	–	–
FLKI	341	***	***	–	–	■	■	–	■	–	■	–	■	■
FLKII	339a	***	***	■	–	–	■	–	■	■	■	–	■	–
FLKII	339b	***	***	■	–	–	■	–	■	■	■	–	■	–
FLKII	780	***	***	■	–	–	■	–	■	■	■	–	■	–
MNKII	2770	***	***	■	–	–	■	–	■	■	■	–	■	–
FLKII	TRI+	***	***	■	–	–	■	–	■	■	■	–	■	–

*The lower case letter identifies the replica when more than one replica per specimen was analysed; ** tools after Leakey (1) and Shipman (2); *** control sample; **** modification after Leakey and Shipman; (x) cut-mark-like grooves associated with punctures.

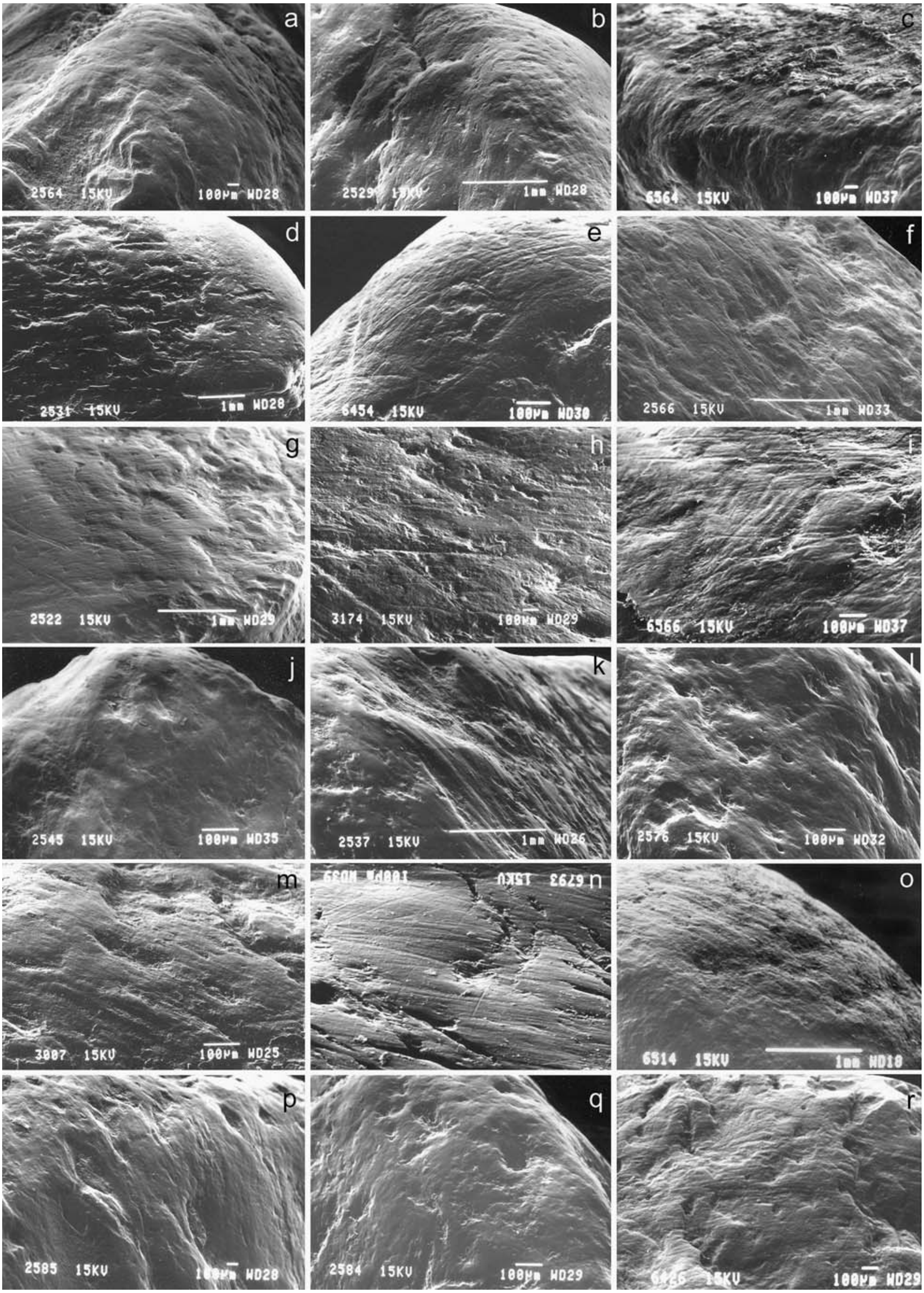

Figure 2. a–n, Wear pattern on bone fragments interpreted as tools by Shipman (**a–d**: smoothing; **e–f**: smoothing associated with sub-parallel striations; **g–h**: parallel striations; **i**: sets of intersecting parallel striations; **j–l**: polish with no striations); **m–n**: wear pattern on areas of the objects interpreted as tools, located away from the purported functional area (**m**: smoothing, **n**: sub–parallel striations on a smoothed area); **o–r**, pieces interpreted by Leakey as tools but rejected by Shipman (**o**: smoothing, **p–q**: polish, **r**: parallel striations). a: BKII 1938b, b: FCIIS 068–6679, c: HWKEII 068–6690, d: FLKII spit5+a, e: BKII 1938a, f: MNKII 1741c, g: FCII 068–6679, h: FLKII spit5+, i: HWKEII 6690, j: MNKII 1731a, k: FCIIS 068–6679, l: SHKII 068–6688, m: BKII 53–9b, n: BKII 1938c, o: BKII 201, p: BKII 1953b, q: BKII 1953b, r: BKII 3122b.

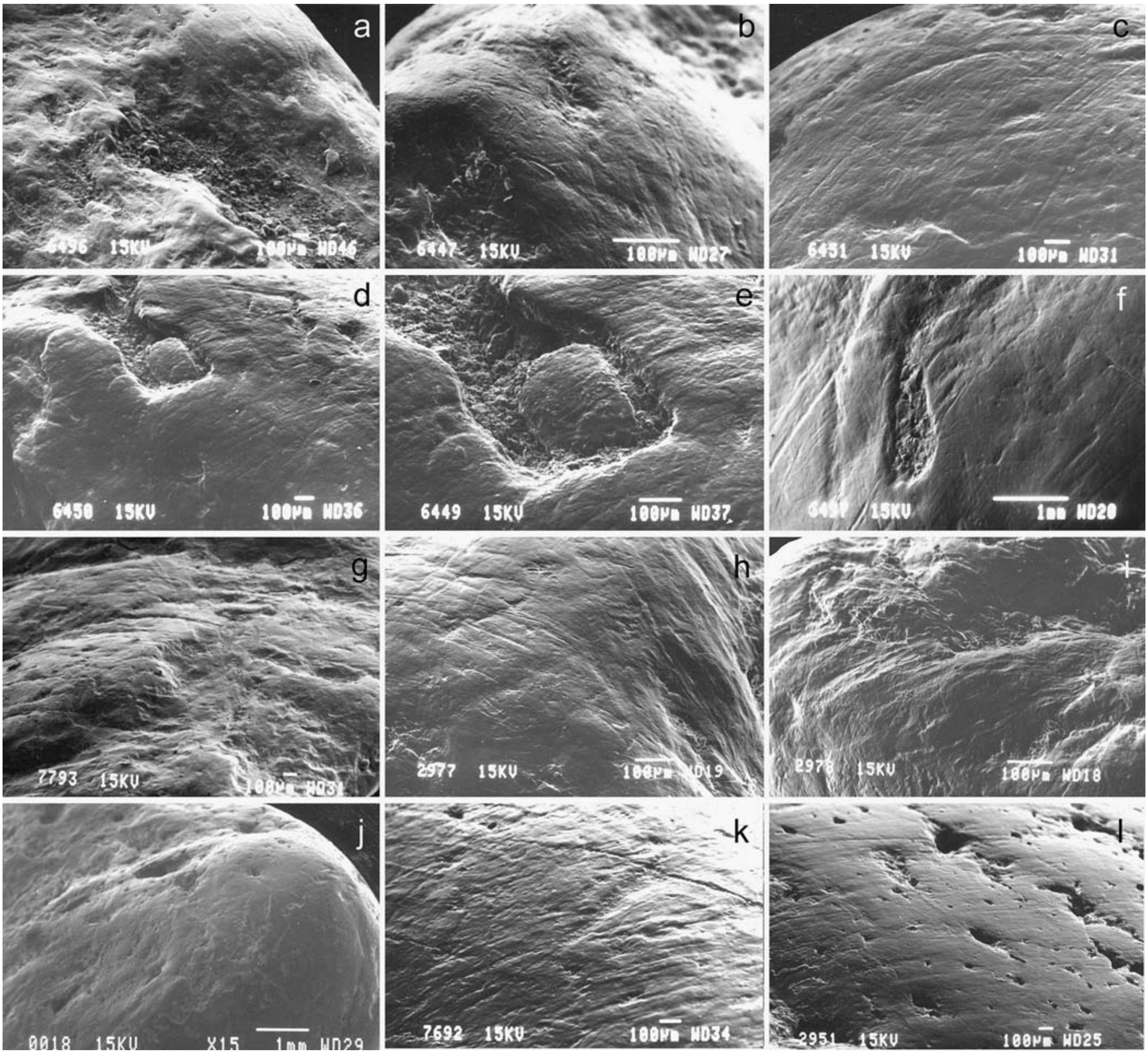

Figure 3. **a–f**, Edges and tips of shaft fragments from the remainder of the Olduvai Beds I–II assemblage not considered as tools by Shipman and by Leakey, and bearing no apparent anthropic traces (**a**: smoothing of elevated areas, **b**: smoothing with randomly oriented striations, **c–e**: smoothing with sets of parallel striations. **e**: close–up view of (d) showing a bone islet resulting from abrasion; **f**: polished area crossed by individual striations); **g–i**, edges of bone pieces from the Homeb Hottentot water hole bearing traces of smoothing and striations; **j–l**, edges of bone pieces from the Bacon Hole hyaena den showing smoothing and areas covered by parallel striations.

Comparative collections

Damage inflicted on bones by non-human agents may also closely match, at microscopic scale, the surface features observed on the edges of the purported tools. Comparable features are observed on bones collected by Brain at the Homeb Hottentot water hole in Namibia, where they were subjected to trampling by goats (Fig. 3g–i). The edges of these pieces record significant smoothing of the more elevated regions often associated with individual and sets of parallel striations. Bone pseudo-tools from the Bacon Hole fossil hyaena den cave site (Stringer 1977) also record comparable modifications, including smoothing of elevated areas (Fig. 3j) and zones covered with broad or fine parallel striations (Fig. 3k–l). In both comparative collections, where these modifications affect the bone surface to a lesser degree, only more exposed areas such as ridges, edges and tips develop a detectable wear pattern that may not appear on the remainder of the object, thus producing a pattern that might be erroneously interpreted as differential wear due to anthropic use.

Wear patterns on experimentally used bone tools

Experimental use of unmodified shaft fragments applied to different tasks produced distinct wear patterns that, in part, overlap with those described by other authors (MacGregor 1975; Campana 1980; Peltier 1986; Shipman 1988, 1989; Brain & Shipman 1993; d'Errico 1993b; Lemoine 1997; Backwell & d'Errico 2001). The working of fresh hides with sand by maintaining the tool perpendicular to the hide, flattens the edge and smoothes a 2–3 mm wide adjacent band (Fig. 5a–e). The edge is

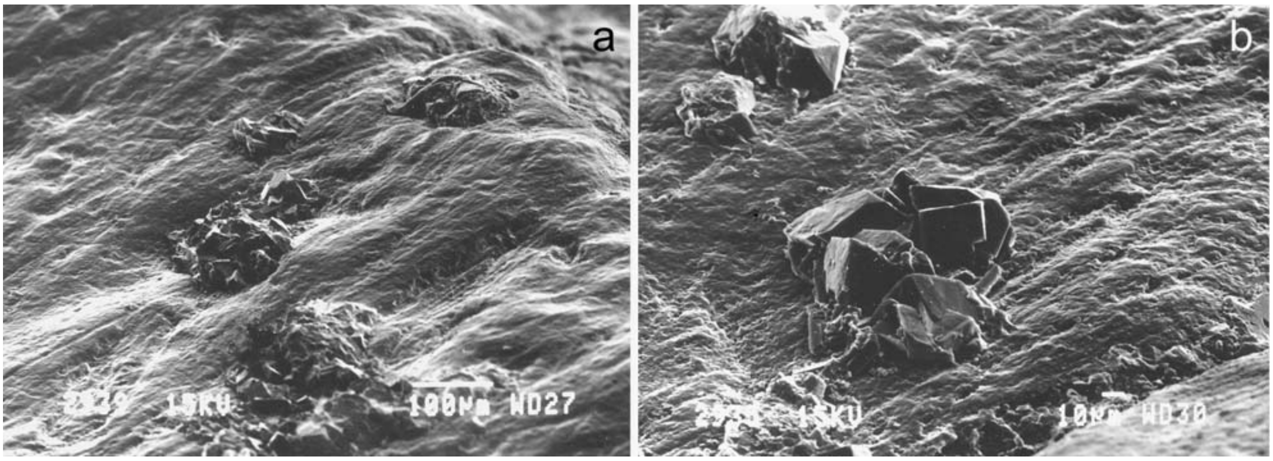

Figure 4. **a–b**, Examples of micro-crystals that developed on an already abraded bone surface (specimen MNKII 2474). Notice the rhombohedral cleavage of the crystal at top left in (b) demonstrating the calcitic nature of the crystals.

intersected by relatively broad superficial striations, and the adjacent band by narrow parallel striations perpendicular to the tool edge. Flaying with a bone tool produces a smoothing of the edge associated with polishing of prominent areas (Fig. 5f). Individual sub-parallel grooves develop on flat underside areas (Fig. 5g). This activity also chemically alters the bone surface, differentially etching the bone structure (Fig. 5h). Bark removal creates a smoothed surface covered by individual sub-parallel striations. Digging in soil produces an association of single and bar-code-like composite broad striations, oblique or parallel to the main axis of the tool (Fig. 5k–l).

Punctured bones

Only two of the four pieces interpreted by Leakey and by Shipman as anvils, a giraffe astragalus (BKII 2933, Fig. 7) and an elephant patella (FLKII 884, Fig. 8), were located in the National Museums of Kenya. Our reappraisal of these pieces has taken into account criteria proposed by other authors for identifying the causes of impressions on bone, as well as observations made on our experimentally broken elephant limb bones. Tooth pits, crushes and punctures produced by carnivores are well known features commonly described in the taphonomic literature (Binford 1981; Haynes 1983; Lyman 1994; Fisher 1995). Tooth pits are superficial, roughly circular markings producing no inward crushing of the bone cortex. Crushes are roughly circular depressions of cortical bone nested in underlying cancellous bone, often in the vicinity of epiphyses. Punctures are roughly circular holes in cortical bone with irregular edges, depressed margins and flaking of the outer wall of the bone pushed into the depression. More regular edges are seen on punctures made on thin cortical bone.

Percussion pits, impact marks, chop-marks, crushing and percussion striae are terms used to describe the alterations created by a hammer-stone striking a bone surface (Binford 1981; Blumenshine & Selvaggio 1988; White 1992; Oliver 1994; Fisher 1995). Though referring to the same phenomenon – the mark inflicted on a bone by a hammer – the first three terms indicate impact marks of variable shape. This shape is determined by the morphology of the contact area of the stone hammer. Tools with knapped edges typically produce deep v-shaped marks (chop-marks), while angular-edged hammer-stones produce irregularly shaped depressions with complex internal morphologies, and fine-grained pebbles result in more uniform superficial depressions. Crushing caused by stone tools is defined as the result of an impact in which thin cortical bone is nested in underlying cancellous bone. These features are often associated with micro-striations resulting from the contact of the hammer-stone tip with the bone surface before or after the impact.

It may be difficult distinguishing between carnivore- and hominid-induced punctures when micro-striations are absent, and the mark produced by the hammer-stone is circular, rounded, and does not display internal features reflecting the irregular morphology of the hammer-stone tip. These features may be mistaken for carnivore activity. Poor surface preservation can also mask diagnostic characters and make the identification of the agent problematic.

Our bone breakage experiments, conducted using dolomite and quartzite blocks as hammers or anvils, confirm the criteria described in the literature for stone tool-generated puncture marks. In our experiments, this activity produced three main features that may or may not be found together (Fig. 6). These are irregular depressions, the morphology of which is determined by the shape of the tool tip penetrating the bone (Fig. 6a), the lifting or detachment of micro-flakes adjacent to the impression (Fig. 6a,c), and the production of broad composite striations visible inside or close to the puncture (Fig. 6b).

The astragalus from Olduvai (Fig. 7) bears on its dorsal face a cluster of overlapping punctures of consistent triangular shape and orientation. Apart from the features already described by Shipman, indicating that these punctures were made by the same stone tip repeatedly striking the object, we have identified striations within two peripheral punctures (Fig. 7c–d), as well as inside the main area of percussion. Although calculating the precise number of punctures is difficult due to overprinting, microscopic analysis suggests that at least 14 blows were inflicted.

The patella records, on the left half of the articular

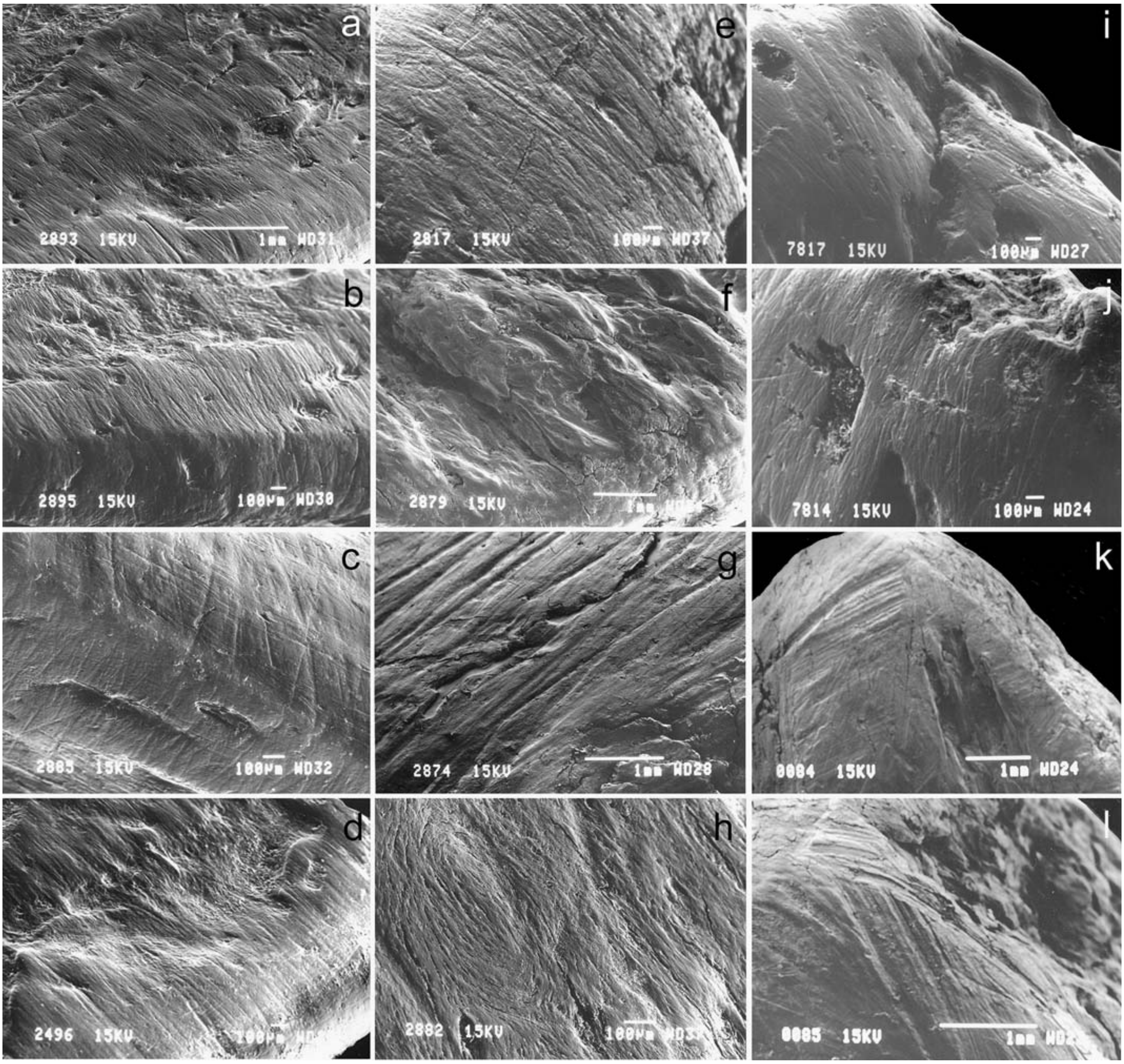

Figure 5. SEM micrographs of the edges of modern elephant bone shaft fragments used to work hide with sand (**a–e**), flay an eland carcass (**f–h**), remove bark from trees (**i–j**), and dig in soil in search of grubs and tubers (**k–l**).

surface, nine scattered punctures (Fig. 8) bearing ambiguous features. Our analysis of these marks (Fig. 8a–i) indicates that in spite of some degree of morphological variability, these punctures were probably made by the same agent striking the surface in a single session, as demonstrated by their similar internal morphology and the consistent orientation of their spindle-like shape. The rounded/oval morphology of a number of them, macroscopically similar to carnivore punctures, and the absence of clean angular edges, makes it difficult to securely attribute them to hominin agency. Macroscopic analysis of marks made on a similar bone by various carnivore taxa, and use of this bone as a hammer on material such as wood, is necessary before reaching a definite conclusion. This experiment might also explain, if the carnivore hypothesis is retained, why no other carnivore damage is present on the specimen, as would be expected if all these marks were made by a large carnivore.

In sum, our analysis confirms Leakey's and Shipman's diagnosis of these bones as anthropically modified. We believe, however, that an interpretation of these objects as hammers used on intermediate stone tools, rather than anvils on which to pierce skins, fits the evidence better. Experimental piercing of leather (d'Errico *et al.* 2003) shows that a rotating motion is needed to effectively perforate this material and leave a suitable non-tearing hole. If exerted against a bone surface, this motion results in circular or semicircular impressions with curved internal striations, not seen on the Olduvai specimens. Also, striking motions are unsuitable for piercing skin at precise locations, as generally required by this activity. Piercing a skin by striking a pointed stone tool against a bone anvil requires a relatively large and stable bone. Neither of the bones appears large enough, and the patella is very unsta-

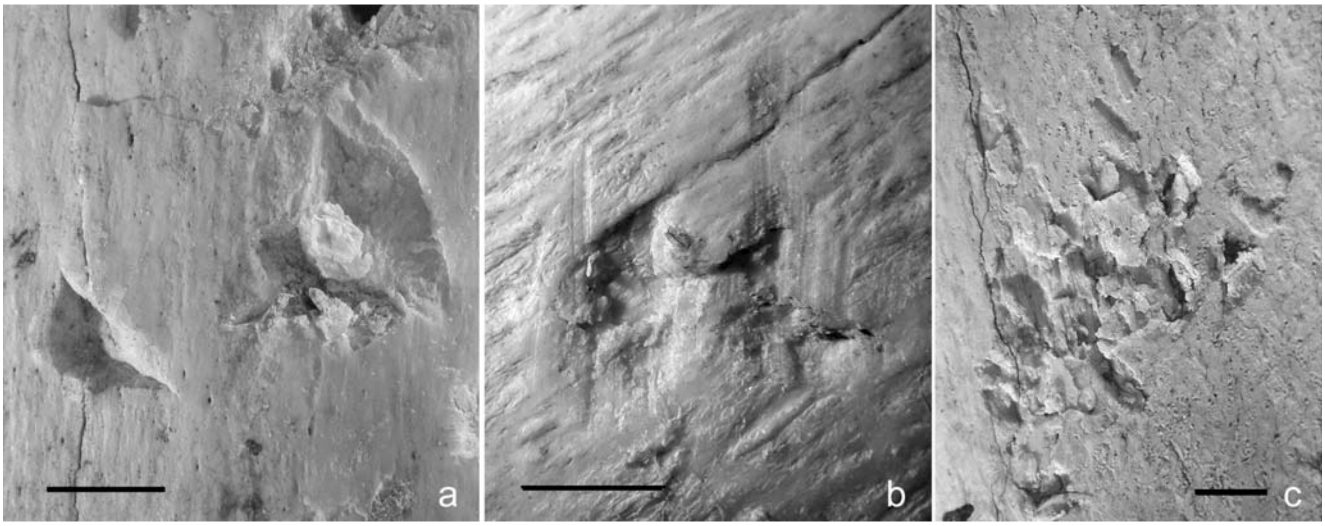

Figure 6. Puncture marks produced experimentally on fresh elephant bone; **a**, impressions of the stone tool tip associated (right) with chipping of the outer bone surface; **b**, impressions with composite striations; **c**, concentration of punctures with lifting of primary bone lamellae. Scale bars = 1 cm.

ble. The dispersed location of the punctures on the patella and the location of some impressions near the edge also cast doubt on the anvil interpretation, since the bone would have been destabilized by the striking force. We argue for now that the astragalus, and perhaps the patella, were instead used in single-session hammering tasks, most likely on intermediate stone wedges used to split bones, fruit or wood. Future research will include a wider range of actualistic studies, including observations of carnivore-generated bite marks and the impressions produced by a number of stone types and tip shapes.

The presence of crude choppers used as hammerstones and evidence of cut-marks and hammerstone-induced fractures on bones from the oldest levels of Bed I (DK), and their persistence through Bed II evidence the regular use of hammers in the subsistence activities carried out at Olduvai. In contrast, anvils occur only in Bed I (DK, FLK, FKLK North), while awls are recorded only in Bed II, appearing first in level 2 at HWK East, and later at SHK and BK, the reworked stream channel deposit.

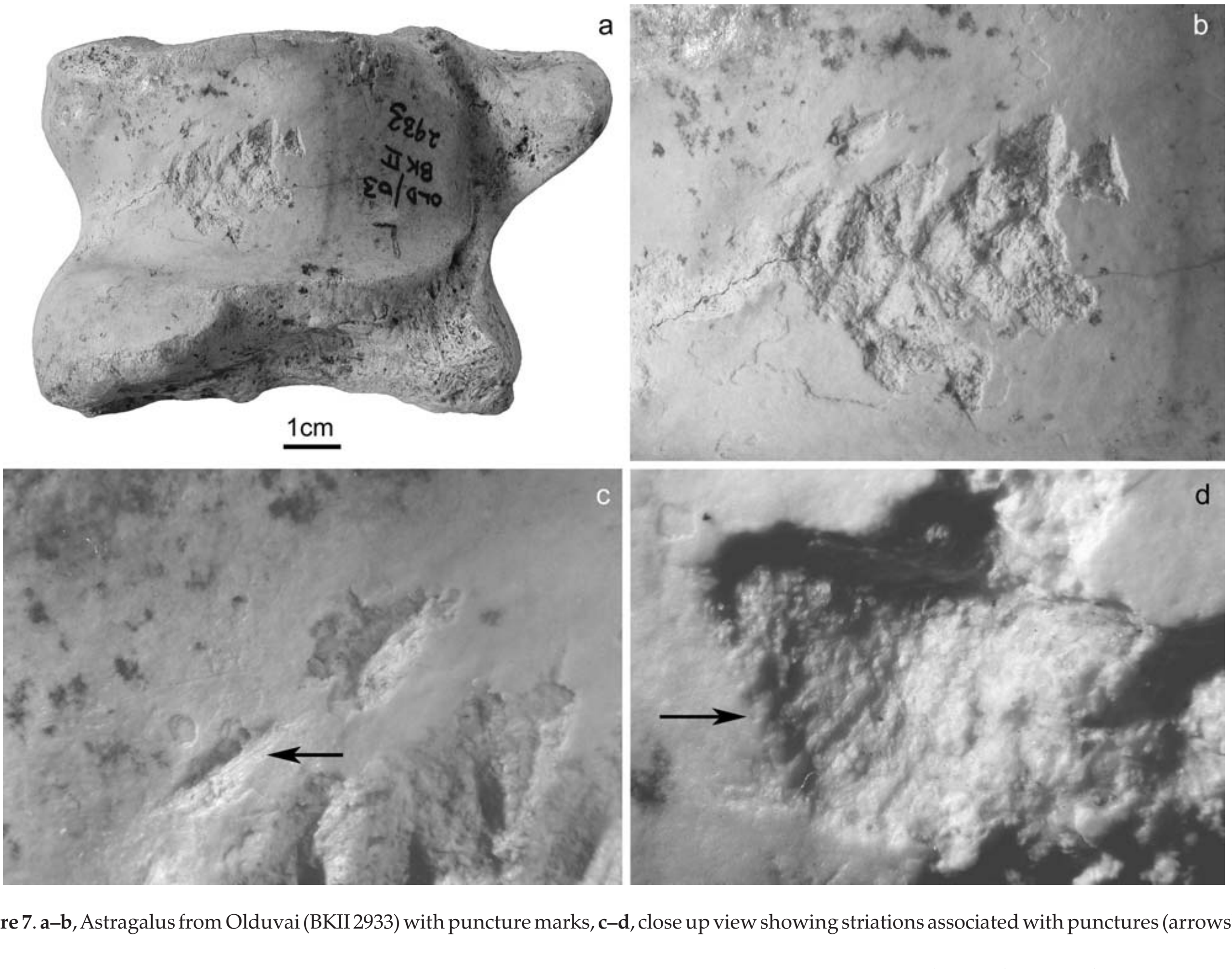

Figure 7. **a–b**, Astragalus from Olduvai (BKII 2933) with puncture marks, **c–d**, close up view showing striations associated with punctures (arrows).

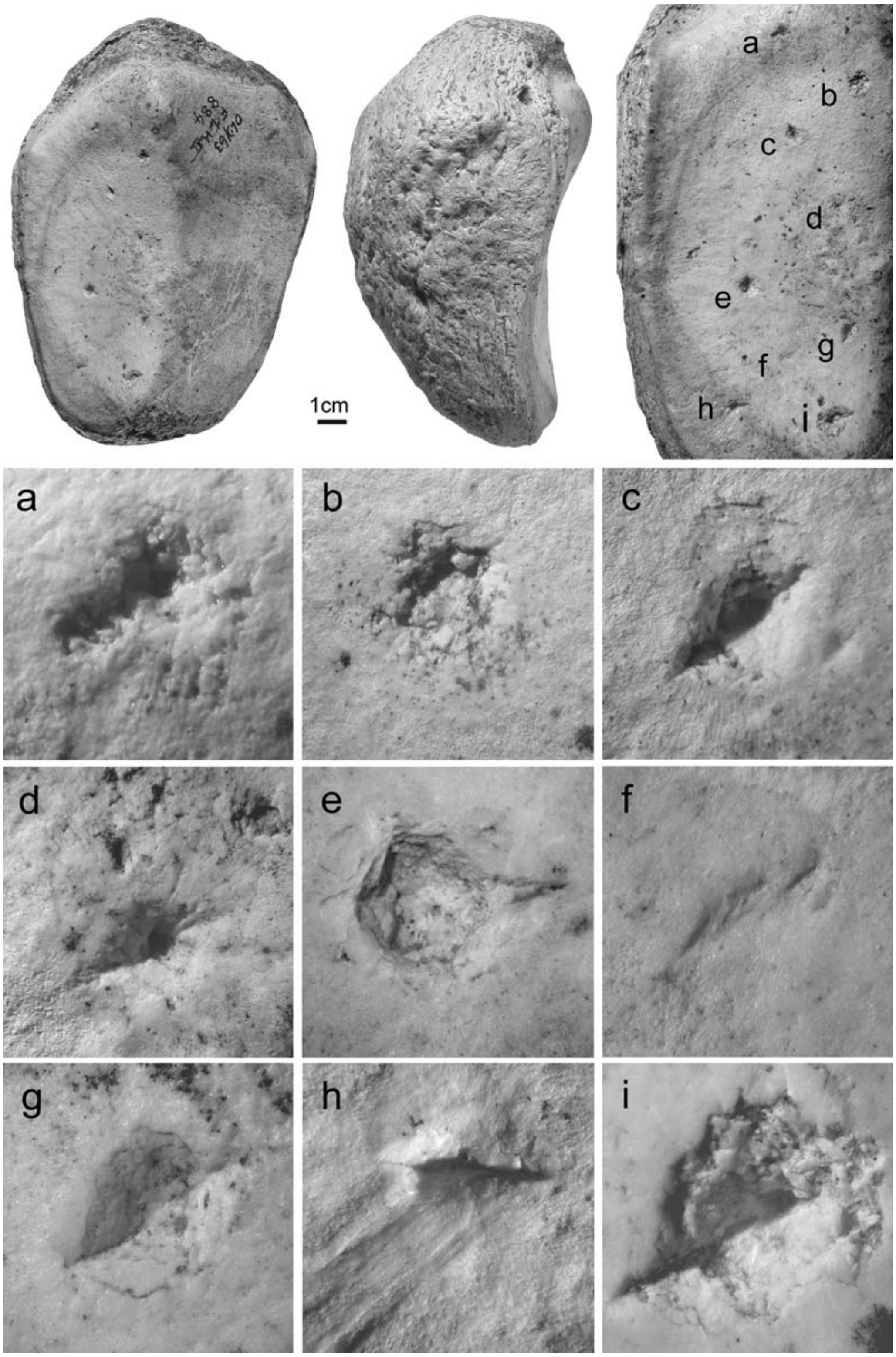

Figure 8. Elephant patella from Olduvai (FLKII 884) with punctures on the articular surface.; **a–i**, close up views of the puncture morphology.

Taphonomic and morphometric analysis

Experimental results

Four techniques were used by the students to break the bones (Table 3). The first involved lifting the bone while holding one epiphysis and repeatedly striking the opposite epiphysis against a rock. This produced in one case a mid-shaft break with no flakes, and in three other cases, breakage with numerous flakes. The second technique entailed throwing the bone repeatedly against a rock. This was used for two bones, which both produced flakes. The third, employed by females, involved throwing a rock at the bone. To avoid the absorption of the striking force by the ground, two bones were stabilized between two rock outcrops, and another inclined against a separate rock. The break of the former produced no flakes in one case and many in the other, while that of the latter resulted in numerous flakes. The fourth technique, attempted by females, consisting of striking the bone with a hand-held rock, was unsuccessful in bone breakage. Once the bones

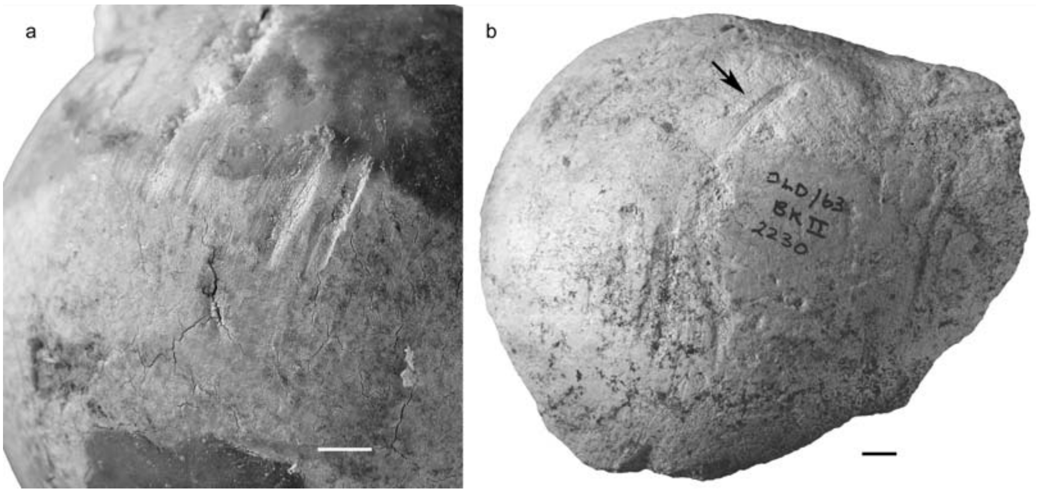

Figure 9. **a**, Head of a modern elephant femur showing scrape marks produced by striking the epiphysis against a rock; **b**, femoral head from Olduvai specimen BKII 2230 bearing weathered carnivore tooth notches, scores and pits as well as a modern scrape mark (arrow).

were broken, students attempted to detach more flakes from the epiphyses by throwing the bones against rocks, rocks against the bones or by using stone wedges. This, however, resulted in the production of very few additional flakes. Shaping the flakes by knapping was also attempted.

Percussion and scrape marks

Half of the flakes bear multiple large percussion marks (Fig. 6), and 23% bear chop marks. Virtually all the pieces with chop marks also have punctures, while only a third of the punctured flakes are associated with chop marks. The epiphyses of the bones struck against rocks show distinct parallel scrape marks resulting from their tangential impact caused by unskilled striking motions (Fig. 9a). The experimentally-produced scrape mark is characterized by parallel grooves with a spindle-like shape, and clear internal striations. A number of Olduvai epiphyses show traces of carnivore scoring which may be confused with strike marks (Fig. 9b). Carnivore marks, however, are seldom parallel, may be curved, do not have clear internal striations, and generally terminate abruptly at one end.

Flake analysis

Breakage of the nine elephant limb bones produced 134 flakes. Data were recorded on 107 of these pieces. Two bones produced no flakes, while the remainder produced between six and 29 flakes each, the highest figure deriving from the weathered bone.

Table 5. Dimensions of flakes produced during the experimental breakage of elephant limb bones.

Flake dimensions	Mean $n = 107$	S.D. mm	Minimum mm	Maximum mm
Length	139	76.6	23	385
Width	50	25.5	10	125
Maximum thickness	21	12.1	2	52
Compact bone thickness	16.5	9.2	2	44

Flakes can be divided into two broad categories; those made exclusively of compact bone (Fig. 10) and those retaining spongy bone (Figs 11 & 12). The compact bone includes slivers resulting from the detachment of primary cortical bone (Fig. 10: Nos 6–10, 14), spindle-like thicker splinters (Fig. 10: Nos 4–5), and rectangular blanks that are flat on the ventral and dorsal aspects (Fig. 10: Nos 2, 3, 11,12). One sliver-like flake is noteworthy (Fig. 10: No. 7) in that it demonstrates that very large blanks made of compact bone (26 × 10 cm) can result from the breakage of very large mammal bone when struck against rocks for the exclusive purpose of marrow extraction. The flakes with spongy bone include large elongated shaft fragments with rounded or pointed ends that retain between half and one third of the shaft section (Fig. 11), and irregularly-shaped chunks with a considerable proportion of cancellous bone (Fig. 12).

Data on the dimensions of the flakes are given in Tables 5 & 6 and Fig. 13. Results indicate that the frequency of flakes in the different size classes remains constant in all bones, with the exception of the weathered bone (Table 6, no. 5), which shows an over-representation of elongated flakes. This difference does not correspond to a change in the general size of the flakes, as demonstrated by the scattergram (Fig. 14) correlating the flake width and length. This scattergram also shows that the size of the flakes is not determined by the bone type or by the breakage technique.

Pseudo-retouch

Fifteen flakes (14%) show removals/flake scars that may be taken as evidence for deliberate shaping (Table 7). Six bear a single removal, seven bear between two and five removals, and only two pieces have eight removals. Removals occur more often on the periosteal surface (eight cases) than on the medullar (three cases). Four pieces have removals on both periosteal and medullar surfaces. Isolated removals generally do not exceed one per specimen, while multiple removals are in almost all cases found in association. Results also show that removals occur more often on the ends of flakes than on their sides. At close inspection, however, only a few of these removals may be taken as negatives of flakes produced by knapping. This is because they lack features that would indicate that percussion was applied. One piece, for example, presents a

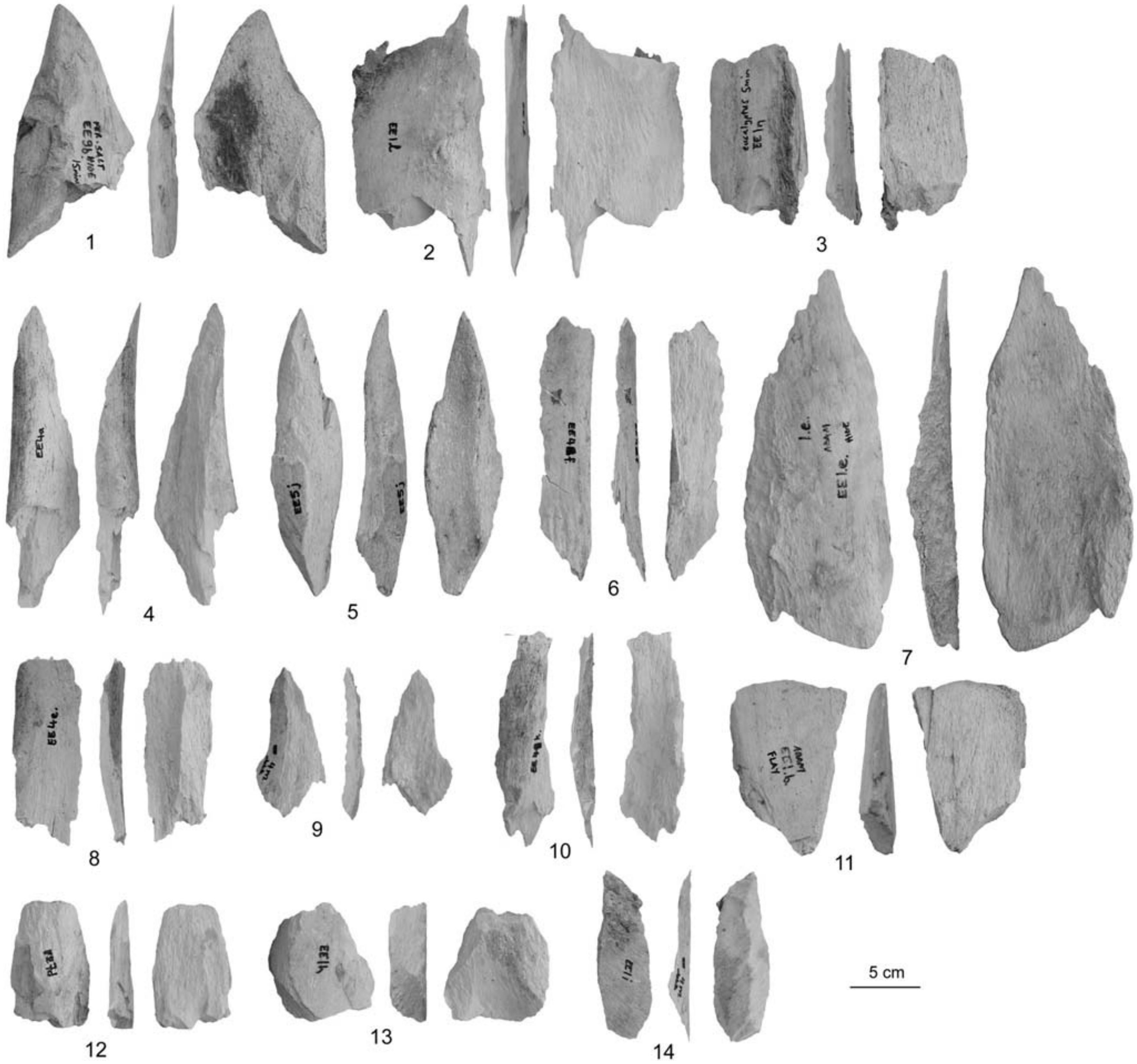

Figure 10. Cortical bone flakes produced by the experimental breakage of elephant limb bones.

wedge-like breakage with opposing flat scars that lack a negative bulb of percussion (Fig. 15a). Another, resulting from the breakage of the weathered bone, has scars due to the lifting of primary bone lamellae opposite to irregularly shaped scars (Fig. 15b). This morphology, difficult to accept as evidence of purposeful modification, is as to be expected, the result of the state of preservation of the bone. Two pieces require special attention. One is a large flake with a pointed end bearing overlapping removals that mimic the tip of a dihedral burin (Fig. 15c). The other is a large flake with a remarkable hand axe-like morphology with contiguous pseudo-removals on both ends that

Table 6. Length of the flakes from experimentally broken elephant bones.

Bone No.	Flake length (cm)								
	0–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	Total
1	1	9	5	2	4	2	0	0	23
2	2	8	1	1	1	0	2	1	16
3	0	2	4	0	0	1	0	0	7
4	0	5	7	3	1	1	1	0	18
5	1	9	8	6	1	4	0	0	29
6	0	0	0	0	0	0	0	0	0
7	0	3	0	2	0	1	0	0	6
8	0	0	0	0	0	0	0	0	0
9	2	2	2	1	1	0	0	0	8
Total	6	38	27	15	8	9	3	1	107

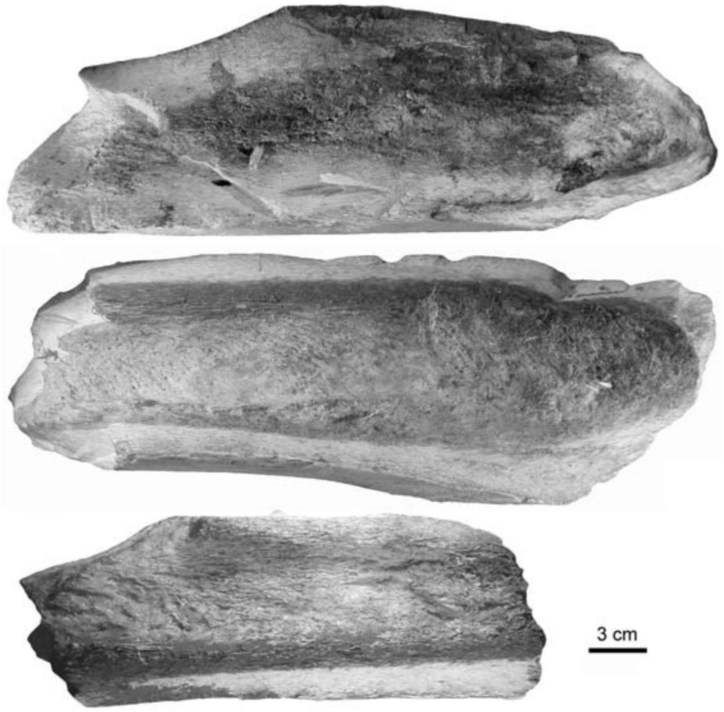

Figure 11. Large bone flakes produced by the experimental breakage of elephant limb bones with a large proportion of spongy bone.

mimic pseudo bifacial shaping at its base (Fig. 16). In spite of its general resemblance to an Acheulean stone hand axe or to one of the Acheulean elephant bone hand axes from the Italian sites (Radmilli 1985; Radmilli & Boschian 1996), this piece has no invasive contiguous bifacial scars.

Experimental shaping by knapping

Knapping of the elephant bone flakes using quartzite and dolomite blocks, attempted by the students shortly after the bone breakage, was unsuccessful. The students were, however, unskilled knappers and the available hammers seemed to be unsuitable for the task. Subsequent knapping, made by one of us (F.D.) using elongated quartzite pebbles weighing *c.* 500 g, took place one year after the breakage experiment, when the bone flakes had dried considerably. Flakes from bones fresh at the time of breakage experiments were difficult to knap, and split longitudinally. The results obtained after soaking them in water for two days were no better. Knapping was successful on shaft fragments resulting from bone weathered at

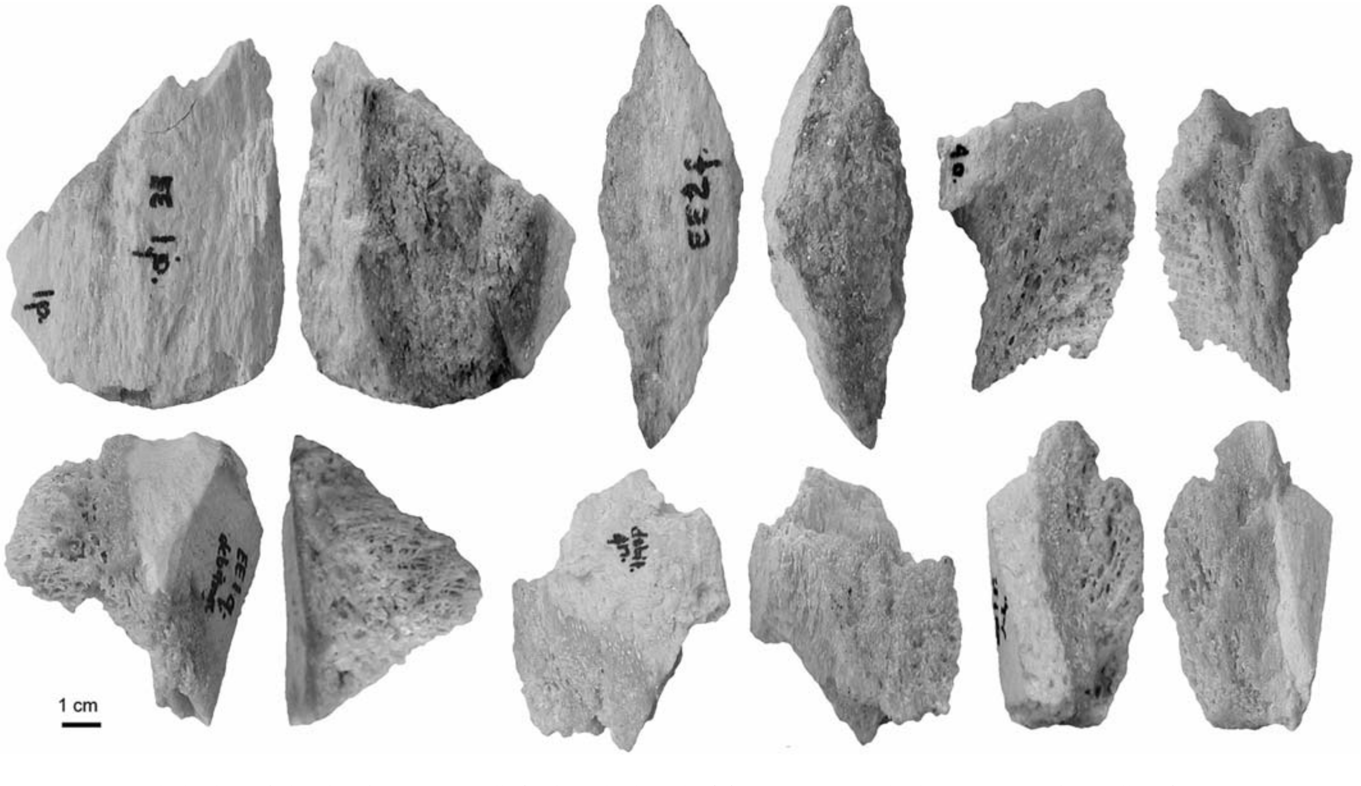

Figure 12. Irregularly shaped chunks of experimentally broken elephant limb bone retaining a high proportion of cancellous bone.

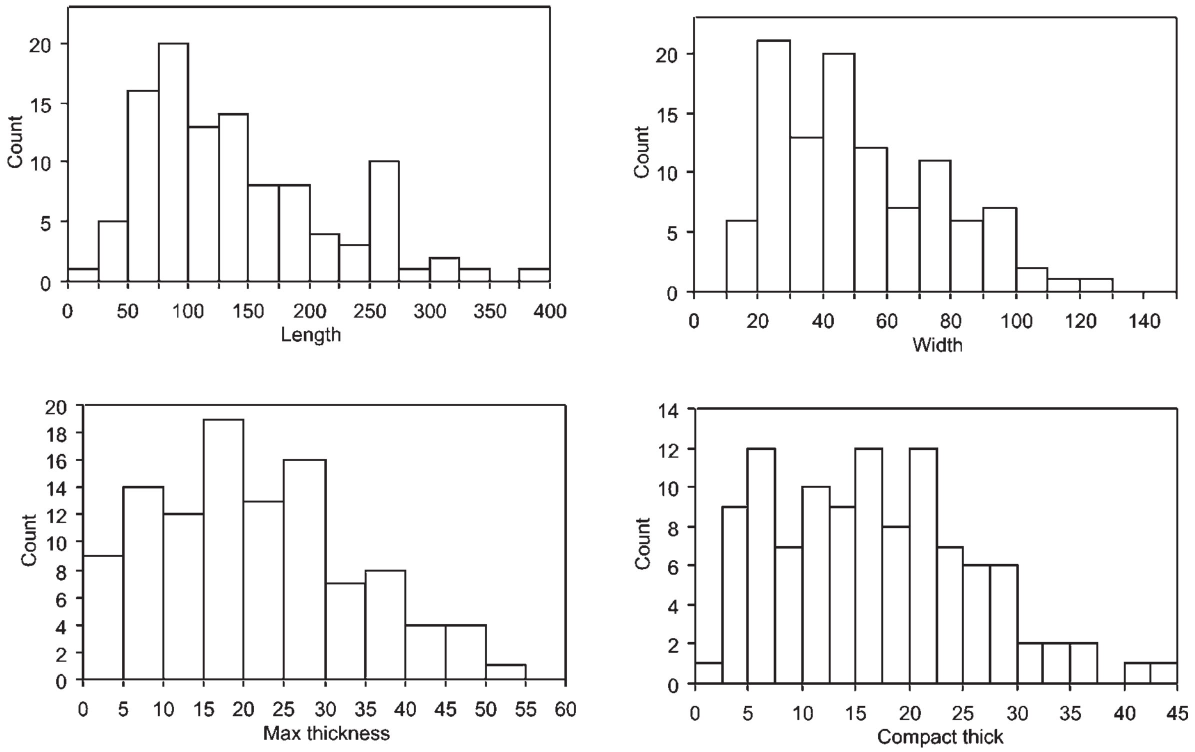

Figure 13. Histograms of the dimensions of flakes produced during the experimental breakage of elephant bone.

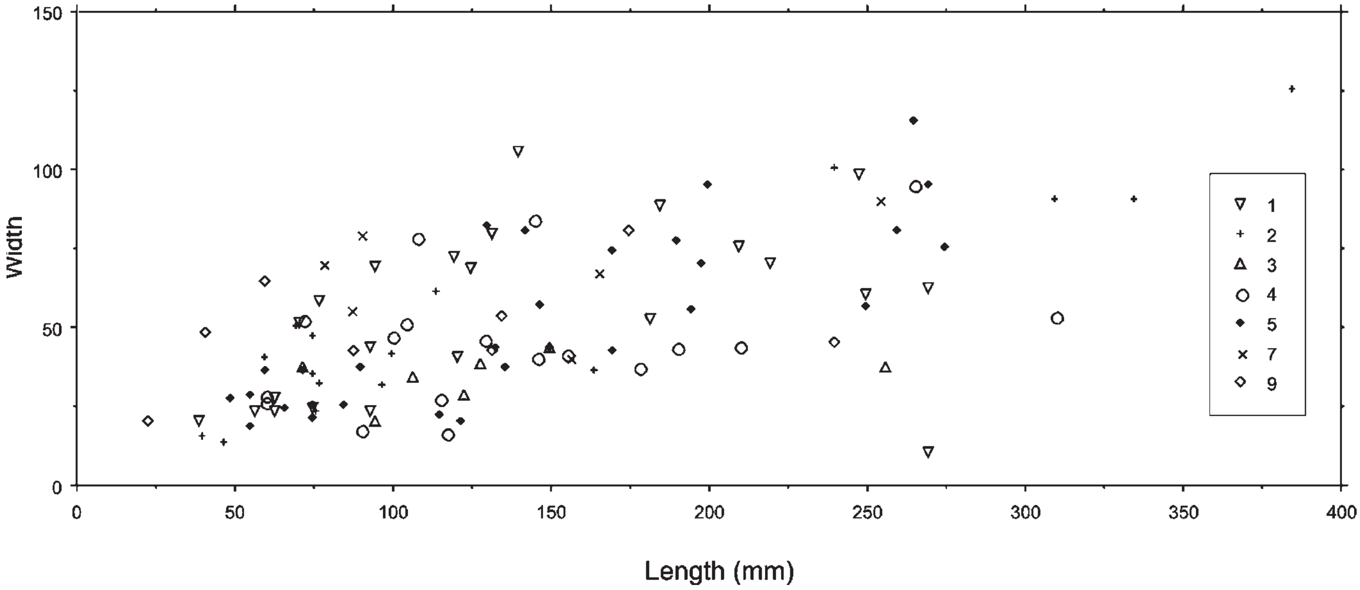

Figure 14. Length/width correlation of the flakes produced during the experimental breakage of elephant bone. Symbols indicate flakes from the same bone (see Table 3 for the bone type and the breakage technique used).

Table 7. Number, association and location of removals on the periosteal and medullar surfaces of flakes produced by the experimental breakage of elephant limb bones.

No. rem. per flake	No. of flakes with removals			Association				Location					
				Periosteal		Medullar		Periosteal			Medullar		
	Total	Peri.	Med.	Isolated	Cont.	Isolated	Cont.	End	End+side	Side	End	End+side	Side
0	92	95	100	103	99	101	106	97	105	106	103	106	105
1	6	4	5	4	0	5	0	3	0	1	3	0	2
2	2	3	0	0	3	0	0	2	1	0	0	0	0
3	1	0	1	0	0	1	0	0	0	0	0	1	0
4	2	3	1	0	3	0	1	2	1	0	1	0	0
5	2	1	0	0	1	0	0	1	0	0	0	0	0
8	2	1	0	0	1	0	0	1	0	0	0	0	0

rem: removals; Peri: periosteal; Med: medulla; Cont: contiguous.

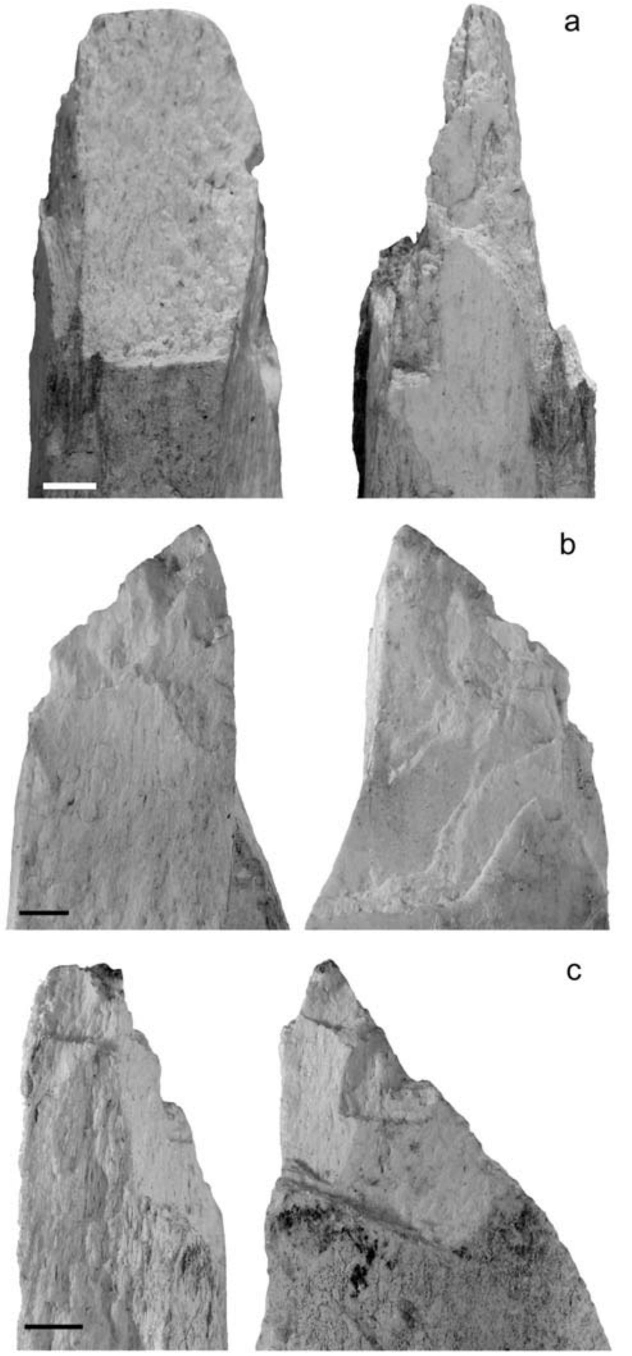

Figure 15. Pseudo-removals resulting from experimental breakage of elephant bones.

the time of the experimental breakage (Fig. 17). The large invasive removals obtained exhibit, however, a rough surface (Fig. 17b–c) different from the fine-grained texture recorded on the scars on many Olduvai purported bone tools. Also, the fracture surface is different, in that after producing a concoidal-like negative, it progresses inward, with its orientation determined by that of the bone lamellae. This gives a portion of the scar a flat appearance not seen at Olduvai.

Olduvai

Leakey bone tool collection and comparative sample composition

The purported bone tool collection we analyse here comprises 106 specimens. Teeth and tusks, as well as complete bones, are not the subject of this paper and complete bones bearing punctures have been analysed above. The photographs of the analysed material are presented in Figs 18–46, by site in alphabetical and numerical order. Most of the analysed pieces are limb bone flakes and shaft fragments (62%). The remainder consists of epiphyses with or without a portion of the diaphysis. Nearly 80% of the pieces come from large to very large mammals (Fig. 47). Owing to their fragmentary nature, most of them are difficult to identify to taxon level. The most commonly identified animals in order of abundance are giraffids, equids, bovids, elephantids, hippopotamids, and rhinocerotids. Our comparative sample is instead mostly composed of flakes and shaft fragments from medium-sized mammals, particularly bovids (Fig. 47). This is because outside of the bone tool collection, the Olduvai assemblage comprises very few large limb bone fragments, making impossible the construction of a more appropriate comparative sample.

Bone preservation and surface modifications

The bone tool collection is generally characterized by an excellent state of preservation. The large majority of the pieces (Table 8) are either fresh (44%) or slightly abraded (40%). Post-depositional breaks and scars, mostly due to excavation and handling, account for 23% and 13% of the collection, respectively. Almost all of the bones underwent a rapid burial process; 48% show no weathering, and 45% show a weathering stage 1 (Behrensmeyer 1978). A moderate degree of trampling and polishing affects *c.* 21% of the pieces. The majority of the pieces have spiral fractures, indicating that the bone was fresh when broken. Hominids are the agent most likely to have been responsible for the breakage, considering that 30% of the bone tool collection bears either cut-marks or clearly lithic-derived punctures (Fig. 48a–e), and an additional 3% bears a combination of both modifications (Table 9).

Carnivore marks, although occurring on 25% of the collection, only consist of superficial tooth scores and pits. No evidence of destruction of epiphyses by gnawing, crenulated edges or a combination of these features

Table 8. Bone surface modifications on Olduvai bones.

Collection	No. pieces	Surface modifications					Weathering stage			Degree of abrasion				Post deposition	
		Carn.	Cut-mark	Perc.	Tramp.	Polish	0	1	2	Fresh	Slight	Mod.	Heavy	Break	Rem.
Control	82	2	10	7	28	3	58	23	1	41	32	8	1	17	2
Leakey/Ship.	106	26	15	22	24	22	51	48	7	46	42	14	3	25	14

Ship: Shipman; Carn: carnivore tooth marks; Perc: percussion marks; Tramp: trampling: Mod: moderate; Rem: removal

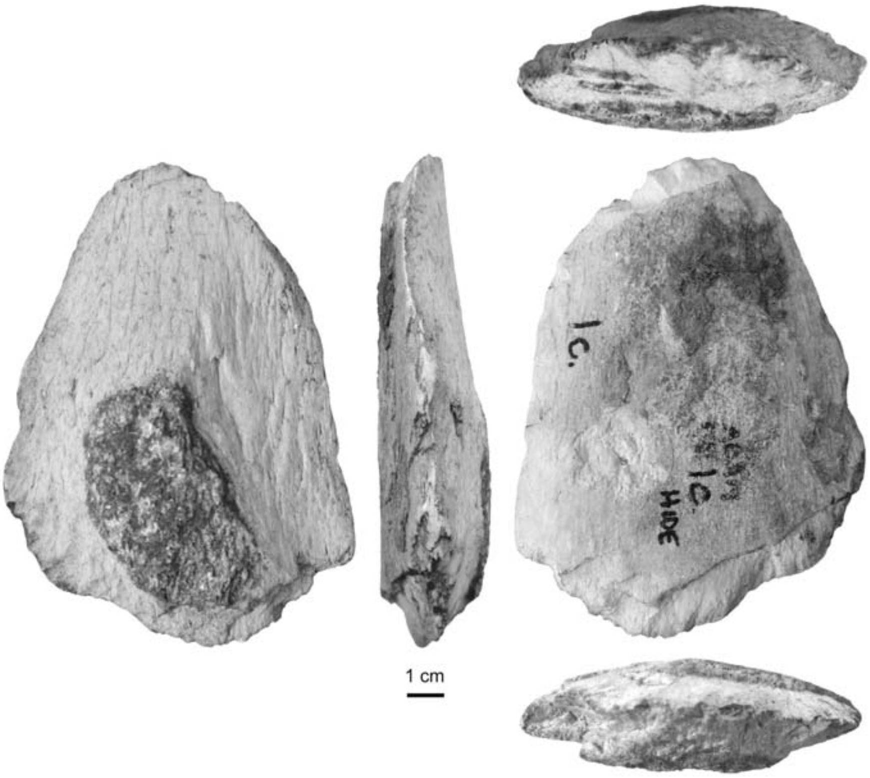

Figure 16. Bone flake resulting from experimental breakage of elephant limb bones with a hand axe-like morphology.

with impact notches is found, suggesting that carnivore involvement was limited and post-dated bone breakage. Figure 48f illustrates the most extreme example of carnivore damage recorded. Carnivore-, percussion-, and cut-marks occur on all bone types and mammal size classes. Their absence from the bones of small mammals is certainly due to the very low proportion of such bones in the sample.

The above surface modifications occur in the Olduvai control sample in proportions that are not significantly

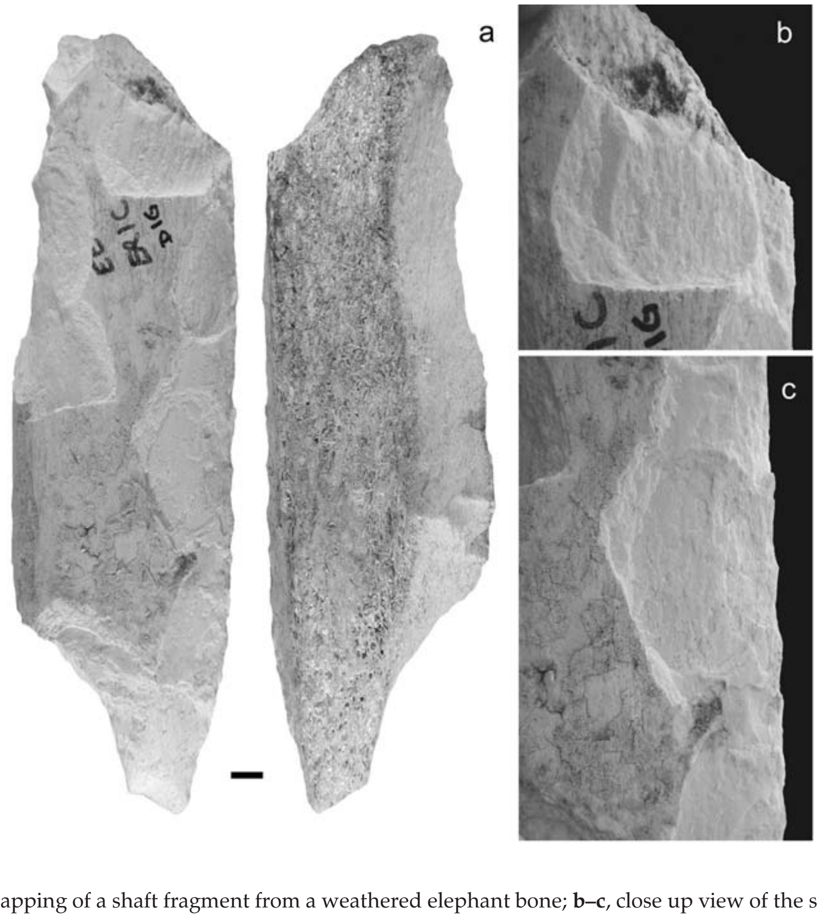

Figure 17. a, Experimental knapping of a shaft fragment from a weathered elephant bone; **b–c**, close up view of the scars.

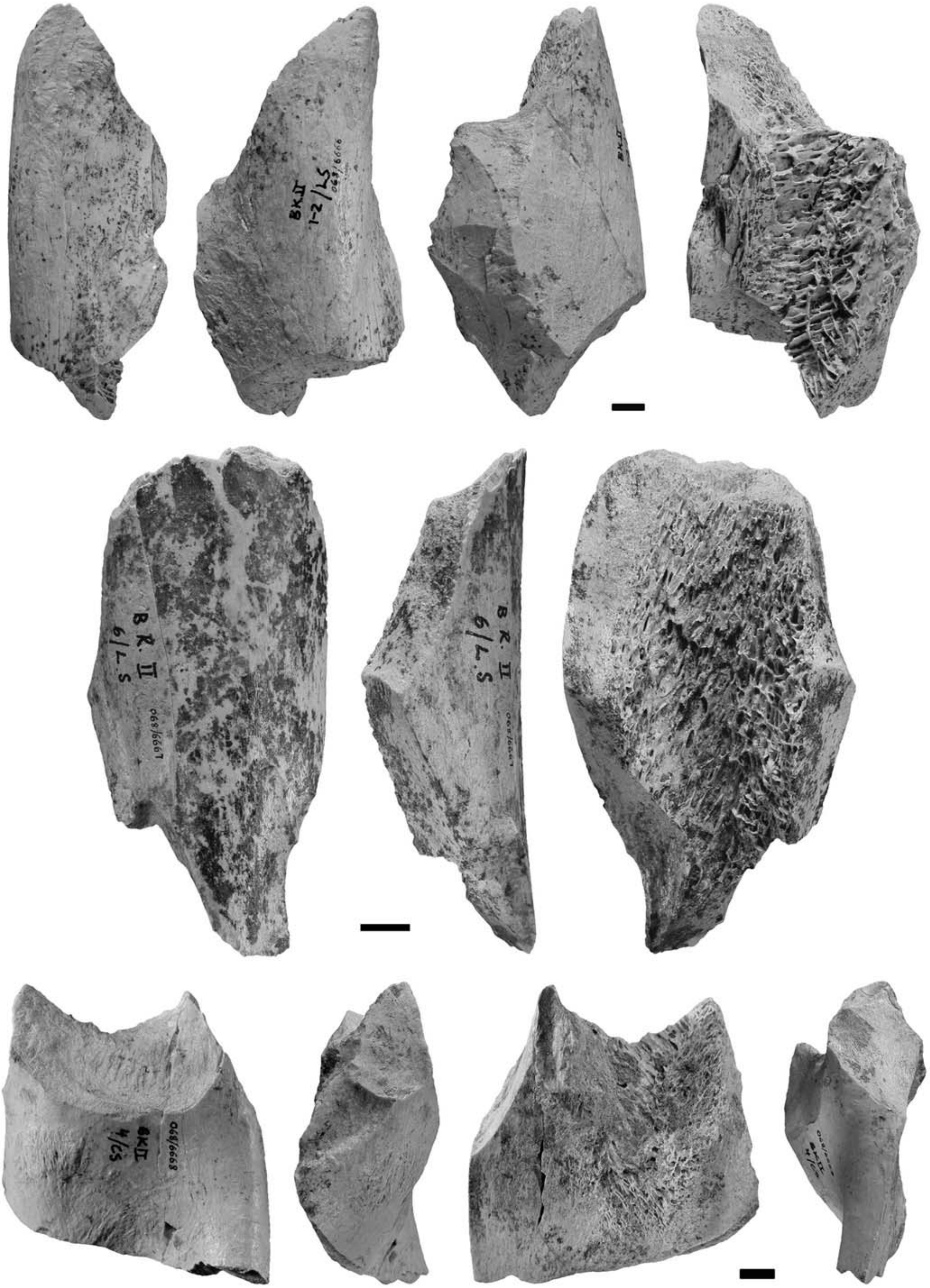

Figure 18. Olduvai bone tools proposed by Leakey. *BKII 068–6666 (**top**), BKII 068–6667 (**centre**) and *BKII 068–6668 (**bottom**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

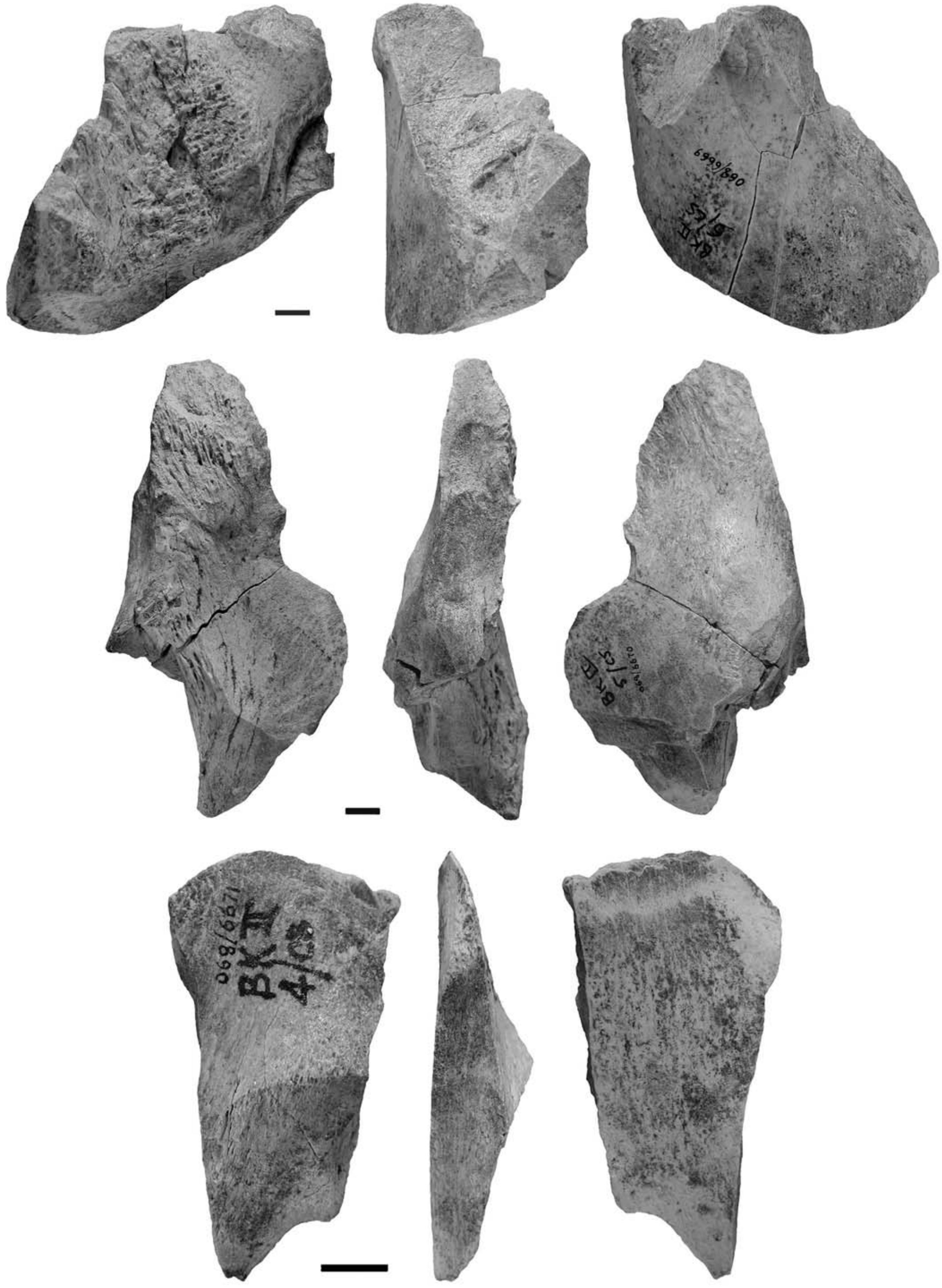

Figure 19. Olduvai bone tools proposed by Leakey. BKII 068–6669 (**top**), *BKII 068–6670 (**centre**) and BKII 068–6671 (**bottom**). Scale bars = 1cm. An asterisk indicates a bone tool according to this study.

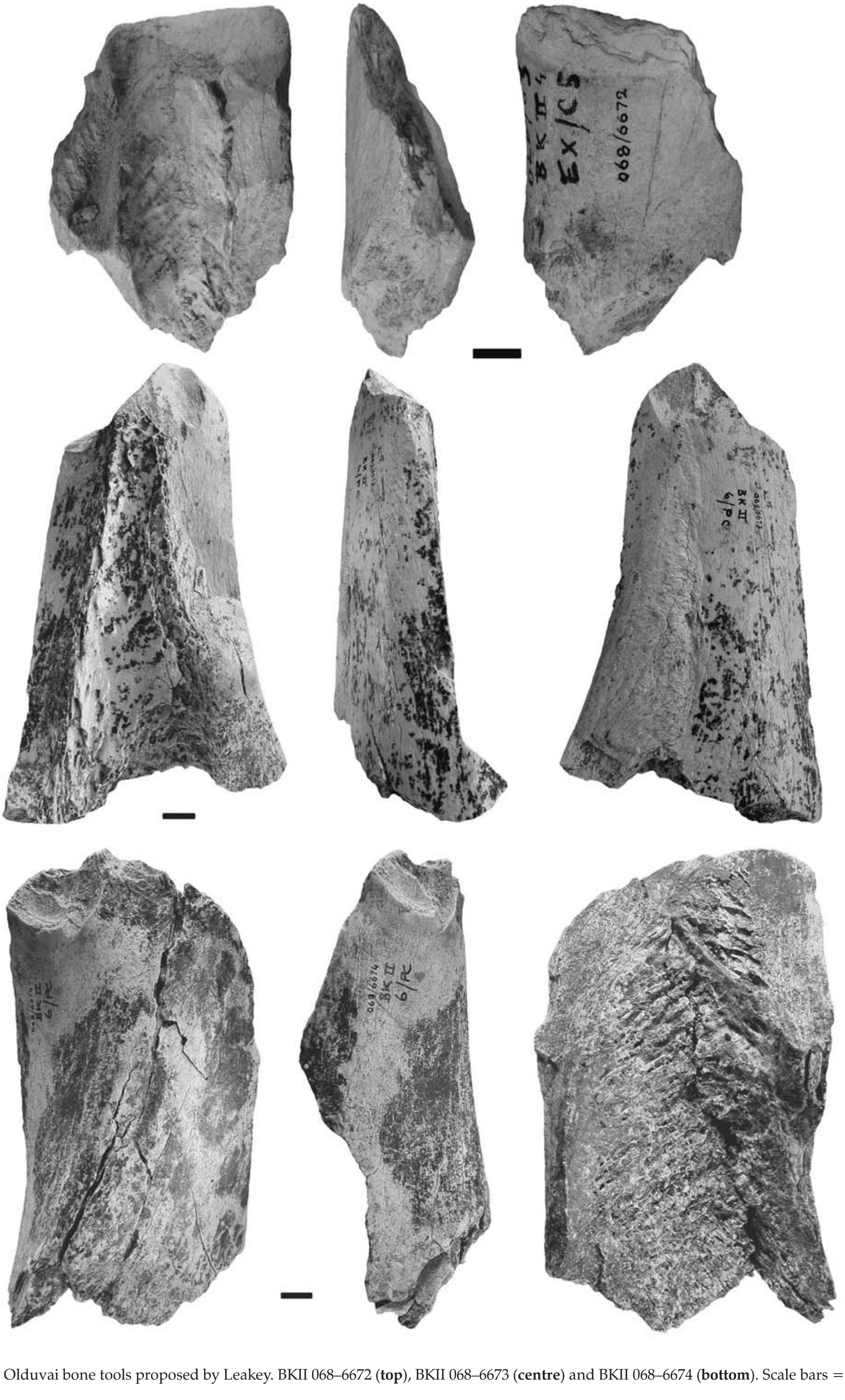

Figure 20. Olduvai bone tools proposed by Leakey. BKII 068–6672 (**top**), BKII 068–6673 (**centre**) and BKII 068–6674 (**bottom**). Scale bars = 1cm.

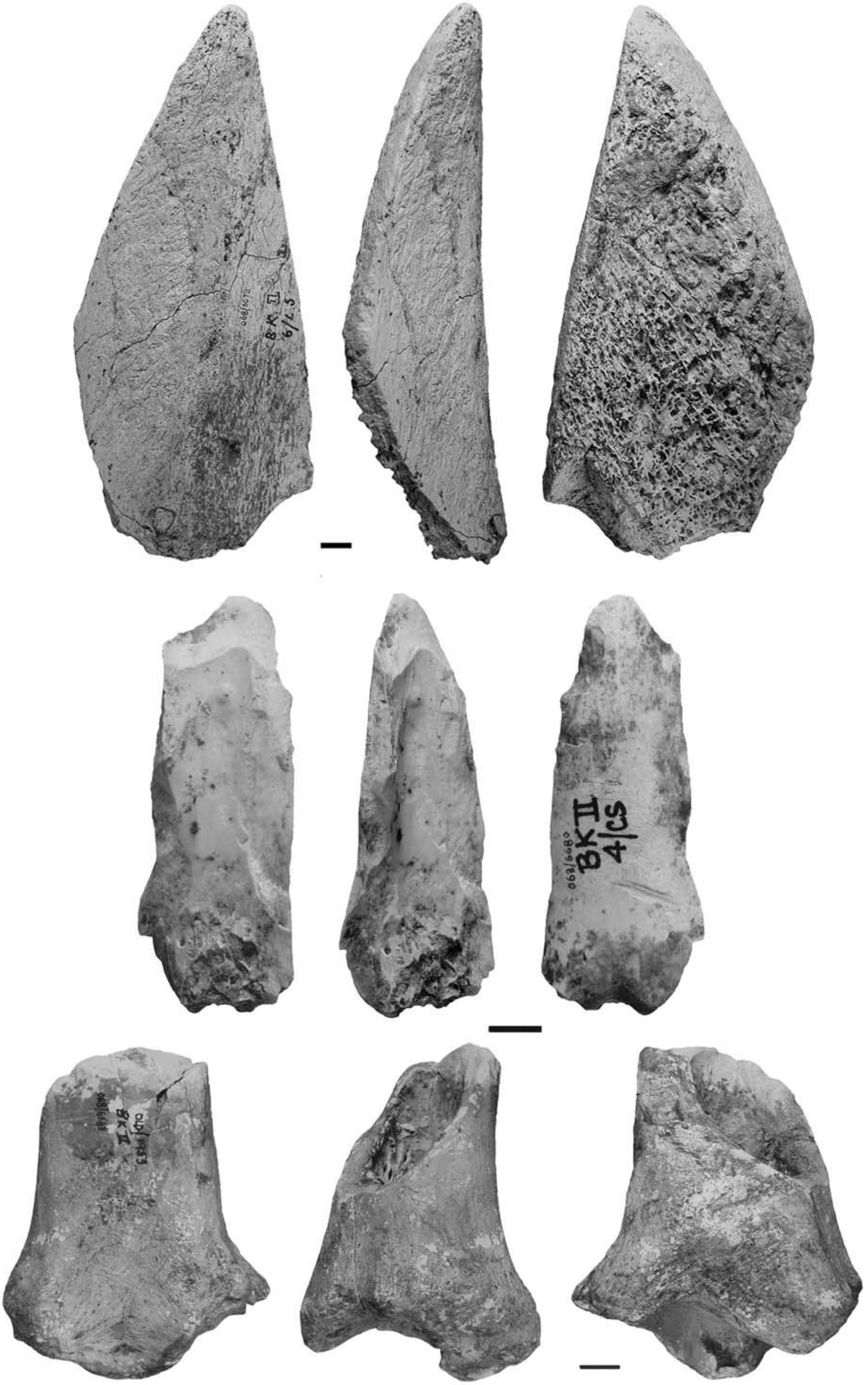

Figure 21. Olduvai bone tools proposed by Leakey, BKII 068–6678 (**top**), BKII 068–6674 (**bottom**), and by Leakey and by Shipman BKII 068–6673 (**centre**). Scale bars = 1 cm.

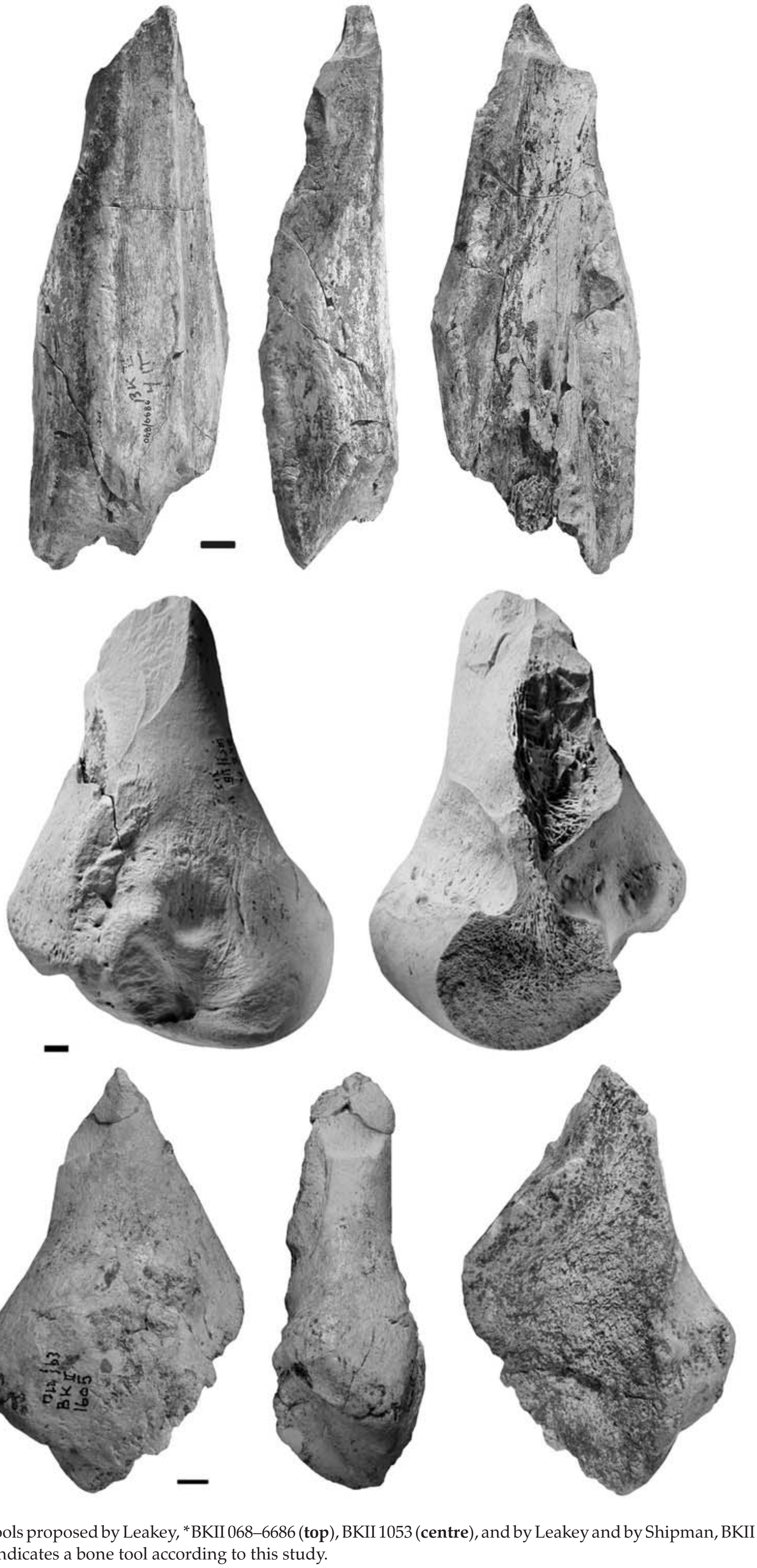

Figure 22. Olduvai bone tools proposed by Leakey, *BKII 068–6686 (**top**), BKII 1053 (**centre**), and by Leakey and by Shipman, BKII 1605 (**bottom**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

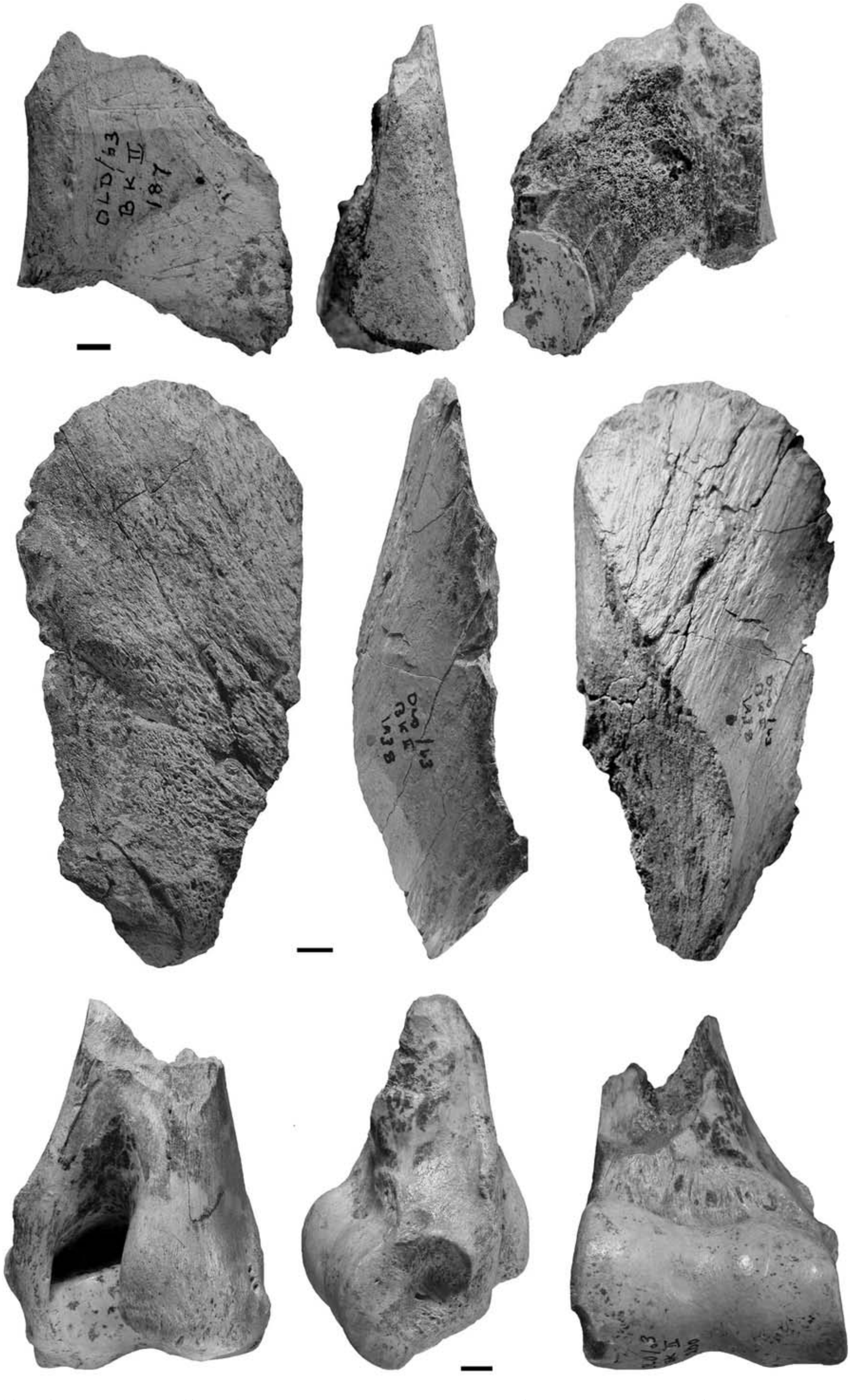

Figure 23. Olduvai bone tools proposed by Leakey. BKII 187 (**top**), *BKII 1938 (**centre**), and *BKII 200 (**bottom**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

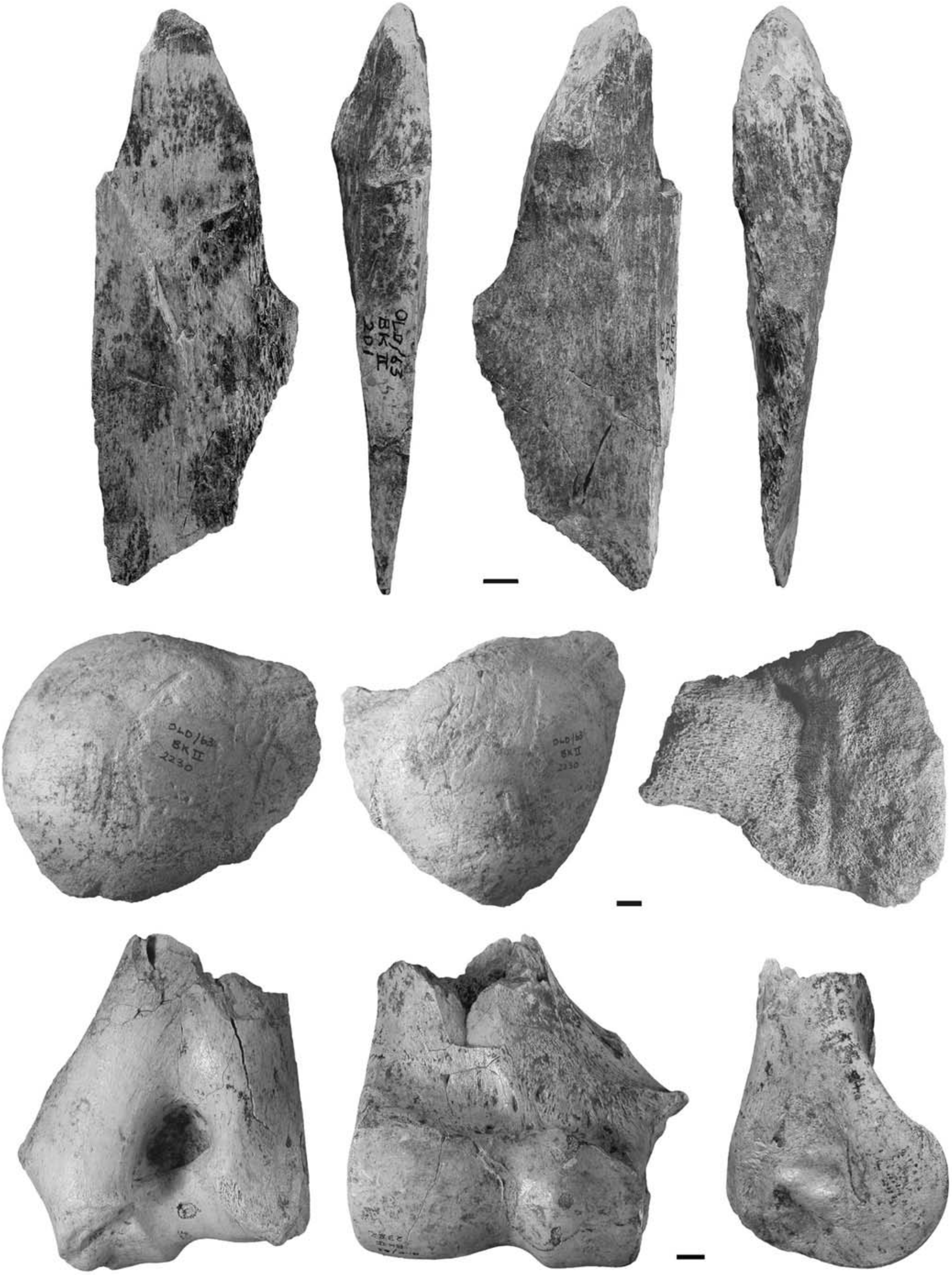

Figure 24. Olduvai bone tools proposed by Leakey. *BKII 201 (**top**), BKII 2230 (**centre**), and *BKII 2382 (**bottom**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

Figure 25. Olduvai bone tools proposed by Leakey, *BKII 2715 (**top**) and BKII 2959 (**bottom**), and by Leakey and by Shipman, BKII 2870 (**centre**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

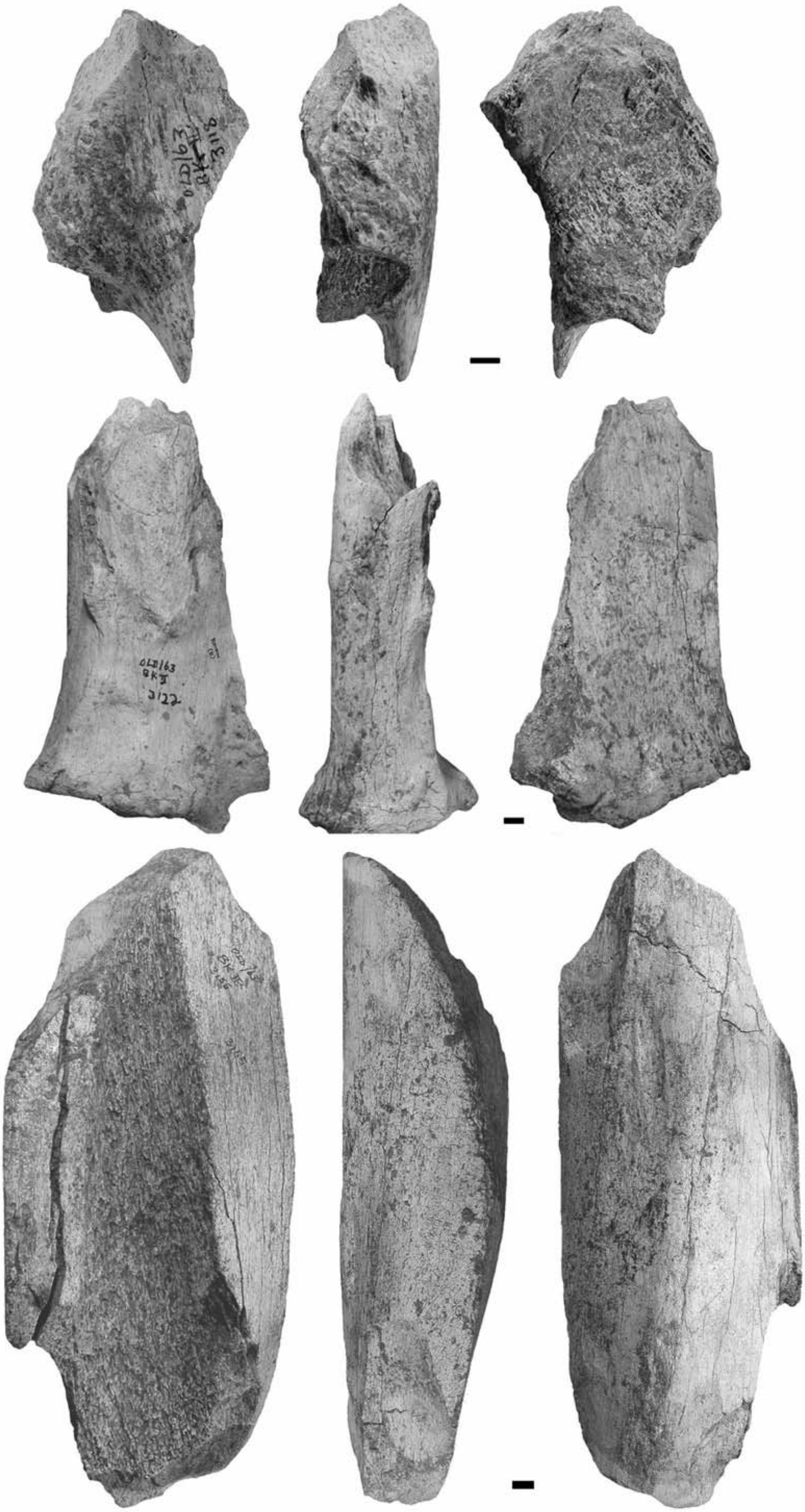

Figure 26. Olduvai bone tools proposed by Leakey, BKII 3118 (**top**) and BKII 3122 (**centre**), and by Leakey and by Shipman, *BKII 3155 (**bottom**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

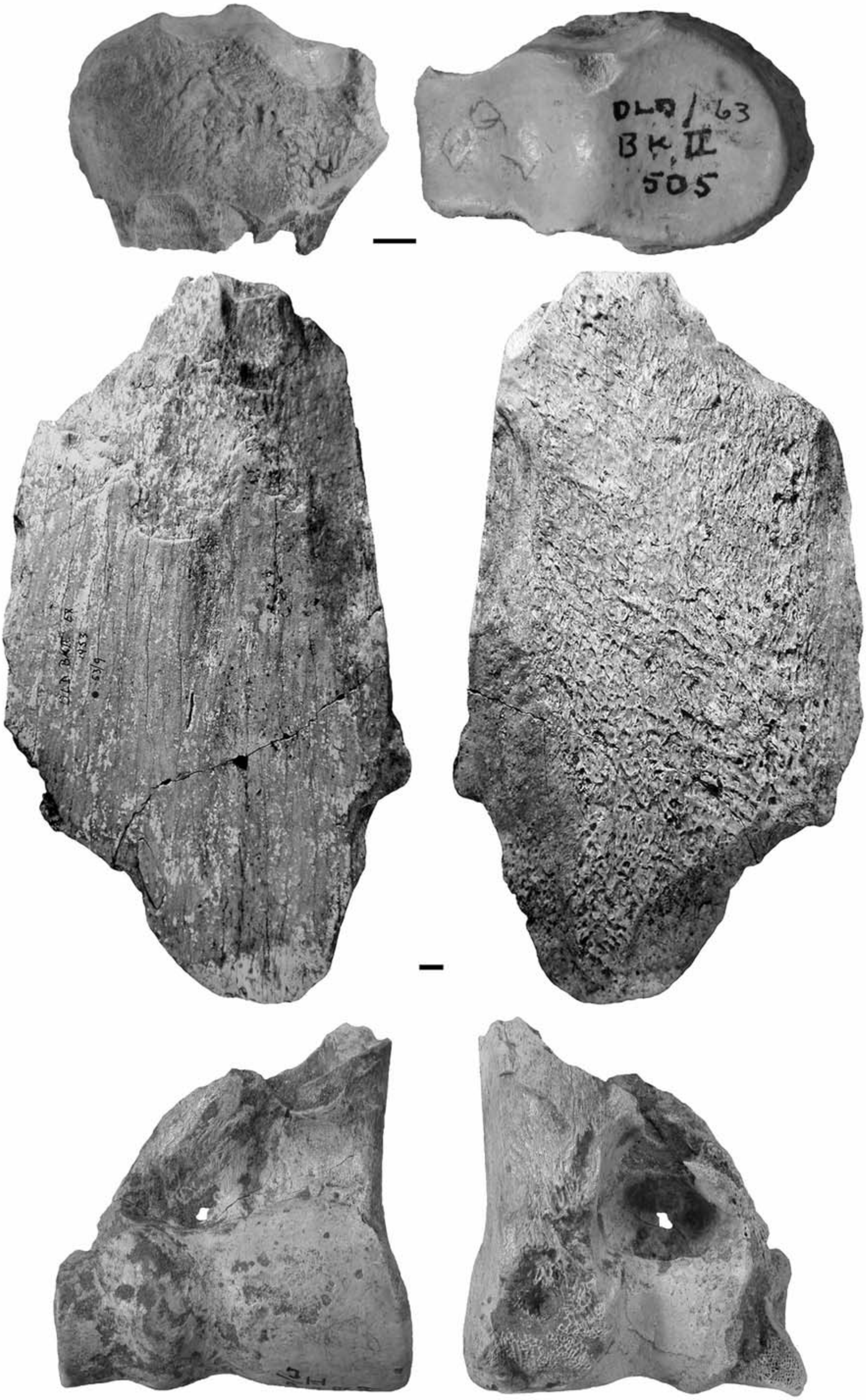

Figure 27. Olduvai bone tools proposed by Leakey, BKII 505 (**top**), *BKII 1953 or 53–9 (**centre**), and by Leakey and by Shipman, BKII 869 (**bottom**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

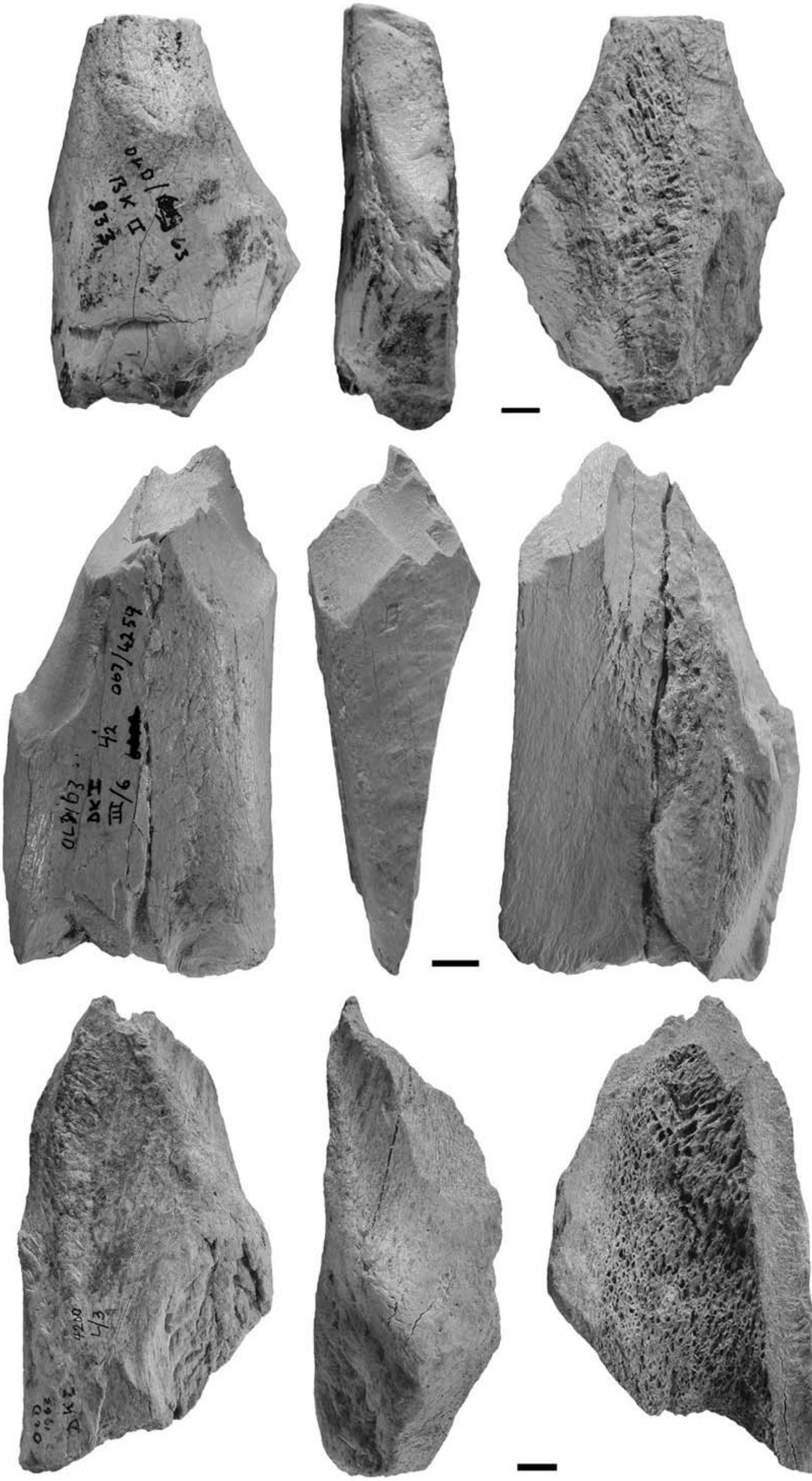

Figure 28. Olduvai bone tools proposed by Leakey, *BKII 933 (**top**), *DKI 067–4259 (**centre**), and by Leakey and by Shipman, DKI 4200 (**bottom**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

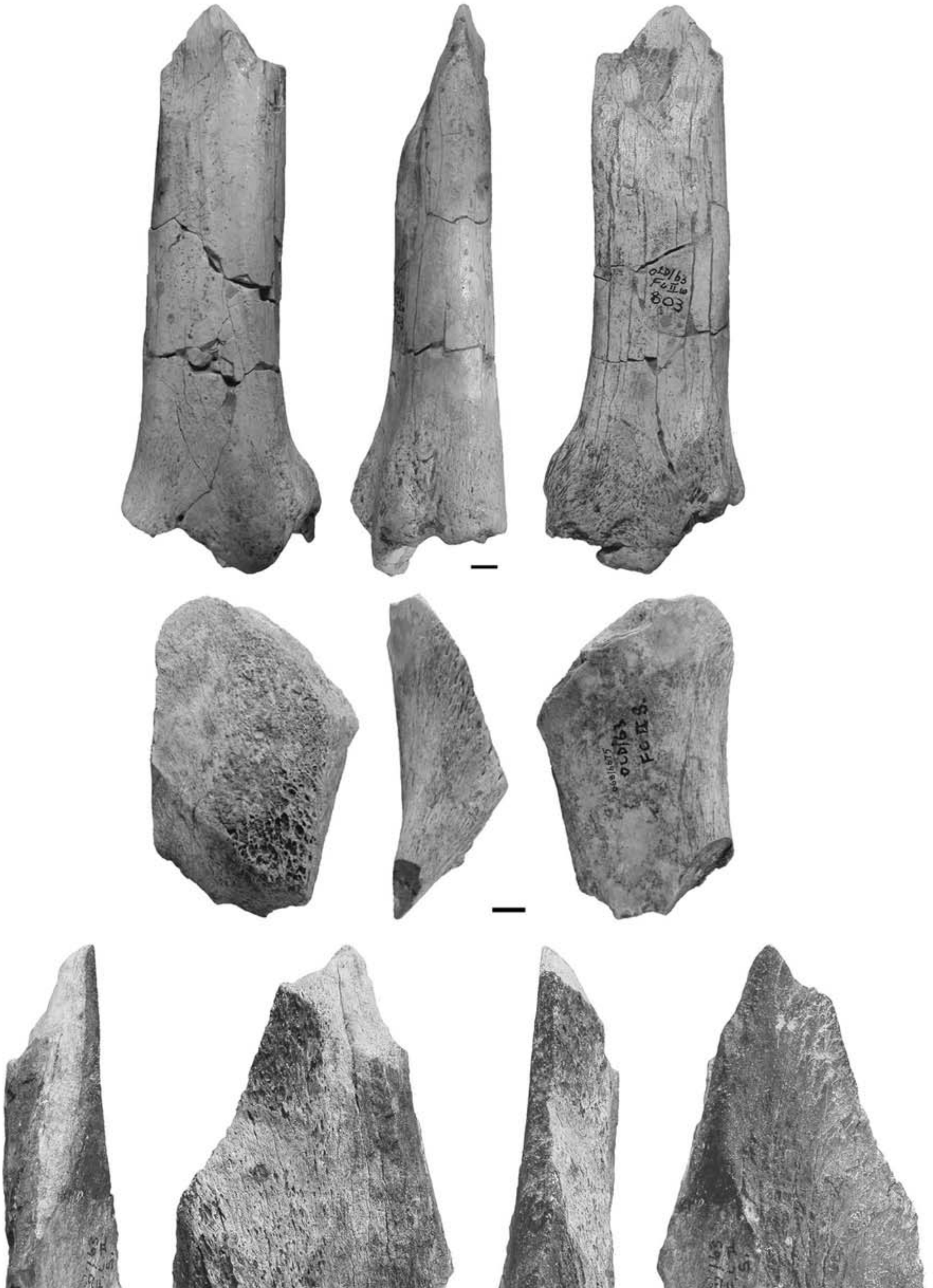

Figure 29. Olduvai bone tools proposed by Leakey, FCII 803 (**top**), FCII 068–6675 (**centre**), and by Leakey and by Shipman, *FCII 068–6679 (**bottom**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

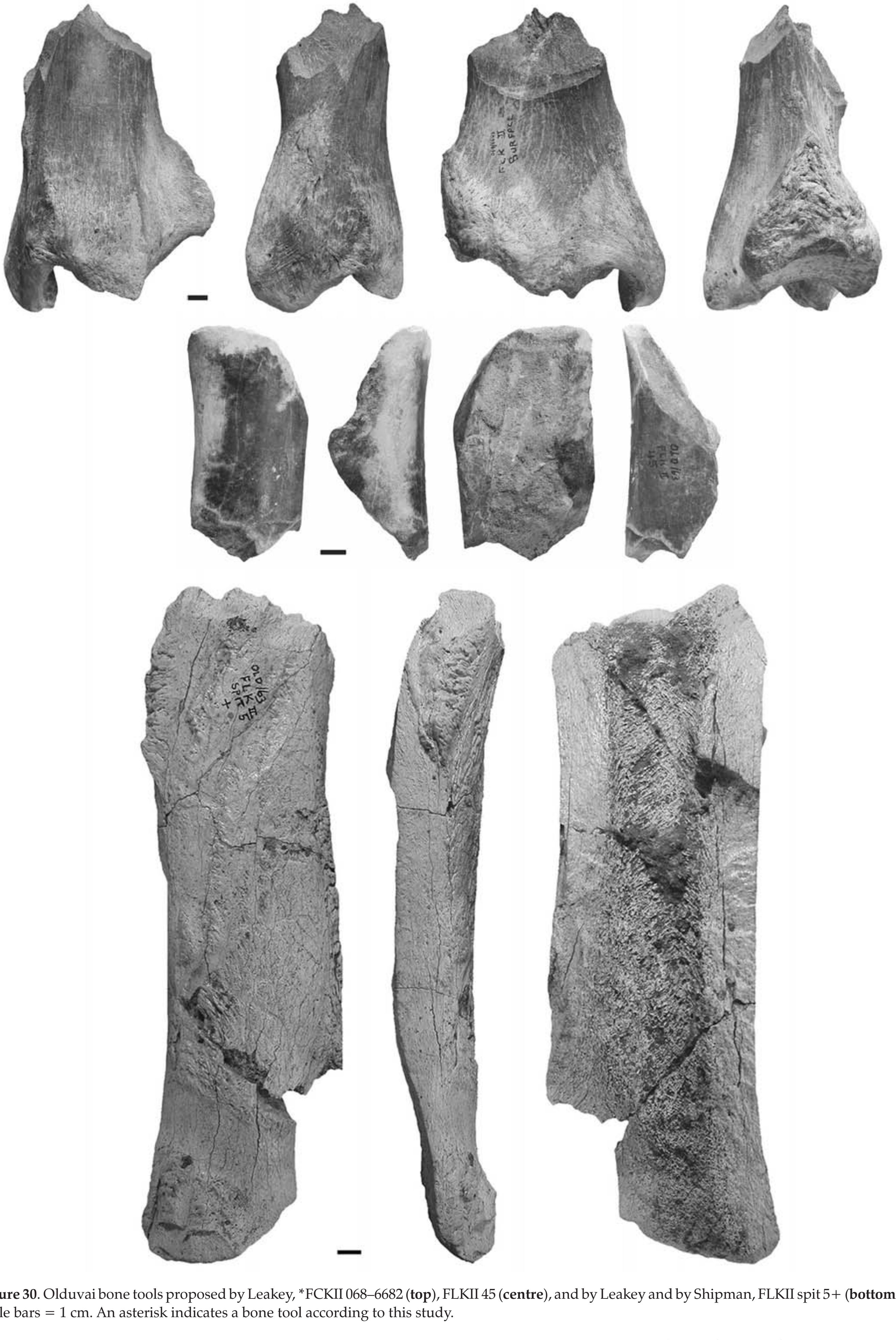

Figure 30. Olduvai bone tools proposed by Leakey, *FCKII 068–6682 (**top**), FLKII 45 (**centre**), and by Leakey and by Shipman, FLKII spit 5+ (**bottom**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

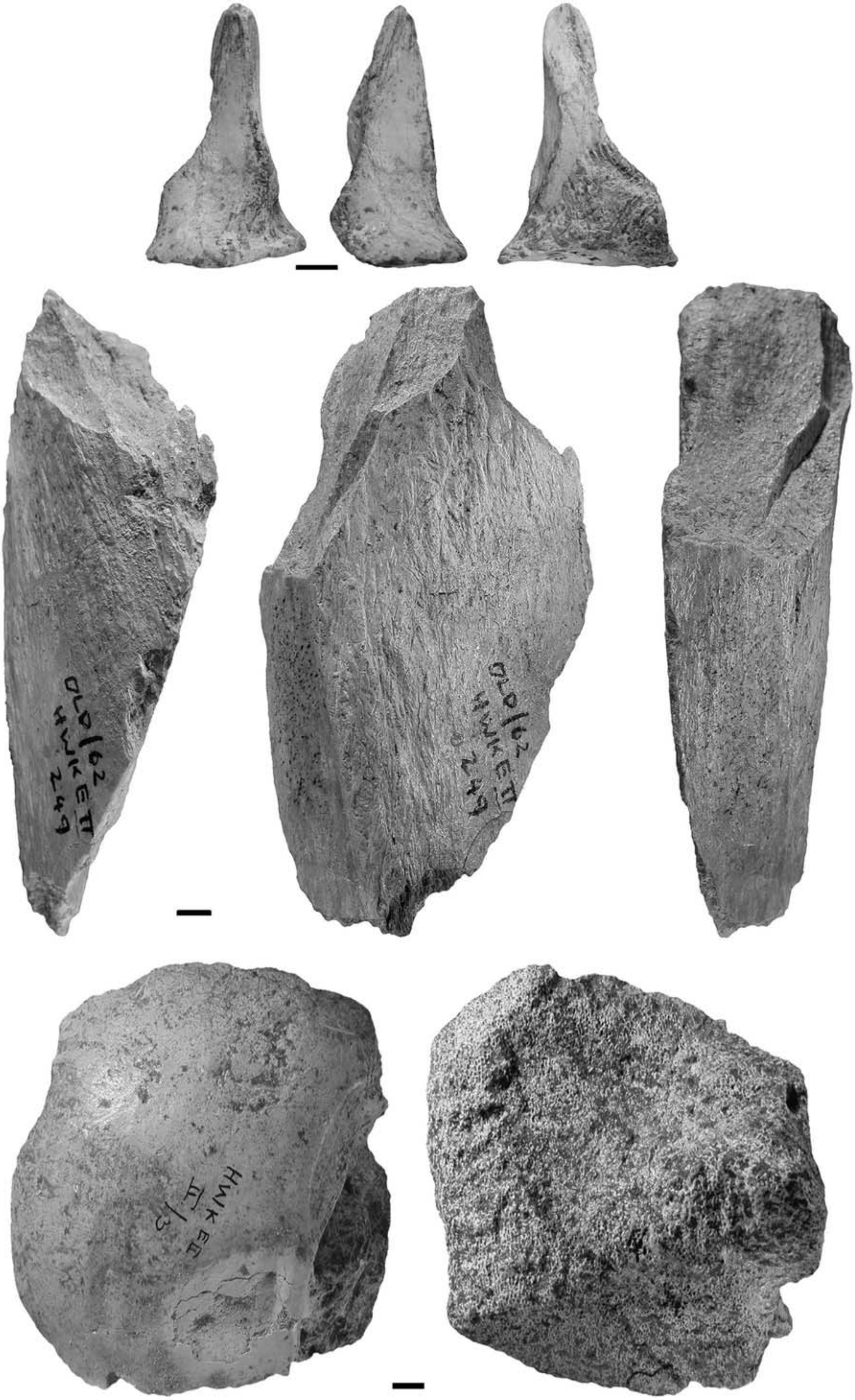

Figure 31. Olduvai bone tools proposed by Leakey and by Shipman, HWKEII 068–6690 (**top**), and by Leakey, *HWKEII 249 (**centre**), HWKEII 3a **(bottom)**. Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

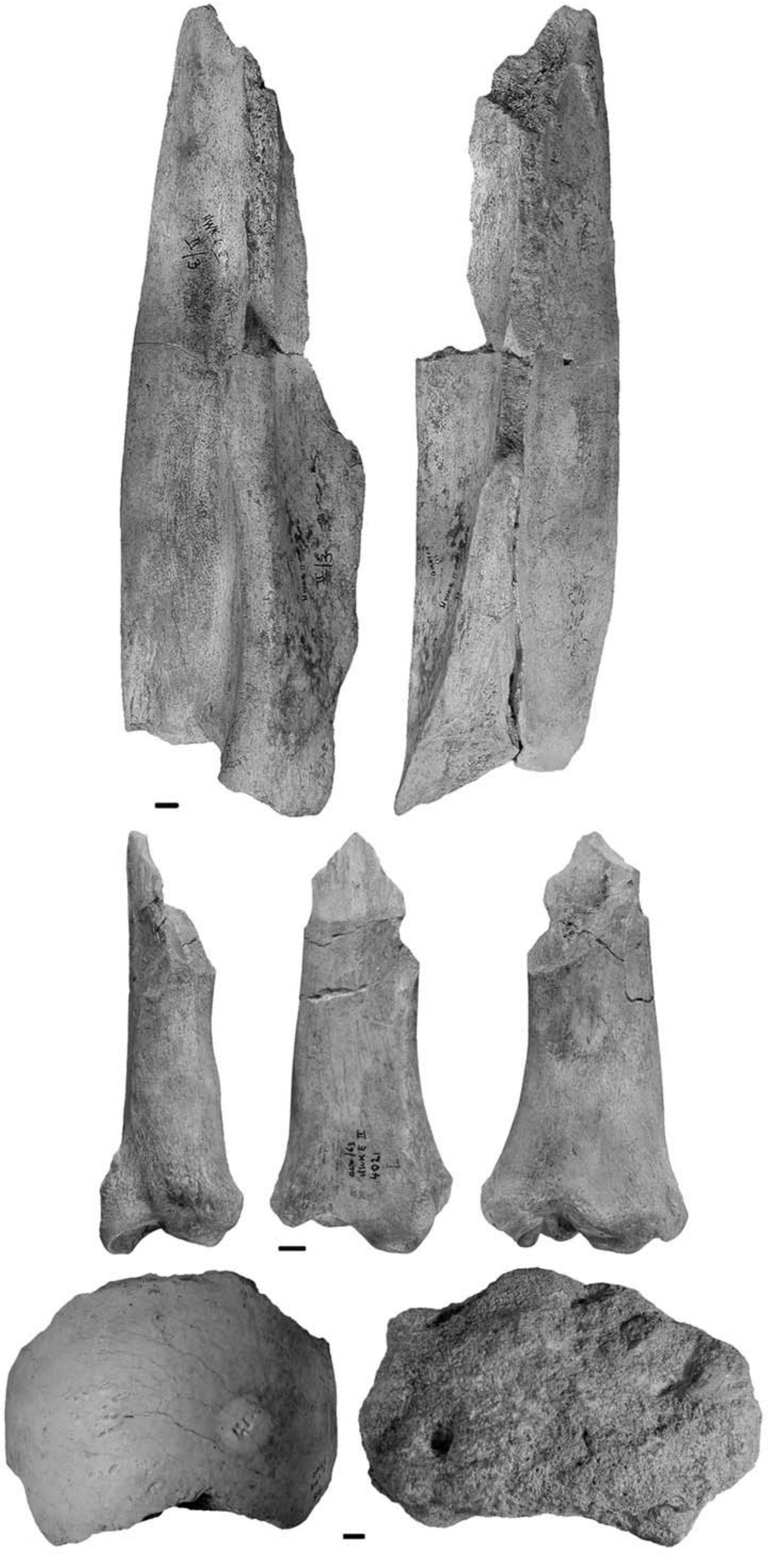

Figure 32. Olduvai bone tools proposed by Leakey, HWKEII 3b (**top**), HWKEII 4021 (**centre**) and HWKEII 866 (**bottom**). Scale bars = 1 cm.

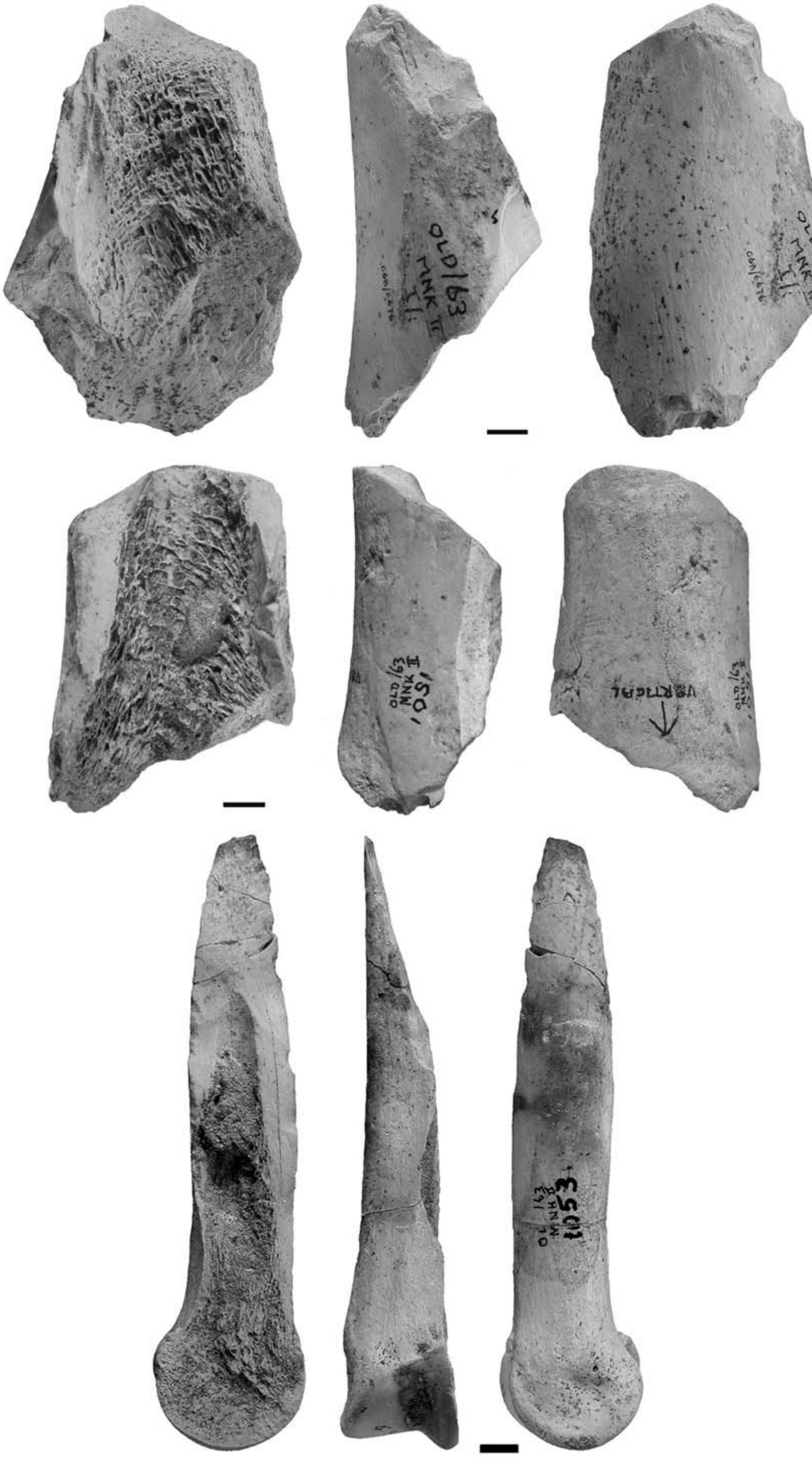

Figure 33. Olduvai bone tools proposed by Leakey and by Shipman, *MNKII 068–6676 (**top**), and by Leakey, MNKII 1051 (**centre**), MNKII 1053 **(bottom)**. Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

Figure 34. Olduvai bone tools proposed by Leakey, MNKII 1059 (**top**), MNKII 1090 (**centre**) and *MNKII 1116 (**bottom**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

Figure 35. Olduvai bone tools proposed by Leakey, *MNKII 1117 (**top**), *MNKII 1133 (**bottom**), and by Leakey and by Shipman, MNKII 1123 (**centre**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

Figure 36. Olduvai bone tools proposed by Leakey, MNKII 1269 (**top**), MNKII 1304 (**centre**), *MNKII 1496 (**bottom**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

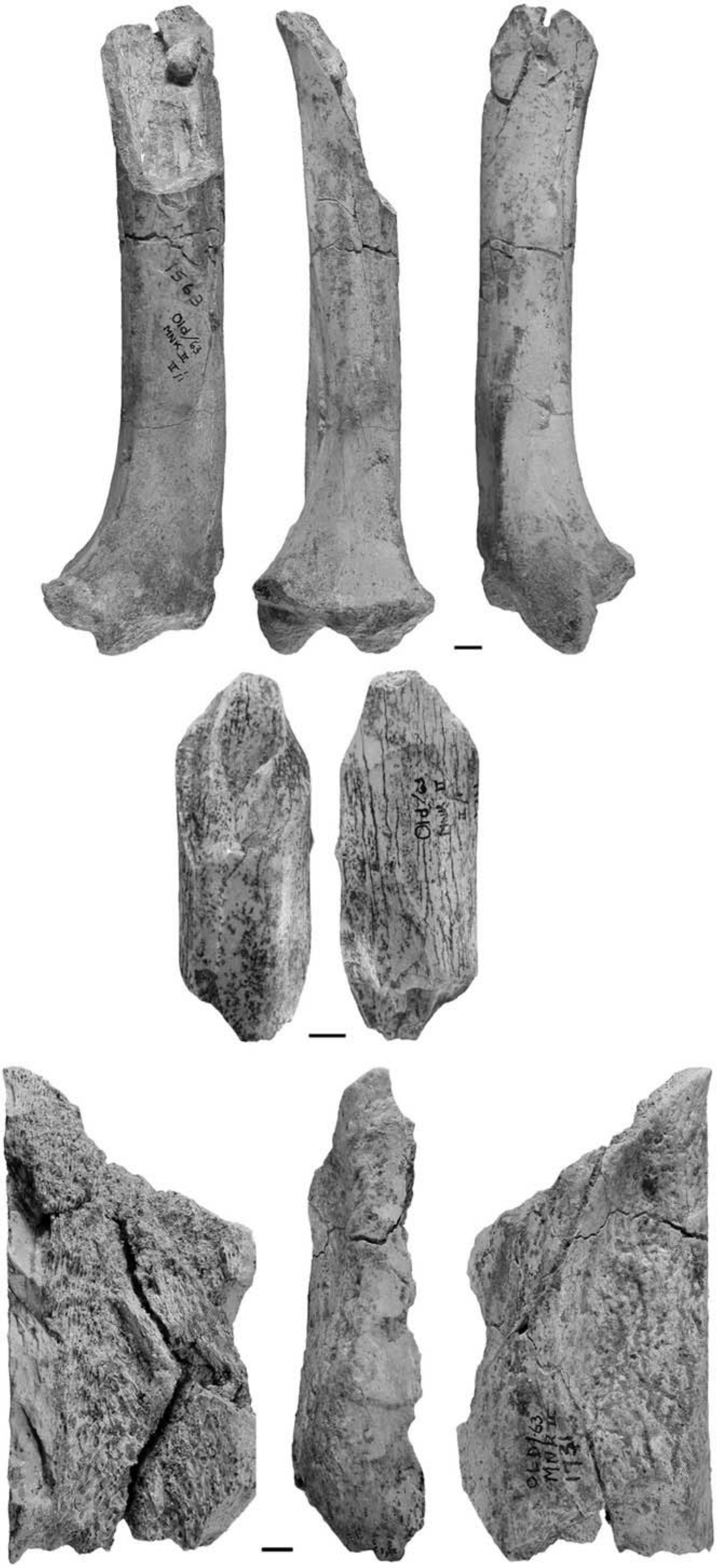

Figure 37. Olduvai bone tools proposed by Leakey, MNKII 1563 (**top**), MNKII 1711 (**centre**), and by Leakey and by Shipman, *MNKII 1731 (**bottom**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

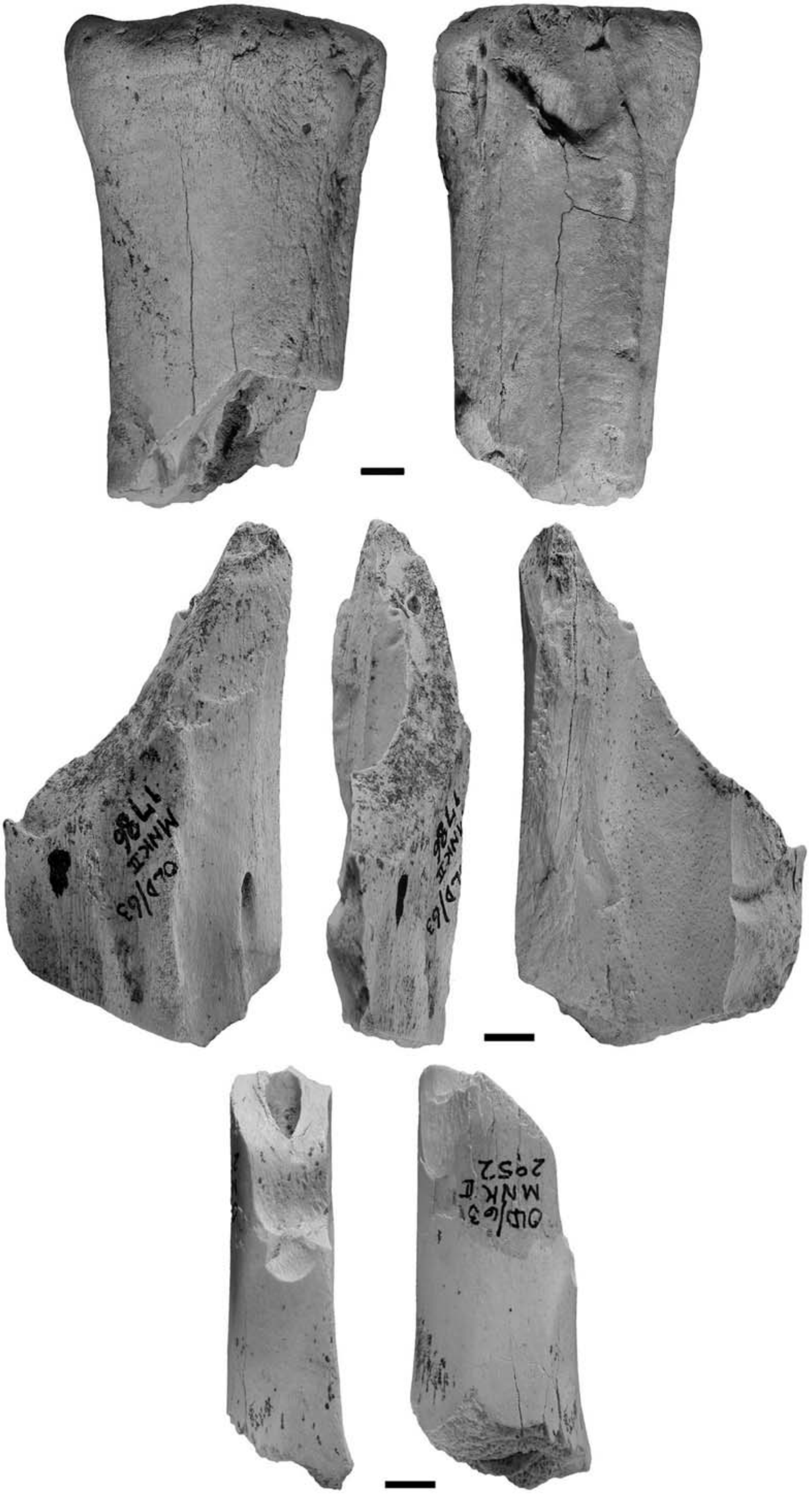

Figure 38. Olduvai bone tools proposed by Leakey, *MNKII 1786 (**centre**), MNKII 2052 (**bottom**), and by Leakey and by Shipman, *MNKII 1741 (**top**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

Figure 39. Olduvai bone tools proposed by Leakey, MNKII 2093 (**top**), MNKII 2355 (**centre**), MNKII 2360 (**bottom**). Scale bars = 1 cm.

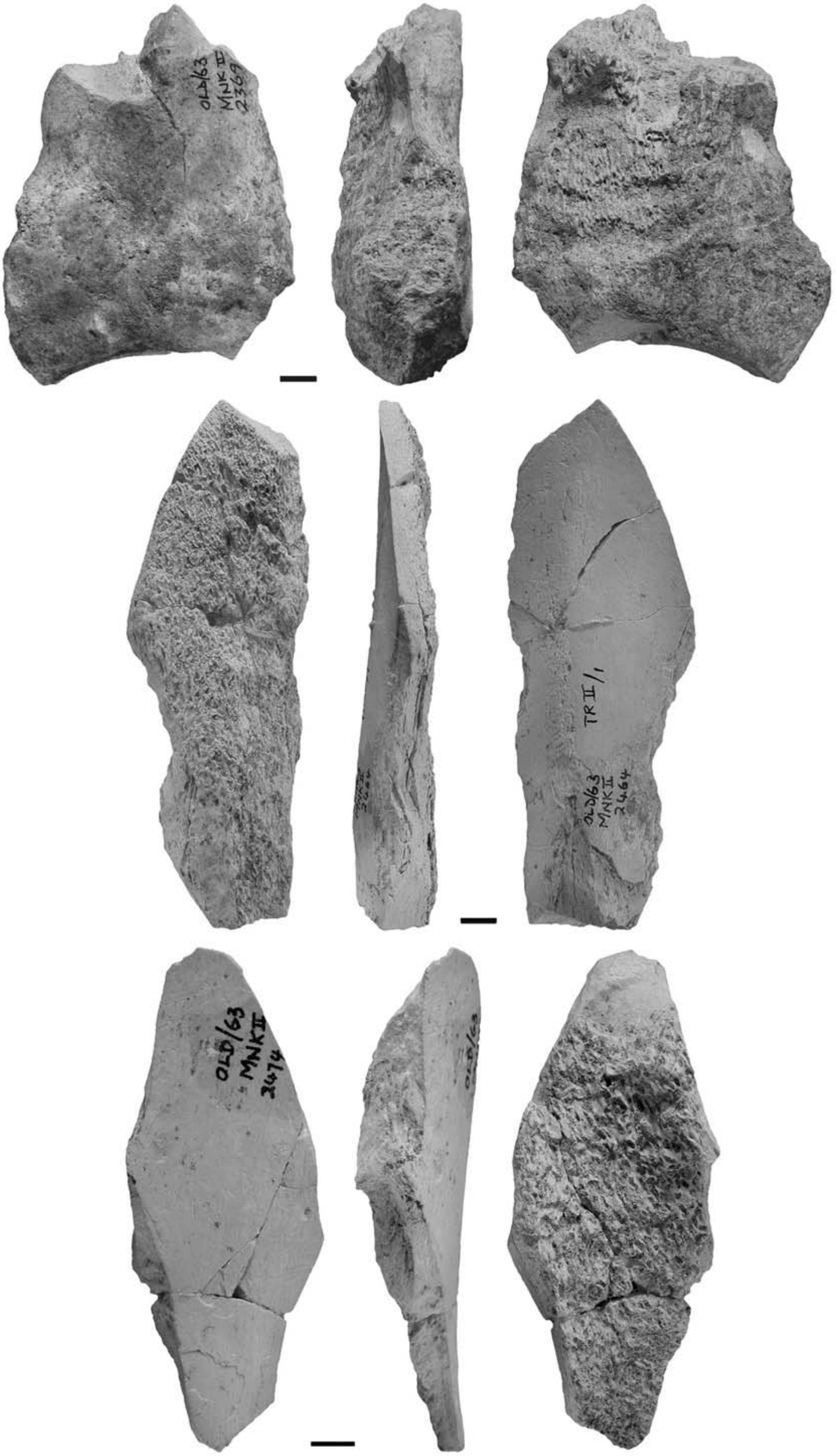

Figure 40. Olduvai bone tools proposed by Leakey, MNKII 2369 (**top**), *MNKII 2464 (**centre**), and by Leakey and by Shipman, MNKII 2474 (**bottom**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

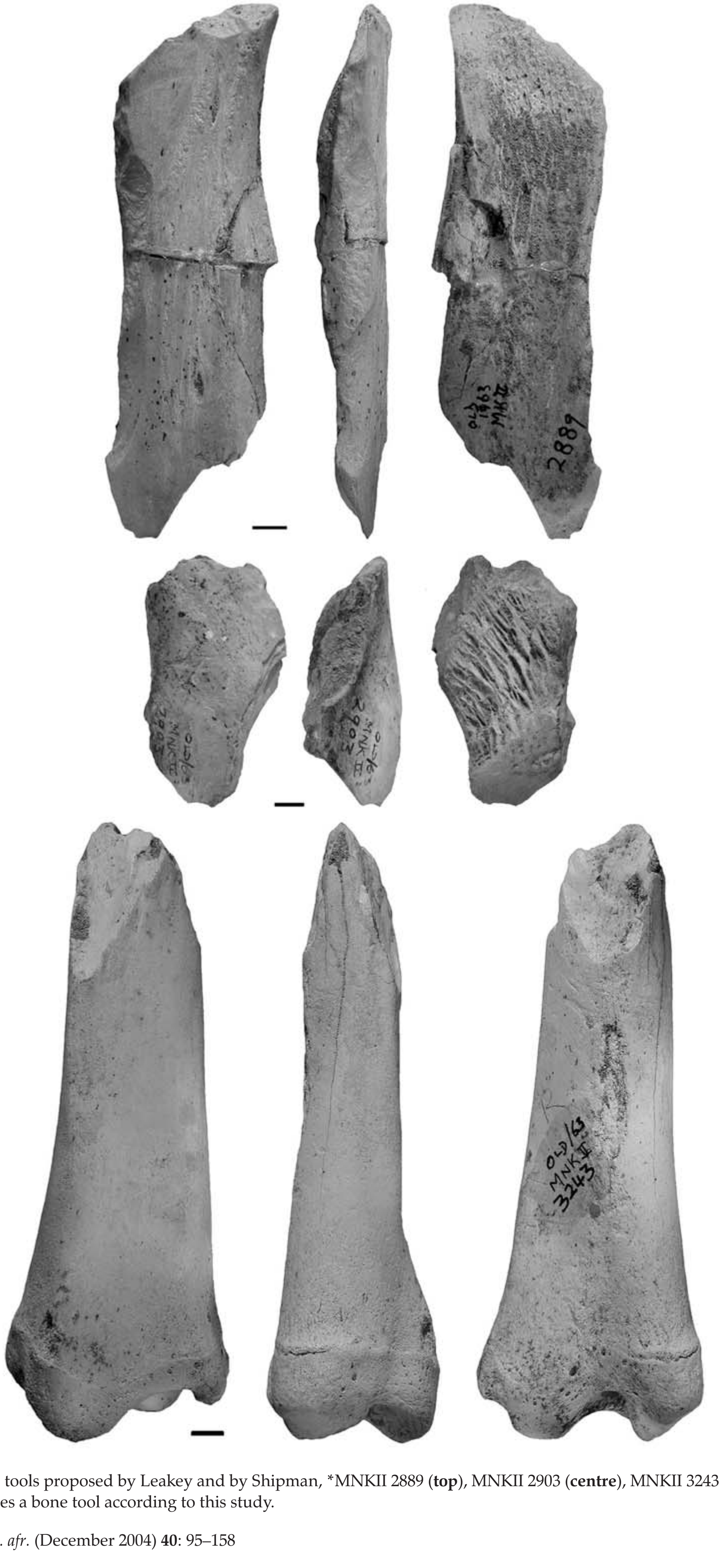

Figure 41. Olduvai bone tools proposed by Leakey and by Shipman, *MNKII 2889 (**top**), MNKII 2903 (**centre**), MNKII 3243 (**bottom**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

Figure 42. Olduvai bone tools proposed by Leakey, MNKII 3335 (**top**), *MNKII 471 (**centre**), and by Leakey and by Shipman *MNKII 475 (**bottom**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

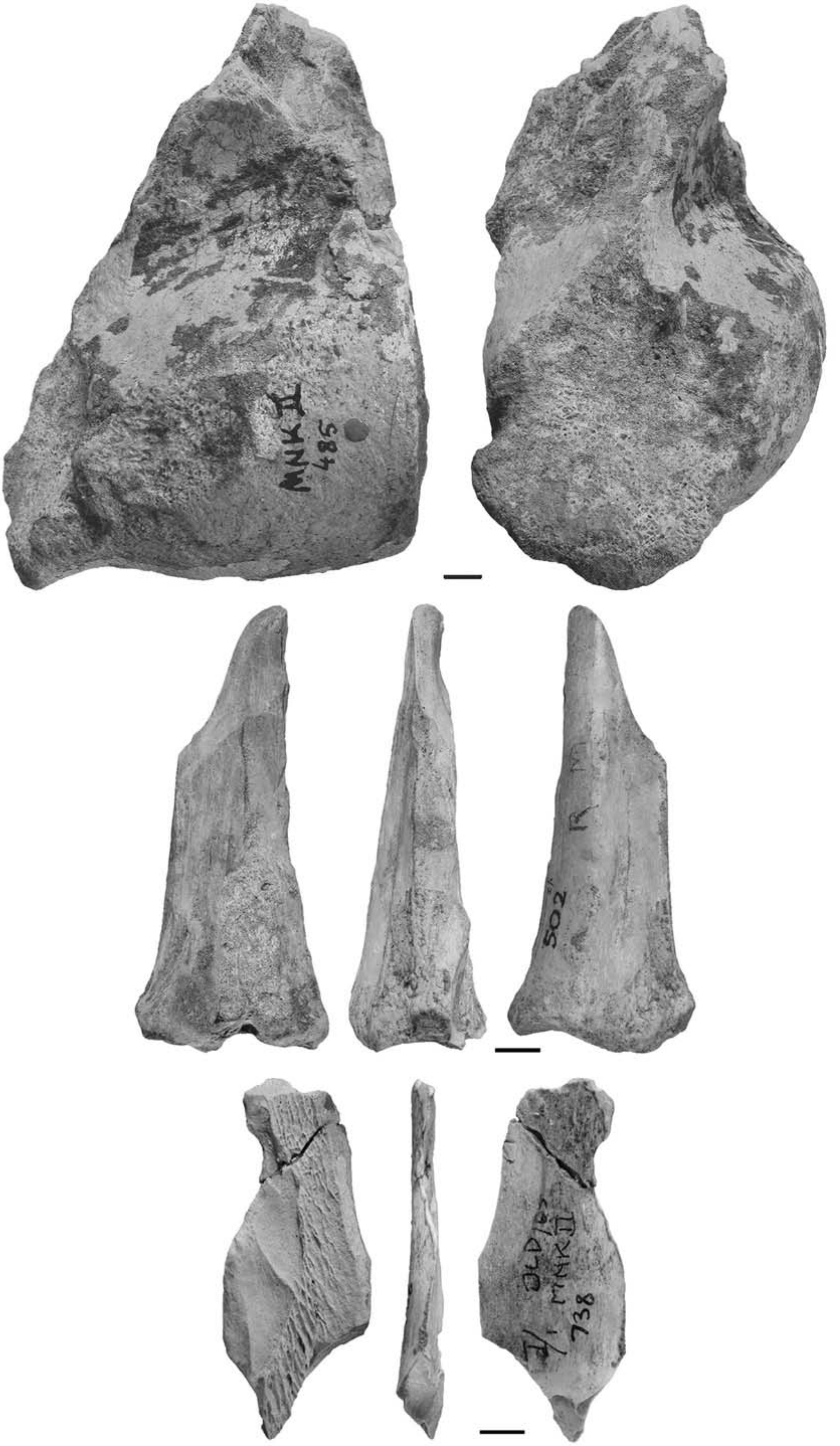

Figure 43. Olduvai bone tools proposed by Leakey, *MNKII 502 (**centre**), and by Leakey and by Shipman MNKII 485 (**top**), MNKII 738 (**bottom**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

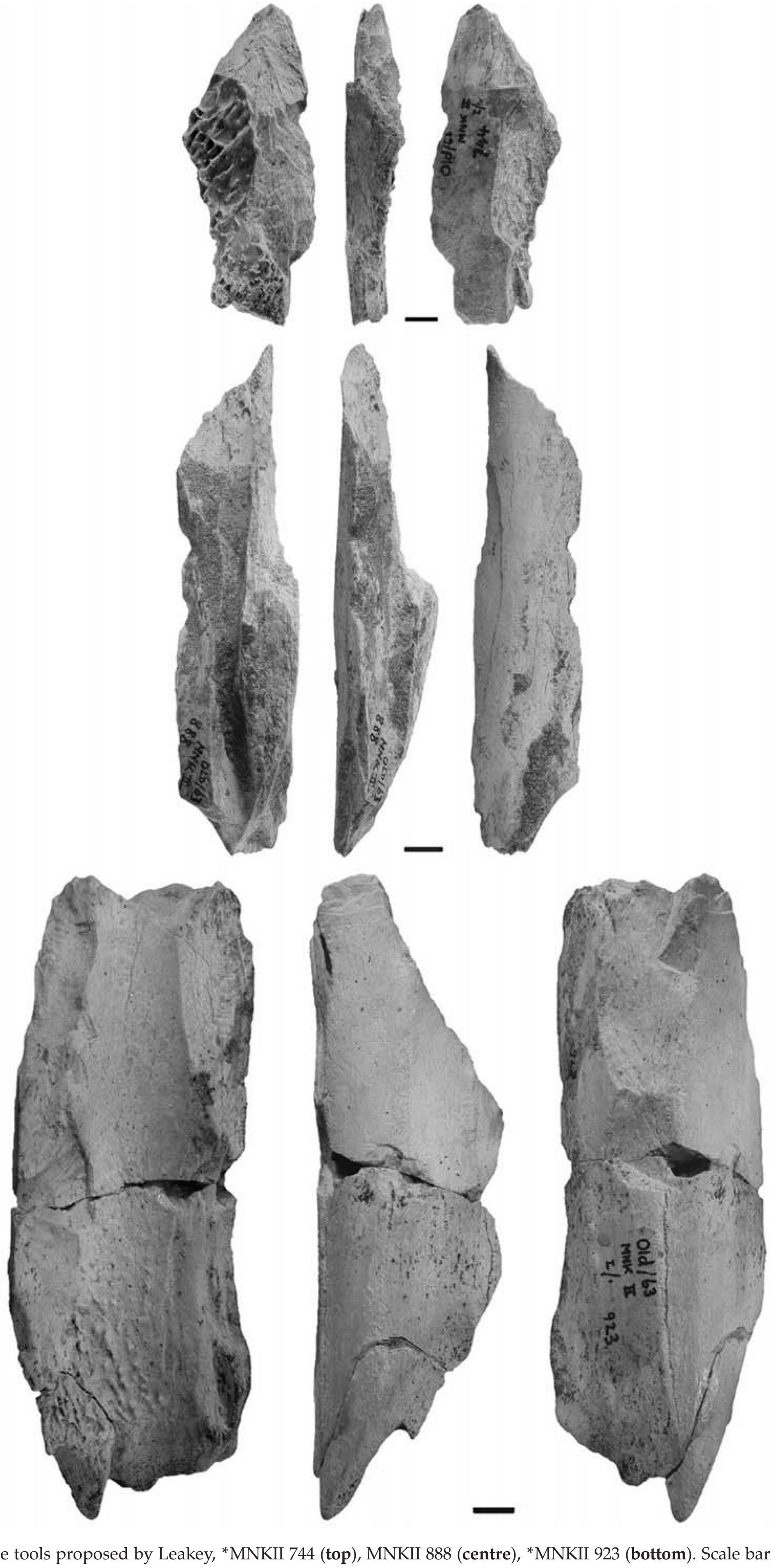

Figure 44. Olduvai bone tools proposed by Leakey, *MNKII 744 (**top**), MNKII 888 (**centre**), *MNKII 923 (**bottom**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

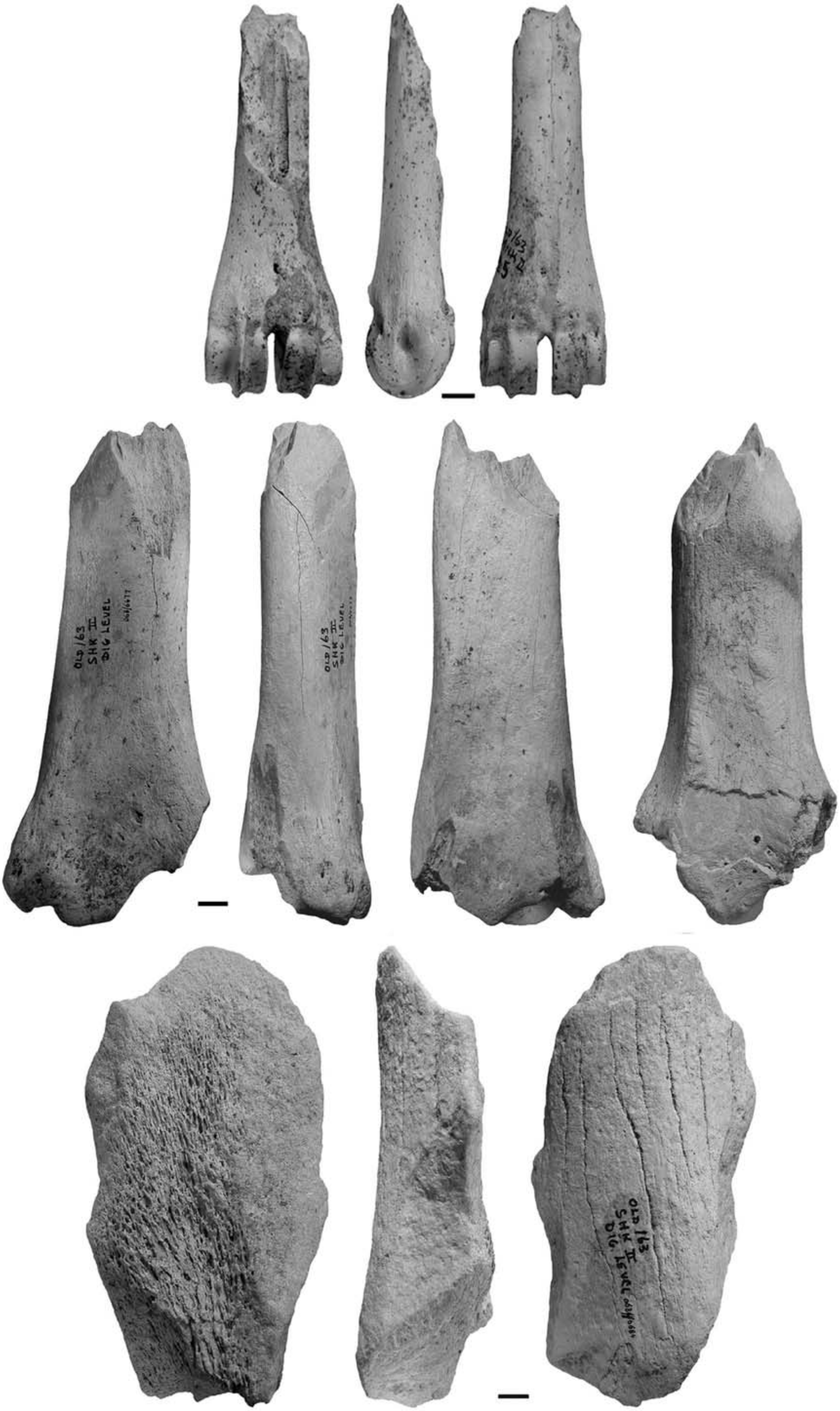

Figure 45. Olduvai bone tools proposed by Leakey, MNKII 925 (**top**), and by Leakey and by Shipman SHKII 068–6677 (**centre**), SHKII 068–6684 **(bottom)**. Scale bars = 1 cm.

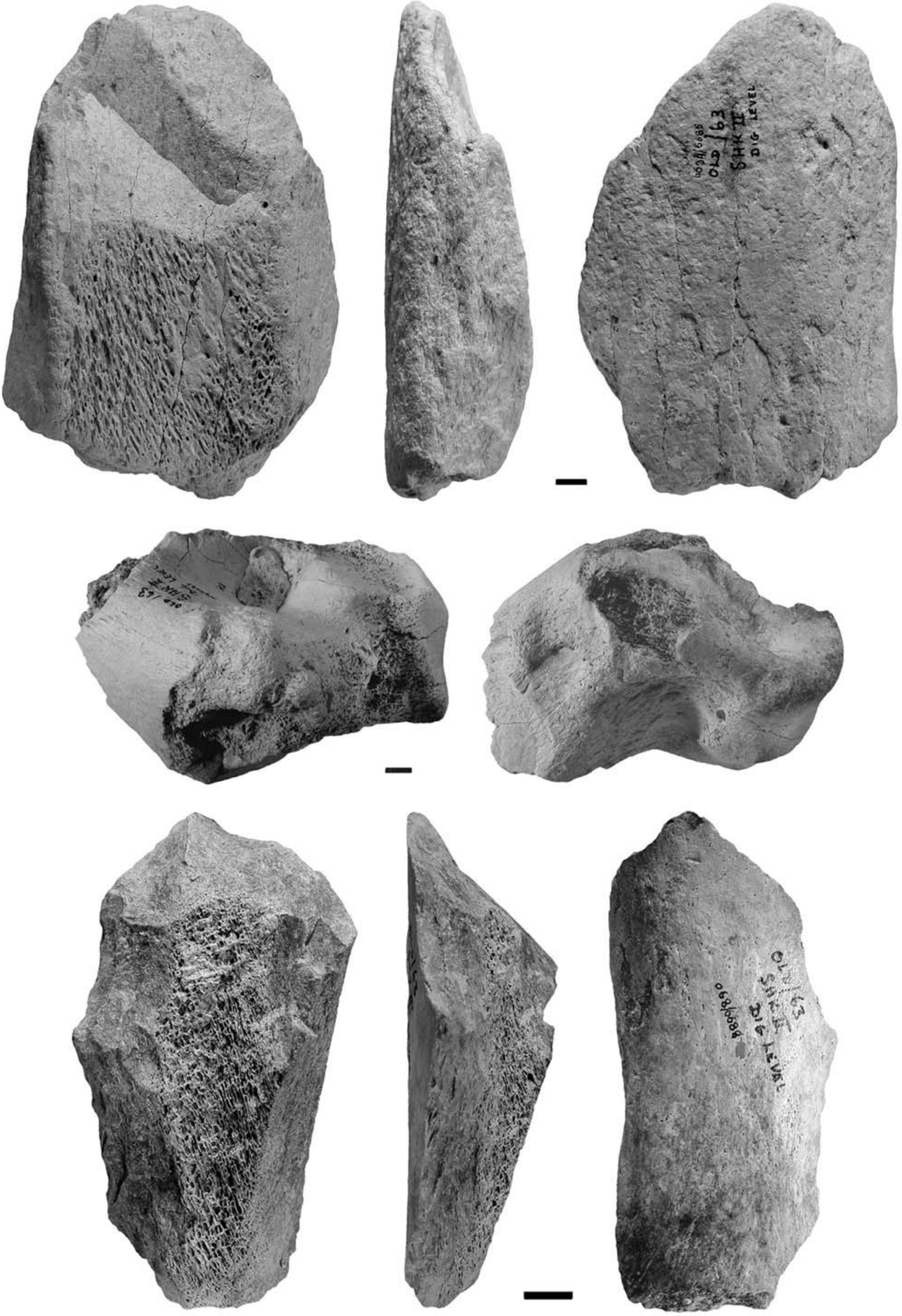

Figure 46. Olduvai bone tools proposed by Leakey, SHKII 068–6685 (**top**), and by Leakey and by Shipman SHKII 068–6687 (**centre**), *SHKII 068–6688 (**bottom**). Scale bars = 1 cm. An asterisk indicates a bone tool according to this study.

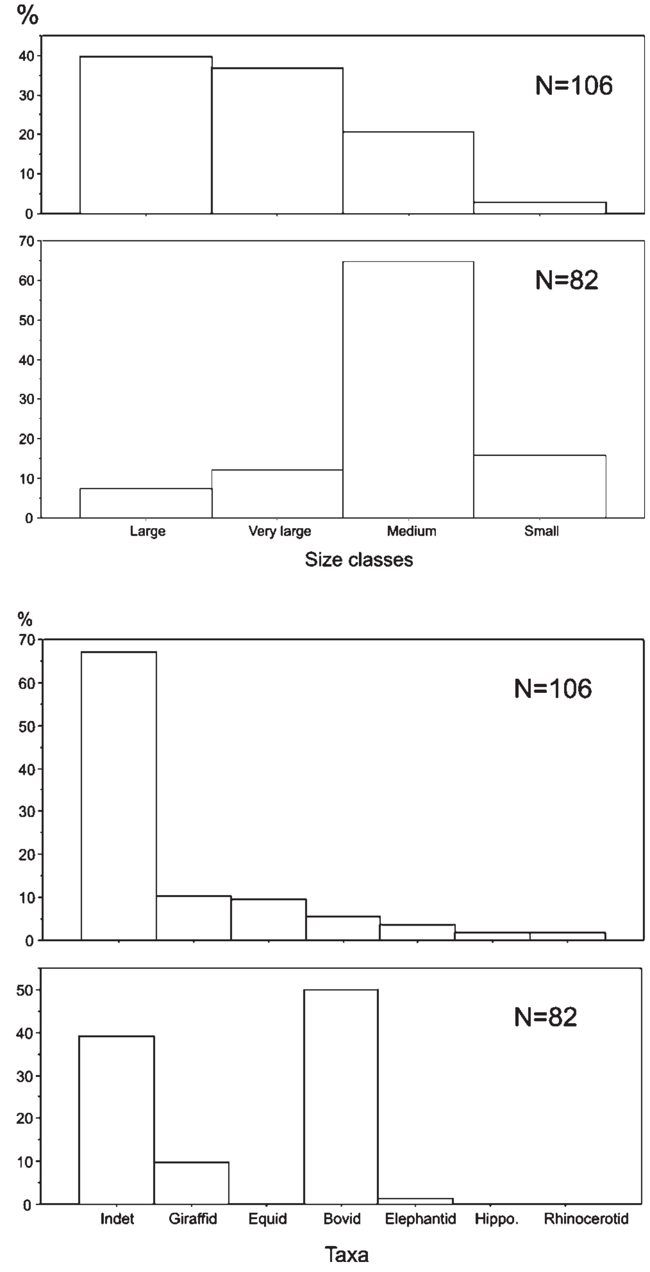

Figure 47. Proportions of mammal size classes (**top**) and taxa (**bottom**) represented in the Olduvai bone tool and comparative collections.

different from those observed on the Leakey collection, with the exception of carnivore traces and percussion marks less represented in the control sample (Table 8). The lower proportion of percussion marks in the control sample is to be expected, considering the smaller size and resistance of the original bones, which broke readily under percussion instead of recording the impact marks. The lower count for carnivore marks in the control sample may be due to specimen size, as smaller bones submitted to the action of carnivores have less chance of survival.

Removals

Bone flakes and shaft fragments described by Leakey and by Shipman as tools, record a significantly higher number of removals suggestive of intentional knapping, than do the Olduvai control sample and the experimental assemblage (Tables 7, 10 & 11). While the Leakey/Shipman collection may have up to 20 removals per piece, no more than four and eight flake scars were observed on the control sample and the experimental flakes, respectively. The Leakey/Shipman collection has an average of four removals per piece, the control sample has 1.2 removals and the experimental collection has only 0.4. In particular, the frequency distribution of the number of removals per piece reveals in the purported tools a marked bimodal trend absent in the other collections (Fig. 49). The second peak in the Leakey/Shipman distribution, composed of pieces having between five and 22 removals each, accounts for nearly half of the specimens. All these pieces come from large- to very large-sized mammals.

Removals do not occur with the same frequency on the periosteal and medullar surfaces of the pieces from the two Olduvai collections (Table 10–11). On specimens from the control sample, flake scars are four times more abundant on medullar than on periosteal surfaces, while on the Leakey/Shipman specimens, a significantly higher proportion of pieces with removals on the medullar surface are only observed on pieces with a single removal. An even more remarkable difference appears when comparing the occurrence of isolated and contiguous removals in the three collections. The Leakey/Shipman collection bears a consistent record of specimens with a considerable number of contiguous removals on both periosteal and medullar surfaces and very few pieces with multiple isolated flake scars. The other two collections have comparatively few pieces bearing contiguous removals, and in the case of the Olduvai control sample, a high proportion of pieces with single removals on the medullary aspect. The number of pieces presenting overlapping removals mimicking stepped retouch is also much higher in the Leakey/Shipman collection than in the other samples (Table 12). Interestingly, only in the Leakey/Shipman collection do a consistent number of flakes (17%) have removals on the same edge and on opposite aspects of the bone flake, creating a bifacial arrangement (Table 12). Moreover, all these pieces belong to large to very large mammal size classes. No such pieces were found in the control sample and only two (2%) among the experimen-

Table 9. Olduvai purported tools with carnivore and hominid modifications.

Carnivore traces	MNKII 1046, BKII 187, MNKII 3243, MNKII 1046, BKII 068/6680, HWKEII/3, MNKII 925, MNKII 2355, BKII 2959, MNKII 1053, BKII 068/6669, BKII 949, BKII 1053, SHKII 068/6677, MNKII 1059, FLKII 323
Cutmarks	BKII 949, BKII 068/6669, MNKII 1053, BKII 1053/315, FLKII 323, MNKII 1059, SHKII 068/6677, BKII 2959, MNKII 1046, MNKII 3243, BKII 187, BKII 068/6680, MNKII 2355, MNKII 925, HWKEII/3
Percussion marks	BKII 068/6683, BKII 949, BKII 1053/315, BKII 068/6678, BKII 068/6674, BKII 2715, BKII 1605, BKII 068/6666, FLKII 45, FLKII spit 5+, MNKII 1741, MNKII 1053, MNKII 475, MNKII 888, MNKII 1115, MNKII 1133, MNKII 1051, MNKII 1304, MNKII 1496, MNKII 502, HWKEII 4021, SHKEII 068/6681

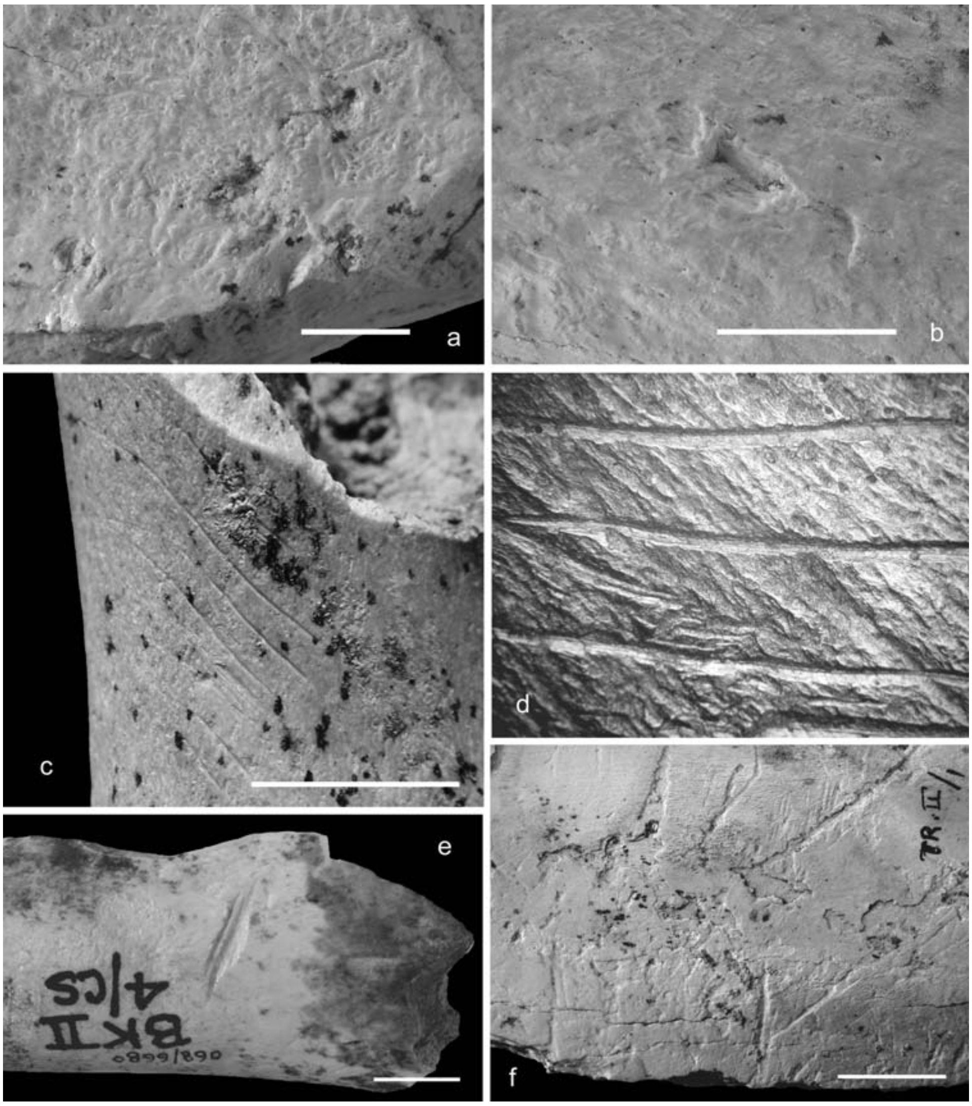

Figure 48. **a–b**, Percussion marks on Olduvai purported bone tools BKII 068/6666 (a) and MNKII 1133 (b); **c–d**, multiple cut-marks on specimen MNKII 925; **e**, cut-marks on specimen BKII 068/6680; **f**, scoring and pits on specimen MNKII 2093. Scale bars = 1 cm.

tal flakes. The location of the removals is not significantly different between the samples.

Additional noteworthy differences appear when analysing the length of the removals. Removals exceeding 40 mm are only present on the Leakey/Shipman and experimental flakes, and those of more than 80 mm occur only in the former sample (Fig. 50). Also, the large majority of the removals on the control sample are less than 10 mm in length (Fig. 50), while those of the same size constitute 40% in the Leakey/Shipman sample and less than 10%

Table 10. Number, association and location of removals on the periosteal and medullar surfaces of Olduvai shaft fragments described as tools.

No. rem.	No. flakes		Association				Location					
			Periosteal		Medullar		Periosteal			Medullar		
	Peri.	Med.	Isolated	Cont.	Isolated	Cont.	End	End + side	Side	End	End + side	Side
0	24	16	55	35	45	36	37	62	57	45	59	45
1	8	17	8	0	17	0	5	0	3	10	0	6
2	9	11	1	8	0	8	8	0	1	8	0	3
3	9	6	2	7	0	6	9	0	0	1	1	4
4	3	6	0	3	0	6	2	0	1	2	0	4
5	4	3	0	4	0	3	1	1	2	0	2	1
6	3	2	0	3	0	2	1	0	2	0	1	1
7	2	1	0	2	0	1	1	1	0	0	1	0
8	1	2	0	1	0	2	1	0	0	0	1	1
9	1	0	0	1	0	0	0	1	0	0	0	0
10	1	1	0	1	0	1	1	0	0	0	0	0
14	1	0	0	1	0	0	0	1	0	0	0	0
20	0	1	0	1	0	1	0	0	0	0	0	1

rem: removals; Peri.: periosteal; Med.: medullar; Cont: contiguous.

Table 11. Number, association and location of removals on the periosteal and medullar surfaces of a shaft fragment control sample from Olduvai.

No. rem.	No. flakes		Association				Location				
			Periosteal		Medullar		Periosteal		Medullar		
	Peri.	Med.	Isolated	Cont.	Isolated	Cont.	End	Side	End	End + side	Side
0	66	39	72	74	54	65	69	77	78	79	52
1	9	23	8	1	23	0	7	2	10	0	13
2	2	8	0	2	3	5	2	0	1	1	6
3	2	9	0	2	0	9	1	1	0	0	9
4	1	1	0	1	0	1	1	0	1	0	0

rem: removals; Peri.: periosteal; Med.: medullar; Cont: contiguous.

Table 12. Frequency of primary/secondary and monofacial/ bifacial removals on the three samples analysed.

Collection	Succession		Arrangement	
	First generation	Second generation	Monofacial	Bifacial
Experimental	34 (71%)	14 (29 %)	12	2
Olduvai control	86 (89%)	11 (11%)	81 (100%)	0
Leakey/Shipman	312 (59%)	216 (41%)	84 (83%)	17 (17%)

among the experimental flakes. One might argue from this evidence, considering the composition of the three collections, that the length of the removals is a function of the bone size. Analysis of removal size according to mammal size classes reveals, however, that those from the Leakey/Shipman collection are in all size classes significantly longer than those on the Olduvai control sample (Table 13). The high standard deviation observed on the purported tools from large and very large animals, in contrast with the low values in the control sample, is due to the fact that these pieces record a succession of large and small, often contiguous and overlapping flake scars. This is supported by the frequency distribution of the lengths of primary and secondary removals, indicating that the putative bone tools are the only sample that records a clear variation in size between first and second

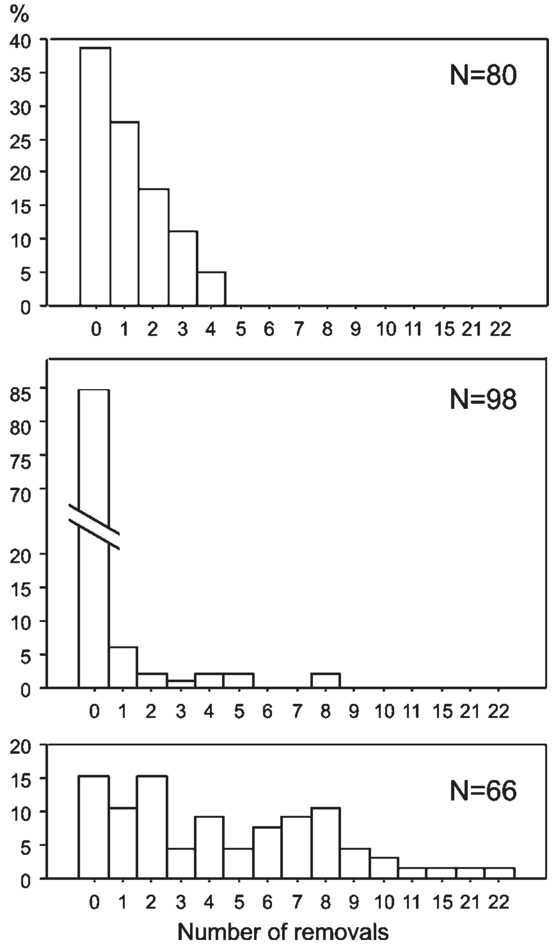

Figure 49. Frequency distribution of the number of removals per piece in the Olduvai control sample (**top**), flakes from the experimental breakage of elephant bones (**centre**), and Leakey/Shipman collection (**bottom**).

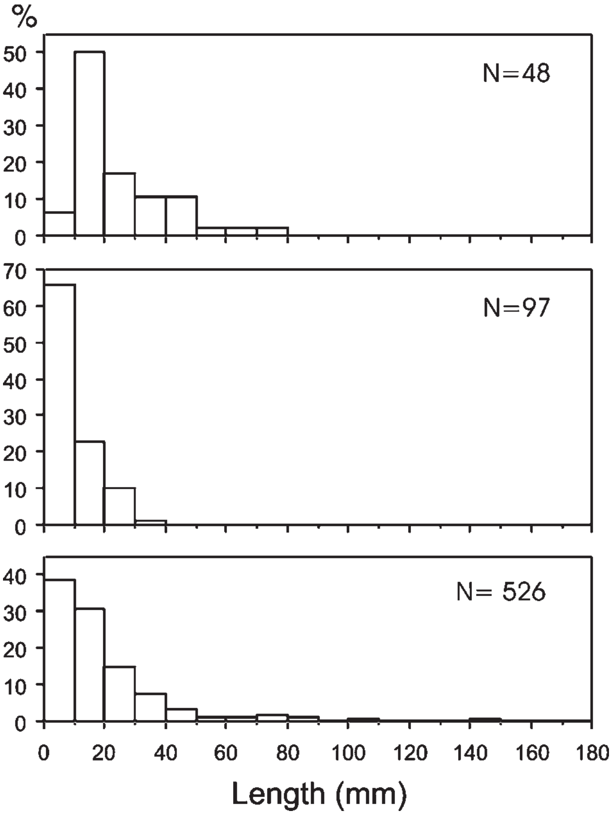

Figure 50. Length of the removals from the experimental flakes (**top**), the Olduvai control sample (**centre**), and the purported bone tools (**bottom**).

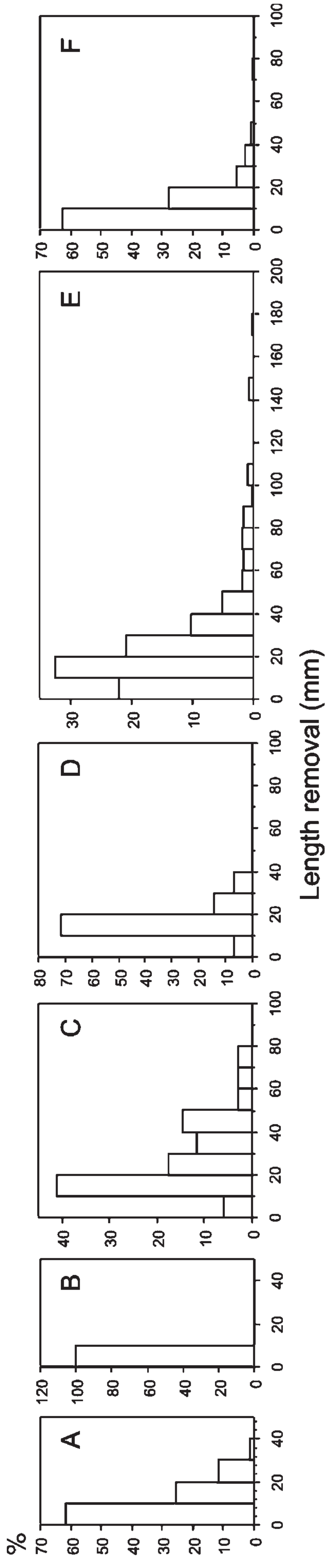

Figure 51. Length of the primary and secondary removals respectively, from the Olduvai control sample (**A–B**), experimental flakes (**C–D**), and the purported bone tools (**E–F**).

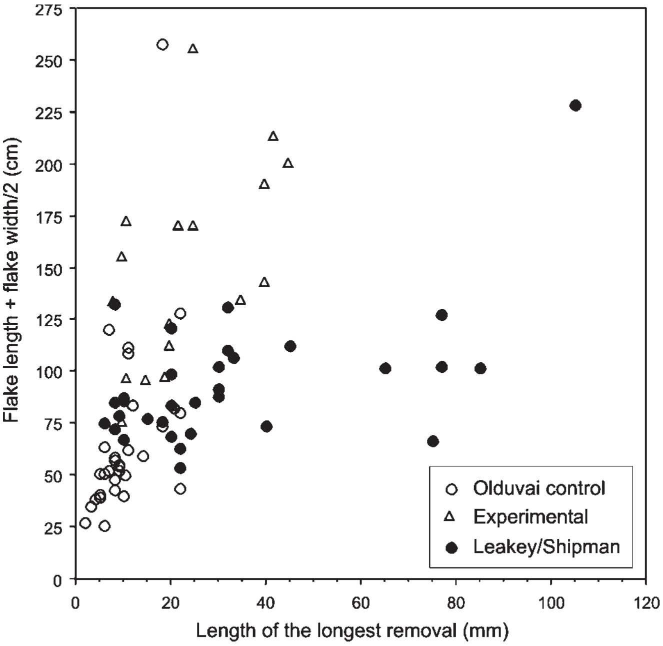

Figure 52. Correlation between the longest flake scar and the shaft fragment size index.

generation flake scars (Fig. 51). The anomalous size of the removals on the Leakey/Shipman sample is also indicated by the correlation of the longest removal with the flake size index, showing that a number of pieces from this collection have removals that exceed the size expected on the basis of the removal/size ratio observed in the other collections (Fig. 52).

According to flake removal data, we identify a reduced number of bone tools (*n*= 36) in Leakey's (1971) purported bone tool collection of 123 specimens. Shipman (1989) identified 41 of these as true bone tools, and even though we identify fewer, some of these pieces are interestingly not considered as tools by Shipman. Bone tools identified by us derive from seven sites (DK, MK, HWK East, SHK, MNK, FC West, BK and FCKII), though site FCKII is not recorded in Leakey's 1971 monograph. We concur that the majority of bone tools occur in MNK and BK, in middle-upper Bed II (Table 2).

In sum, our results seem to identify within the purported tools, a cluster of pieces that appear idiosyncratic when compared with the available non-artefactual analogues. They consist of fresh bone shaft fragments and epiphyseal pieces from large and very large mammals, bearing five or more flake scars, some of which are contiguous, with one or more anomalously invasive primary removals. Table 14 lists the 37 specimens from the Leakey collection that have more than five removals. Most of them share the features mentioned above and reveal a particularly high proportion of bifacially arranged removals, accounting for 14 of the 17 cases recorded in this collection. Importantly, they are virtually unaffected by carnivore damage. The anthropic origin of the removals on many of the specimens belonging to this sample is supported by the few pieces on which the removals are the likely result of carnivore activity because of their close proximity to typical carnivore damage (BKII 869, MNKII 2093, MNKII 2360, MNKII 2369, MNKII 3335, SHKII 068/6687). The removals on these

Table 13. Length of removals according to mammal size class.

	No. of removals			Leakey		Control sample		Experimental	
	Leakey	Control	Exp.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Very large	112	13	48	20.1	21.5	13.7	6.1	22.3	15.4
Large	111	14	0	15.8	15.8	7.7	4.7	–	–
Medium	62	28	0	11.6	9.3	7.1	3.2	–	–
Small	8	8	0	10.9	8.4	7.8	6.5	–	–

pieces may be contiguous but are rarely invasive.

Clearly, a number of these pieces are difficult to interpret as bone tools. This is certainly the case for the distal epiphyses of humeri (e.g. BKII 2382, BKII 200, MNKII 475) that do not seem to differ from similar fragments found at Olduvai and in numerous other collections.

Although bearing a striking amount of invasive contiguous removals, which could suggest their intentional shaping, some other pieces may also be explained as the outcome of bone breakage for marrow extraction (e.g. BKII 068-6668, MNKII 1133, DKI 067-4259 and perhaps HWKEII 249, MNKII 923, BKII 068-6674 and MNKII 1117, all from sites considered as occupation floors by Leakey). These flakes may have been detached as a consequence of repeated percussion made with a hammer or against an anvil, inflicted obliquely on the broken end of a shaft piece. In one specimen (MNKII 1133), these percussions were followed by a strike inflicted on the cortical bone close to the broken end, which was successful in the detachment of the flake and produced a characteristic impact notch on the medullar surface. A similar interpretation may also be proposed for a few other flakes (MNKII 1786, BKII 068-6686, MNKII 1116, MNKII 744) that present a pointed end with adjacent burin-like removals that may

Table 14. Olduvai specimens with five or more removals and a suite of features that appear to differentiate them from the remainder of the Leakey collection.

Site	Spec. No.	Size class	Body part	Bone region	Carn.	Perc.	Total rem.	Periosteal			Medullar			Bifacial	Tools after	Fig. No.
								No. rem.	Type	Loc.	No. rem.	Type	Loc.			
BKII	068/6666	VL	Humerus	Shaft	n	y	8	5	Cont.	Side	3	Cont.	Side	No	1	18
BKII	068/6668	VL	Humerus	Shaft	n	n	6	5	Cont.	E+S	1	Isol.	End	Yes	1	18
BKII	068/6670	VL	Indet.	Shaft	n	n	5	3	Cont.	End	2	Cont.	Side	No	1	19
BKII	068/6686	L	Tibia	Shaft	n	n	9	1	Isol.	End	8	Cont.	E+S	No	1	22
BKII	1938	VL	Humerus	Shaft	n	n	6	3	Cont.	End	3	Cont.	Side	No	1.2	23
BKII	200	M	Humerus	Epi.	n	n	9	4	Cont.	End	5	Cont.	End	No	1	23
BKII	201	L	Indet.	Shaft	n	n	5	3	Cont.	End	2	Cont.	End	Yes	1	24
BKII	2382	VL	Humerus	Epi.	n	n	10	1	Isol.	End	9	Cont.	End	No	1	24
BKII	2715	L	Humerus	Shaft	n	y	22	2	Isol.	Side	20	Cont.	Side	No	1	25
BKII	3155	VL	Indet.	Shaft	n	n	7	3	Con+Is.	End	4	Cont.	End	Yes	1.2	26
BKII	3385	VL	Humerus	Epi.	y	n	5	1	Isol.	End	4	Cont.	End	No	1	–
BKII	53/9 1953	VL	Indet.	Shaft	n	n	15	9	Cont.	E+S	6	Cont.	E+S	Yes	1.2	27
BKII	6674	VL	Humerus	Shaft	n	n	8	3	Cont.	End	5	Cont.	Side	No	1	–
BKII	933	VL	Indet.	Shaft	n	n	8	6	Cont.	Side	2	Isol.	Side	No	1	28
DKI	067/4259	L	Indet.	Shaft	y	n	7	7	Cont.	End	0	–	–	No	1.2	28
FCII	068/6679	VL	Indet.	Shaft	n	n	8	5	Cont.	Side	3	Cont.	E+S	Yes	1.2	29
FCKII	068/6682	L	Femur	Epi.	n	n	7	5	Cont.	End	2	Cont.	End	Yes	1	30
HWKEII	249	VL	Pelvis	Shaft	n	n	7	6	Cont.	End	1	Isol.	End	Yes	1	31
MNKII	068/6676	L	Indet.	Shaft	n	n	8	5	Cont.	End	3	Cont.	Side	Yes	1.2	33
MNKII	1116	L	Indet.	Shaft	n	n	7	3	Isol.	End	4	Cont.	Side	Yes	1	34
MNKII	1117	VL	Humerus	Shaft	n	n	6	3	Cont.	End	3	Cont.	End	No	1	35
MNKII	1133	L	Humerus	Shaft	n	y	11	10	Cont.	End	1	Isol.	End	Yes	1	35
MNKII	1140	M	Tibia	Epi.	n	n	5	3	Cont.	End	2	Cont.	End	No	1	–
MNKII	1496	M	Humerus	Shaft	n	y	5	2	Cont.	End	3	Cont.	Side	No	1	36
MNKII	1731	VL	Femur	Shaft	n	n	7	1	Isol.	End	6	Cont.	Side	No	1.2	37
MNKII	1741	VL	Metatar.	Epi.	n	y	7	4	Cont.	End	3	–	–	No	1.2	38
MNKII	1786	L	Tibia	Shaft	n	n	6	4	Cont.	End	2	Cont.	End	Yes	1	38
MNKII	2360	VL	Scapula	Blade	y	n	8	8	Con+Is.	E+S	0	–	–	No	1	–
MNKII	2464	VL	Indet.	Shaft	n	n	8	4	Cont.	Side	4	Cont.	Side	Yes	1	40
MNKII	2889	M	Tibia	Shaft	n	n	7	7	Cont.	E+S	0	–	–	No	1.2	41
MNKII	471	VL	Humerus	Shaft	n	n	8	0	–	–	8	Cont.	Side	No	1	42
MNKII	475	VL	Humerus	Shaft	n	y	9	8	Cont.	End	1	Isol.	End	No	1.2	42
MNKII	502	M	Metapod.	Shaft	n	y	6	1	Isol.	Side	5	Cont.	E+S	No	1	43
MNKII	744	L	Indet.	Shaft	n	n	10	6	Cont.	Side	4	Cont.	Side	No	1	44
MNKII	923	L	Tibia	Shaft	n	n	9	4	Cont.	End	5	Cont.	E+S	Yes	1	44
SHKII	068/6688	L	Indet.	Shaft	n	n	10	0	–	–	10	Cont.	E+S	No	1.2	46

Tools after Leakey (1) and Shipman (2).
Spec. no: specimen number; Carn: carnivore; Perc: percussion marks; rem: removals; No. rem: number of removals; Loc: location; Fig. no: figure number; VL: very large; L: large; M: medium; Indet: indeterminate; Epi: epiphysis n: no; y: yes; Cont: contiguous; Isol: isolated; Con + Is: contiguous and isolated; E + S: end and side.

Figure 53. Distal tibiae (SHKII 068–6677, MNKII 3243, HWKEII 4021, FCII 803, FCKII 068–6682) interpreted by Leakey as tools, showing centripetal removals at the broken end of the shaft.

result from repeated strikes to the broken end of a shaft, as with the pieces mentioned above.

That this technique was employed at Olduvai is evidenced by the presence of several distal tibiae (SHKII 068-6677, MNKII 3243, HWKEII 4021, FCII 803, FCKII 068-6682 and perhaps BKII 068-6670) interpreted by Leakey as tools, which show centripetal removals on fresh bone at the broken end of the shaft, with the likely intention of reducing the shaft length to access the marrow (Fig. 53). It is also noteworthy that the single piece (Fig. 14c) from the experimental breakage of elephant bone, which has a pointed tip with similar removals, derives from a limb bone struck against a rock. This seems to confirm the kinetic mechanism we have proposed for the detachment of these flakes. One may argue that marrow could be extracted with less effort by using a probe, and that both the distal tibiae and the flakes described above must have been knapped with the intention of using them as tools. This explanation fits particularly well the distal epiphysis of a giraffid tibia showing a large number of invasive centripetal removals around an exceedingly small marrow cavity (Fig. 54). Although we have no basis on which to favour one of these two hypotheses, which moreover, are not mutually exclusive, it would appear that this flaking technique is peculiar to bone from large animals at Olduvai, as no flakes with similar adjacent removals are found in the control sample, mostly composed of bones from smaller animals.

A flake with a pointed end and burin-like removals (BKII 201, Fig. 24), although similar to those discussed above, represents a special case in that its tip shows a marked macroscopic rounding in contrast to the unaltered

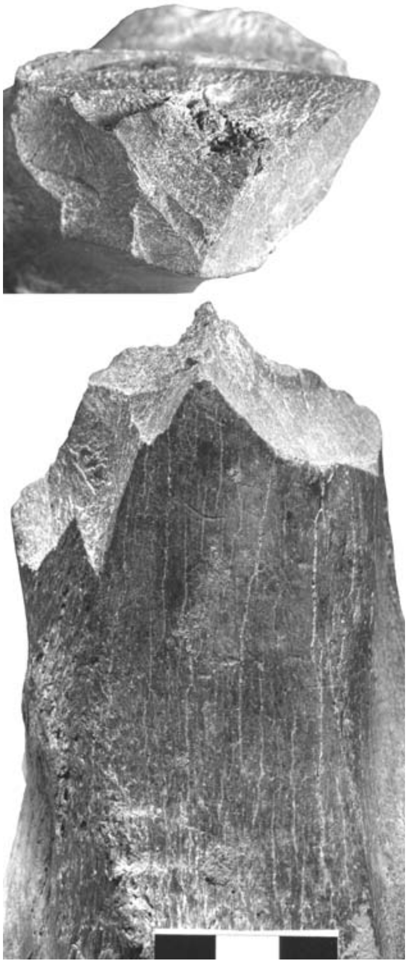

Figure 54. Distal epiphysis of a giraffid tibia with numerous invasive centripetal removals (FCKII 068–6682).

appearance of the remainder of the piece. This is the only specimen in the Leakey collection presenting a clear association of localized rounding with removals. This wear could not have been produced by percussion of the tip, as no evidence of battering is seen at microscopic scale in this area (Fig. 2o), making this piece a good candidate for having been used as a tool. The BKII site is however a reworked channel stream deposit, which may account for the anomalous rounding of the tip.

Other pieces are difficult to interpret as the mere by-product of butchering activities. In some specimens (MNKII 1731, MNKII 471, BKII 2715, the two sites with the highest concentration of bone tools according to Leakey, Shipman and this study), contiguous removals occur along both edges of the shaft fragment on the medullar aspect. The detachment of these flake scars seems to have taken place subsequent to the detachment of the shaft piece from the bone, which is inconsistent with marrow extraction. A large elephant flake (BKII 1938, Fig. 23) shows a continuous sequence of removals on its medullar side, which postdates the detachment of the flake; this continuous sequence is not seen on our experimental breakage pieces. A stronger case can be made for a smaller piece (SHKII 068-6688, Fig. 46) presenting a multiple-stepped, markedly invasive suite of removals on one side of the medullar edge, which postdates the detachment of the flake. Invasive bifacial removals associated with diagnostic percussion marks and a percussion notch are recorded on specimen BKII 068-6666 (Fig. 18). While the flake scars on the medullar aspect, near to the percussion notch, may be a function of the blow, those on the opposite edge, occurring bifacially, and made after the detachment of the piece, can hardly be explained in these terms. Two large elephant flakes deserve special attention; FCII 068-6679 (Fig. 29) and BKII 1953 or 53-9 (Fig. 27). The first, described by Leakey and by Shipman as a biface, bears on the periosteal aspect five contiguous removals that occur on a surface fracture, which indicates that the resulting flakes must have been removed after the detachment of the blank from the elephant bone. The second piece presents on both faces contiguous bifacial removals that appear particularly invasive on the periosteal surface at one end. Removals on the last two pieces are of dimensions considerably longer than those on elephant flakes resulting from experimental breakage. A proximal epiphysis of a giraffid metatarsal (MNKII 1741, Fig. 38) shows on its medial aspect along the edge of the articular surface, contiguous removals resulting from percussions applied to the articular surface, as evidenced by percussion marks close to the margin. The opposite end has a smoothed edge and one removal. The location of these modifications is compatible with an interpretation of this piece as a wedge.

DISCUSSION

There are two means by which to establish the artefactual nature of potential bone tools showing ambiguous traces of manufacture and use. The first entails the documentation of possible evidence of utilization and the demonstration that the recorded modifications, if interpreted as resulting from use, cannot be the outcome of other taphonomic processes. Apart from two pieces bearing traces of use as hammers, and a probable wedge, as well as a flake with a macroscopically worn tip, the remainder of the Olduvai purported bone tools do not seem to provide unambiguous evidence of utilization. Comparative microscopic analysis of different areas of the purported Olduvai tools, and of the edges of bone pieces from the rest of the bone assemblage (control sample), suggests that possible modifications due to utilization are indistinguishable from features attributed to post-depositional abrasion. This conclusion is reached after a systematic microscopic survey of the purported bone tools and control sample from Olduvai. Experimental and comparative non-human modified bone collections involving optical and scanning electron microscopic inspection of hundreds of specimens were similarly surveyed. Additionally, further visual comparison and the recording of features on a comparable amount of SEM micrographs were conducted. We cannot exclude the possibility that similar research by Shipman has made her more adept than we are in the identification of anthropic use-wear, as distinct from other causes. If this is the case, however, one has to acknowledge that her criteria for making this distinction and differentiating between task-specific tools are not clear-cut. Robust criteria are essential if inferences from this type of archaeological evidence are to be made, accepted by a scientific community, and become shared knowledge reinforced by repeatable results. Future analyses of the identification of anthropic use-wear should include the quantification of possible worn areas and the development of appropriate analogues. At present, the SEM is perfectly suited to documenting microscopic features; however, if it is the only diagnostic tool used, it may provide deceptive results for this site, in that gentle, mechanical sedimentary abrasion appears to have affected most of, if not the entire Olduvai assemblage, overprinting potential evidence of use-wear.

It is noteworthy that experimentally used bone tools show that tasks involving a high degree of mechanical abrasion, such as digging in soil or working hide with sand, produce distinct localized macroscopic modifications on the active zone of the tool. Considering the excellent state of preservation of the more probable Olduvai tools, one would expect that the presence of use-wear generated by these aggressive tasks should be easily detectable on the edges of tools. With the possible exception of two pieces (BKII 201, Fig. 24; MNKII 1741, Fig. 38), no evidence of localized macro-wear is observed on the probable tools. This suggests that they may have been used in activities such as butchering, which does not significantly alter the tool edge.

The second means by which to identify ambiguous bone tools is through the recognition of intentional modifications for the purpose of shaping the artefact, and the demonstration that such modifications cannot be ascribed to natural agents, or be the by-product of other subsistence activities. The purpose of Shipman's comparison between possible bone tools and the remainder of the Olduvai assemblage, was not to identify bone tools, but to identify differences between pieces she had previously selected as bone tools, based on the presence or absence of microscopic traces of utilization. Her objective was to characterize hominid preferences for certain bone types. Since our microscopic results challenged her findings, our comparison between purported tools and non-tools had a different objective, namely to contrast the occurrence of taphonomic features and potential traces of manufacture in the Leakey bone tool collection, the Olduvai control sample, and the experimental bone breakage collection, with the objective of isolating an idiosyncratic population of specimens, for which a robust argument could be made for their identification as tools.

Although it is difficult to formally demonstrate that some of the bones from the Leakey collection were intentionally flaked, we believe that our results strengthen this interpretation for a number of the specimens. For the first time, their artefactual nature was assessed using a step-by-step analysis involving different types of variables. This highlighted to what degree each of these pieces bears features interpretable as evidence of intentional shaping.

Villa & Bartram (1996) report on bones of medium- to large-size herbivores from the Pleistocene hyaena den of Bois Roche in France, bearing continuous scars that in some cases mimic scaling retouch. They correctly caution against the interpretation of flaked bones as evidence of bone shaping without the support of contextual and taphonomic analysis of the bone assemblage. A carnivore origin for the flake scars on the more convincing Olduvai bone tools cannot be advocated for a number of reasons. Almost all of the Bois Roche 'flaked' bones show clear signs of hyaena damage in the form of heavy gnawing of articular ends, and pitting and scoring on shafts, features that are rare at Olduvai and virtually absent on the specimens interpreted as tools. Instead, the majority of these pieces record diagnostic stone-induced percussion marks, in a number of cases clearly associated with flake scars. Additionally, pseudo-retouch at Bois Roche is small relative to bone size and does not invade the surface of bones from large mammals by more than 15 mm on the pieces illustrated by Villa and Bartram. This is in stark contrast to the more invasive removals recorded on the Olduvai bone tools. Finally, if carnivores were responsible for the production of flake scars at Olduvai, we should find the same number and proportion of contiguous removals in the Olduvai control sample pertaining to bone from medium- to large-size mammals, as those recorded on the bone tool collection, which is not the case.

In sum, our results indicate that Mary Leakey was correct in isolating a collection of bones, that in her opinion, looked different from the others emerging at Olduvai, and in proposing their interpretation as tools. This was mainly intuitive, relying on morphological similarities between flake scars on stone and putative bone tools. Our results show that many pieces comprising her original collection do not differ significantly from the control sample, or may be similarly interpreted as intentionally-shaped tools, or the result of marrow extraction. We also identify a reduced number of specimens, based on flake removal data (Table 14) that confirm her contention that the bones were tools used by hominids. In order to differentiate between marrow extraction and intentional shaping, future research will focus on the experimental breakage and knapping of extremely fresh bone from very large mammals. Recorded differences in the morphology of the flake scars produced on experimentally-broken elephant bones suggest that those on Olduvai specimens were produced immediately after the animals' death. The breakage of large bone in the same condition can provide an appropriate analogue by which to gather more informed inferences on early bone tool use by East African hominids. A reassessment of the tusk fragments interpreted as tools also needs to be conducted, and analogues compiled to verify the anthropic nature of potential signs of use and manufacture.

An interesting aspect of our results lies in the stratigraphic occurrence of the pieces we are inclined to interpret as bone tools. While for Leakey and Shipman bone tools are present in all beds, we identify, with one possible exception, bone tools only in Bed II (Table 2). This suggests modification of bone fragments by knapping is not a behaviour associated with the Oldowan, but with the more developed phases of this technological tradition (Developed Oldowan B) and/or the Early Acheulean. This observation may have implications for the identification of the maker of these tools. Knapped bone tools appear more systematically, according to our results, in coincidence with the appearance of remains of *H. erectus* in middle and upper Bed II. The presence in a Bed II site of an intentionally knapped bone hand axe (FCII 068-6679, Fig. 29) constitutes supplementary evidence that *H. erectus* was responsible for at least a part of these bone tools.

The alternative hypothesis is that the use of this raw material represents an innovation within a cultural tradition, developed by one or more pre-existing hominin taxa. We favour for a number of reasons the first hypothesis. The relatively low number of bone tools found at Olduvai compared to stone tools is not due to taphonomic reasons, which indicates that modification by knapping of this raw material was occasional and can be interpreted as an extension of motions applied to stone. The size of the mammals involved, and the freshness of the bone used, suggests this extension may have been practiced to facilitate the butchering of large animals, perhaps on occasions when suitable raw material was not immediately available, or could not be transported to the butchering site before the arrival of competitors. Since the production of this type of tool pertains more to the domain of expedient adaptation than to technological innovation (*sensu stricto*), and considering that instances of large mammal butchering are recorded at Bed I sites, one may expect to find occurrences of the same practice in the lower levels, but this is not the case.

The reason may lie in the neuro-motor abilities of various East Africa hominin taxa, enabling some or all of them to knap stone, but only few to effectively knap bone, or do it in a way that has left detectable removals. Though limited, and not made on very fresh bone, knapping experiments conducted in the framework of this study confirm what was known from previous experiments (Bonnichsen 1979; Stanford *et al.* 1981; Haynes 1991; Vincent 1993; Peretto *et al.* 1996), that particular skills are required to produce contiguous invasive removals on long bone shaft fragments. This is due to the elastic and anisotropic nature of bone matter, which obliges the knapper to develop specific adaptations in the strength and control of the blow.

Hovers (2001), notes that both physical and mental capacities are factors that must be considered when inferring knapping skills from archaeological finds. On the one hand, anatomical characteristics dictate the dexterity of a stone tool maker and the ability to manipulate various raw materials in applying the correct force and direction of blows during the reduction process. On the other hand, technical knowledge, or the cognition necessary to implement a mode of tool production (Roche 2000), sets the objectives of the action. Knapping skills may therefore be hampered by limitations in one or both of these broadly defined domains.

Chimps in the wild do not knap stone. Cracking nuts can occasionally produce irregular flakes due to the breakage of the stone hammers (Mercader *et al.* 2002) but the resulting blanks are significantly different from those found at Oldowan sites. Although showing some skills in knapping activities, bonobos trained in captivity do not seem to be able to reach the level of control required to produce Oldowan tools, and even less so Developed Oldowan or Early Acheulean tools (Toth *et al.* 1993). In light of the cognitive competence shown by these animals in other domains, and the well-known strength of their muscles, these restrictions must be attributed to differences in neuro-physiology and anatomy, rather than cognition or strength.

Whether australopithecines were anatomically capable of stone knapping, and if so, which species had these abilities, is debatable (e.g. Susman 1991, 1998; Marzke 1997). The date for the oldest occurrence of stone tools in East Africa (2.6 Mya), which slightly predates the oldest evidence for early *Homo* (Semaw *et al.* 2003), indicates australopithecines could have been be the authors of these early knapping traditions. It does not demonstrate, if this was indeed the case, that australopithecines could extend such abilities to bone matter. Early *Homo* instead appears to have had many, if not all the specific elements of precision grip necessary for habitual tool-making (Marzke 1997). It is possible that these features enabled this hominid to efficiently (albeit occasionally) knap bone, a material that for others was difficult to modify using these motions.

Our identification of ground horn cores at southern African sites shows that the barrier was not a cognitive one, as we see these hominids develop techniques specifically conceived to modify bone in a different cultural and environmental context.

CONCLUSION

We do not consider the results presented here as the last word on the early use of bone tools. In spite of our efforts to tackle the problem from a multi-angled perspective, the definitive identification of flaked bone tools remains a tricky endeavour for a number of specimens. However, evidence gathered in the framework of this study, indicates that bone tool use is attested at different Olduvai localities between 2.1 and 1.15 Mya. It consists of complete bones used as hammers, long bone shaft fragments intentionally shaped by knapping, and possible wedges. This evidence contrasts sharply with findings from a number of contemporaneous South African sites. The use of bone at Olduvai involves large to very large mammals, is confined to limb elements that include an astragalus and patella, applies to very fresh pieces, adopts motions similar to those used for knapping stone, appears to be expedient and occasional, concerns multiple tasks, and is probably restricted to large mammal carcass processing. South African bone tools found at early hominid sites derive from medium-size bovids, are made almost exclusively of weathered limb bone shaft fragments and horn cores, are occasionally shaped by grinding – a technique peculiar to this raw material, and were systematically used in digging activities that probably involved termite or tuber extraction.

One may argue that these discrepancies are due to the different nature of the sites preserving the faunal remains, and that bone tools similar to those from Olduvai may have been used by South African hominids at sites located far from the catchment basins that preserve the bone digging tools. However, this hypothesis is contradicted for Olduvai, considering the good state of preservation of the faunal assemblage and the absence of bone digging implements at this site. We therefore conclude that the remarkable behavioural differences recorded between these two regions indicate that we are dealing with different subsistence strategies, suggesting distinct cultural traditions. Whether these can be interpreted as the expression of regional variants in the adaptation of a single hominid species, or the product of different species, if not genera, is hard to tell at this stage. The emergence of bone tool utilization in both regions is not coincidental with the emergence of the genus *Homo,* and the time span for which bone tools were used, ends with the extinction of the robust australopithecines. This suggests, in light of the virtual absence of bone tools in the African Acheulean and early Middle Stone Age, that early bone tool industries do not represent, as often postulated in the past, a first step in a process of increasing sophistication, the beginning of which has been seen as the behavioural counterpart of the emergence of our genus. The hand axe morphology of one of the flaked bone tools from Olduvai (FCII 068-6679, Fig. 29) may be taken as an indication that bone shaping by knapping is associated with an Early Acheulean industry traditionally assigned to *Homo erectus.* Broken stone bifaces are reported from the same Olduvai locality where the hand axe-like bone tool was found, but this does not exclude other hominids such as *Australopithecus boisei* or *Homo habilis* as the potential makers and users of these tools.

We dedicate this paper to the memory of Mary Leakey, who first identified the Olduvai Gorge bone tools and recognized the significance of this discovery. We thank P. Bushozi of the Ministry of Natural Resources and Tourism in Tanzania and

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A non-destructive investigation of the skull of the small theropod dinosaur, *Coelophysis rhodesiensis,* using CT scans and rapid prototyping

Anthea Bristowe[1*], Andrew Parrott[2], Jonathan Hack[3], Mervyn Pencharz[3] & Michael Raath[1]

[1]*Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand,*
Private Bag 3, WITS, 2050 South Africa
[2]*School of Mechanical, Industrial and Aeronautical Engineering, University of the Witwatersrand, Johannesburg*
[3]*Drs Spiro, Wilson, Duncan and Fourie Inc., Sunninghill Radiology, P.O. Box 5566, Rivonia, 2128 South Africa*

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To solve preparation problems encountered in an exceptionally fragile skull of the small theropod dinosaur, *Coelophysis rhodesiensis,* CT scans were taken of the partially prepared skull, from which a three-dimensional wax model was built using a 'reverse engineering' rapid prototyping technique. The resulting wax model was then consulted to trace and describe cranial elements of the dinosaur that were otherwise concealed by the matrix or overlying bones, which could not be removed without risk of damage to the original fossil bone.

Keywords: *Coelophysis rhodesiensis, Syntarsus,* dinosaurs, Theropoda, CT scans, computed tomography, rapid prototyping, stereolithography.

INTRODUCTION

Skeletal material of the small Early Jurassic theropod dinosaur, *Coelophysis rhodesiensis* (formerly *Syntarsus rhodesiensis*), is notoriously fragile and delicate, especially its skull material (Raath 1977, 1985, 1990; Bristowe 2004). Recent preparation of a partially disarticulated skull of a juvenile specimen of this dinosaur encountered problems relating both to the fragility of the individual cranial elements and to the degree of disarticulation which had resulted in some bones from neighbouring parts of the skull being flattened together inextricably during burial (Bristowe 2004). To solve these problems, use was made of the well-established non-destructive technique of CT (computed tomography) scanning combined with the relatively new technology of rapid prototyping. Prototypes have become useful tools in engineering and biomedical applications, being used to prove constructional details and problem-solve manufacturing difficulties, as well as in designing prostheses, planning reconstructive surgery, or simply to find out how an object or product in development will finally look (Webb 2000). The comparable combination of magnetic resonance imaging with 3-D stereolithography has also been successfully used recently to study a mouldic fossil from Scotland (Clark *et al.* 2004).

The specimen studied in this project, catalogued as QG165 in the collections of the Zimbabwe Natural History Museum, Bulawayo, was recovered from a bone-rich deposit in the Early Jurassic fine-grained Forest Sandstone Formation in the Chitaki River, north-central Zimbabwe (approx. 16°07′S, 29°30′E) (Raath 1977). Within this deposit, poorly sorted isolated bones and occasional articulated partial skeletons were preserved jumbled together in a small fluvial channel within a thick aeolian sandstone unit.

Specimen QG165 consists of an incomplete partial skull of a juvenile individual in which the cranial elements are closely associated although partially disarticulated (Fig. 1). This degree of association is unusual for material from the Chitaki River deposit, where by far the bulk of the assemblage consists of isolated individual skeletal elements that have been randomly mixed together (Raath 1977). In spite of this, the preservation of the bones in QG165 is generally excellent (Fig. 2) and there is little evidence of abrasion or predation, thereby offering a rare opportunity to study each cranial element as an individual piece while at the same time clarifying contacts between adjacent bones whose association in a single individual is beyond question. However, to study the skull at this level of detail meant that extensive and detailed preparation was necessary. In order to avoid damage to the vulnerable fossil bone, it was decided to take physical preparation as far as it was considered prudent to go, and then to supplement this with alternative, non-destructive, methods that would allow the otherwise obscured details to be revealed without risk to the specimen.

Data from CT scans can form the basic framework for a computer-assisted three-dimensional reconstruction, which can then be visualized and manipulated in any number of other applications, and studies involving use of this technology are becoming commonplace in palaeontology (see e.g. Brochu 2003; Stokstad 2000; Torres *et al.* 2003). One of the problems, though, when CT-scanning fossils is variations in density between bone and matrix – the smaller the difference between the two, the more problematic the scan. Recent CT scans of a skull of *Tyrannosaurus rex* presented not only this problem, but also one related to its sheer size; it was too long to fit into the single rotational envelope of most industrial scanners, so a means had to be found whereby the one-ton skull could be scanned resting on its occipital plate where the

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[*] Author for correspondence. E-mail: bristowea@yahoo.co.uk

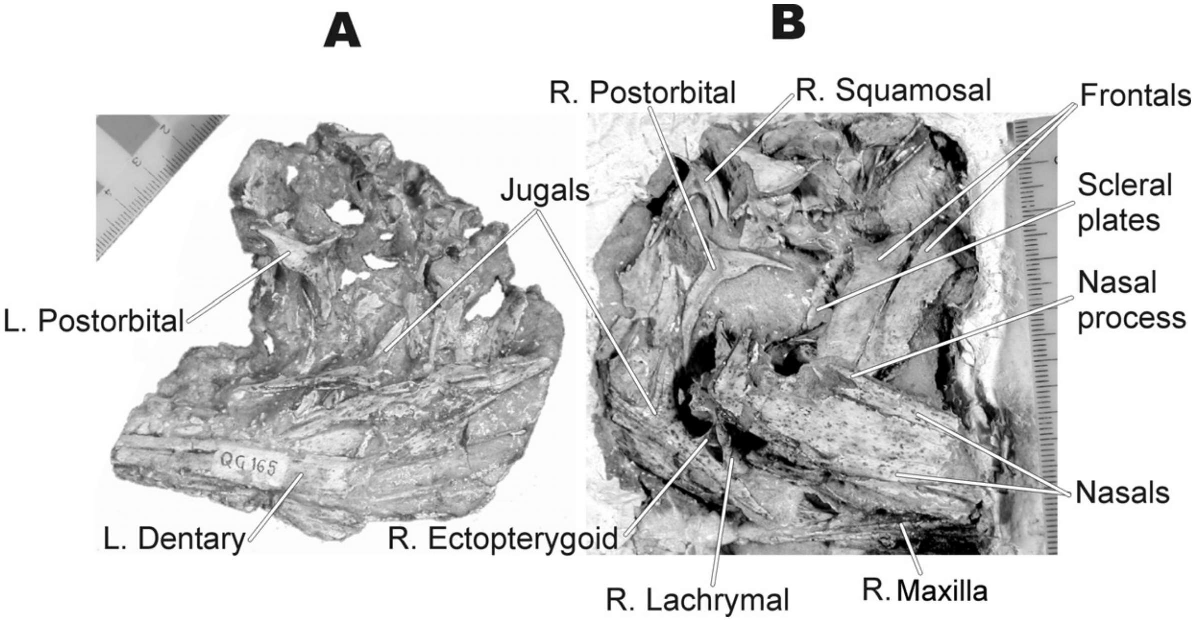

Figure 1. Two sides of the specimen QG165, showing slightly displaced elements of a juvenile skull. (Scale divisions = mm.)

bones are hollow and 2 mm thick (Brochu 2003). It was then discovered that most of the matrix filling the skull was a sandy siltstone that at times was nearly as dense as the bone, confounding attempts to digitally prepare the skull, or generate models of individual bones or internal structures (Brochu 2003). Specimen QG165 posed no such problems, as there was relatively little density-related 'noise' from the matrix and the specimen was small enough to be handled conveniently by a hospital-based CT-scanner.

The CT scans of QG165 were used to build a three-dimensional replica of the dinosaur skull in wax, by reference to which several of those cranial elements that were concealed by the matrix or by overlying bones could be traced and described.

MATERIALS AND METHODS

CT (computed tomography) scans

Specimen QG165 was scanned at the Sunninghill Hospital, Sandton, Johannesburg, in a series of fine slices using a Philips MX 8000 Multi-channel spiral scanner with effective slice thickness of 0.6 mm with 50% overlap, on a pitch of 0.875. Imaging was performed at 120 kV and 222 mAs, using an ultra high resolution algorithm, on a 512 × 512 image matrix. The resulting images (Fig. 3) were manipulated on a Philips MxView workstation using maximal intensity projection imaging techniques, and saved on CD in DICOM format. The thickness of the slice is critical to the success of the process, and while the slice thickness achieved in the project reported here was more

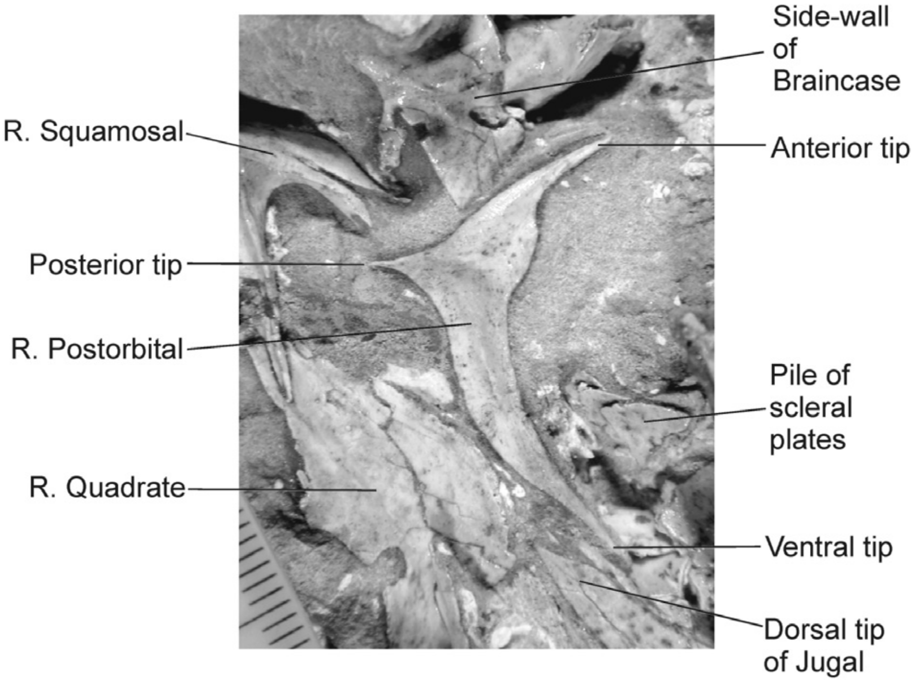

Figure 2. Right postorbital of QG165 in association with adjacent cranial elements, showing the perfect preservation of even delicate processes. (Scale divisions = mm.)

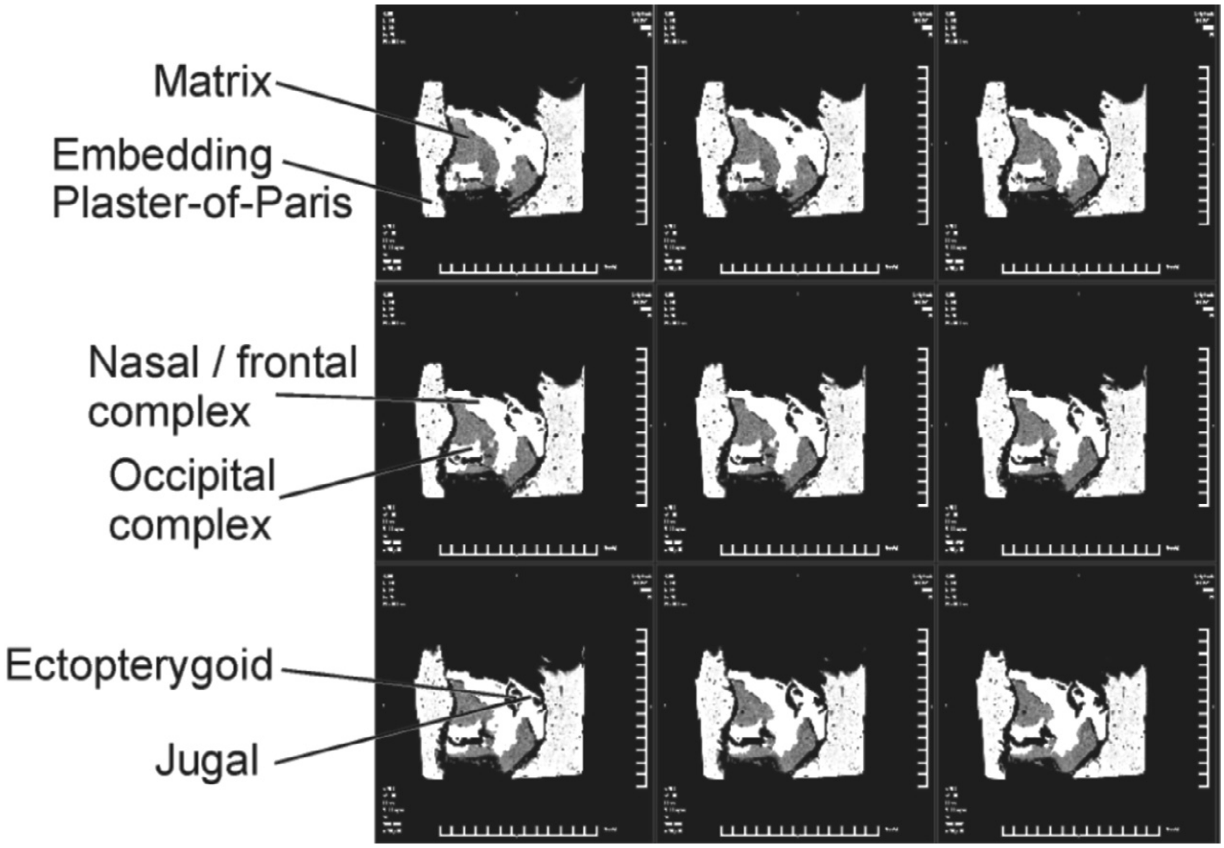

Figure 3. Selection of adjacent slice images derived from CT scan data.

than satisfactory for the purpose, when compared with achievable slice thicknesses of 0.2 mm or better on rapid prototyping machines, CT scans with a minimum slice thickness of 0.6 mm could be a limiting factor in some investigations (Webb 2000).

Using the Mimics Materialize software package (version 7.3), the formatted scan images of QG165 were converted into a digital volume where they were previewed and the density of the different substances, namely bone and matrix, were evaluated in order to establish their threshold values (Fig. 4). Once these were established it was possible to isolate bone from matrix. Threshold values were measured on a sliding scale in Hounsfield Units (HU), and these values were manipulated in order to eliminate as much of the matrix as possible from the image. It was not possible to eliminate all the matrix in the specimen because some of the densities were too close to those of the bone; densities of the dinosaur bone measured between 2000 HU and 3000 HU and those of the matrix were less than 2000 HU and greater than 3000 HU.

Building the model

The file was exported to .STL (stereolithographic) file format, a format that can be used to create physical three-dimensional parts. At this stage two methods of model building were investigated: a haptic modelling system using the FreeForm system (Sensable Technologies, MA, U.S.A.). Haptic interaction is a means of performing virtual preparation on the specimen in a virtual environment. A haptic modelling tool, known as a phantom haptic device, provides a sense of 'touch', making it possible to prod and probe the specimen and cut 'virtual matrix' away from the 'virtual bone'. However, the complex layering of the individual elements of bone in QG165 was unsuited to this approach, so haptic modelling was abandoned and the second method, that of rapid prototyping, was adopted.

The STL file was submitted to a commercial prototyping firm, Rapid Design Technologies, in Olivedale, South Africa, where it was directed to a Thermojet printer which grew the model in wax on a solid platform at a scale of 1:1 (Fig. 5). In common with all rapid prototyping systems, a

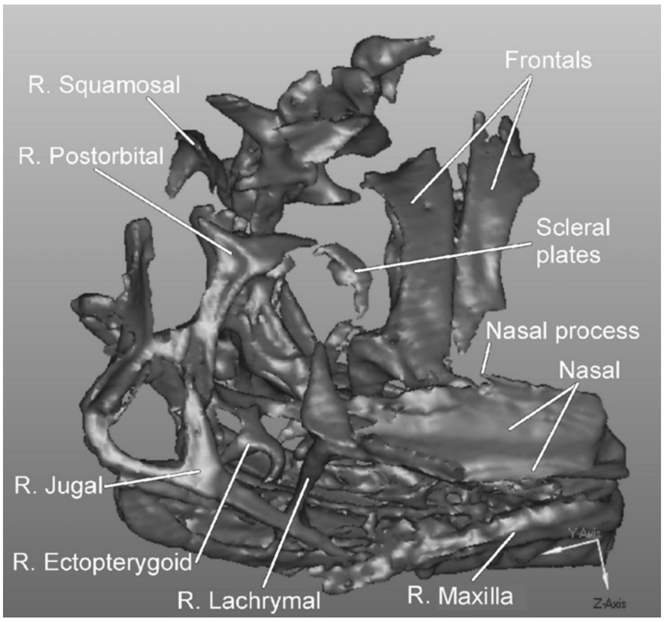

Figure 4. Digital volume of formatted images of right side of QG165, showing resolution of individual cranial elements.

layered manufacturing technique was used, which means that the model was built up in a series of physical slices, with each layer or slice being approximately 0.2 mm thick.

Voids around and within the resulting model are supported by regularly spaced fine pillars of wax, through which the general shape of the three-dimensional model is visible (Fig. 5). The model of QG165 was left on its platform with all its wax supports in place because it was small and delicate, and required support to protect the wax proxies of delicate and fragile processes on the original bones. The fine and brittle wax supports were easily brushed away when access to obscured parts of the model was needed. The three-dimensional model was used to supplement examination of areas of QG165 where details were obscured by overlying matrix or bone and where further physical preparation of the original fossil would have risked severe damage to the bone.

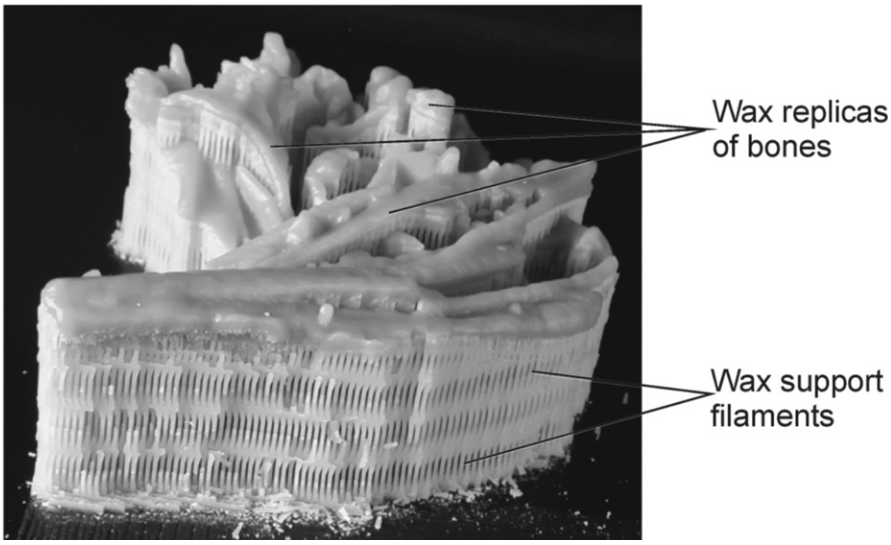

Figure 5. Wax replica of QG165 at a scale of 1:1 grown from the digital volume represented in Fig. 4.

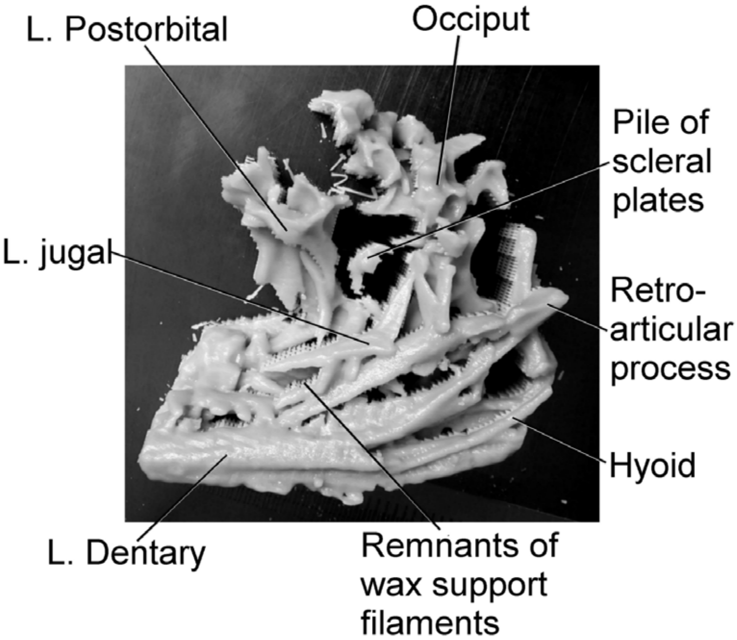

Figure 6. Wax replica of QG165 with most of the supporting wax filaments removed. Individual cranial elements are identifiable, including the previously unrecognized hyoids. Density differences were not sufficient to permit resolution of individual scleral plates.

RESULTS

The wax model of QG165 made it possible to identify and describe previously contested elements such as the hyoids, which are exceptionally slender and delicate bones (Fig. 6). In QG165 they were partially embedded in the matrix and therefore hidden from view. By examining the model it was possible to locate their contact with the dentary bones precisely. The left lachrymal was also located through examination of the model; during deposition of the specimen the skull had begun to disintegrate, as a result of which the nasal bones drifted over the left lachrymal, completely covering it and obscuring it from view. Physical excavation to expose it would have unavoidably damaged both the nasals and the frontal bones. The left maxilla was also tracked through the medium of the wax model as it too was buried deep beneath the nasal. This was especially useful as its posterior end was still preserved, unlike that of the right maxilla, so it was possible to reconstruct the maxilla-lachrymal-jugal contact (another contested region of the skull of *C. rhodesiensis*) using what could be directly observed on the right side of the skull combined with information on the morphology of the left maxilla gleaned from examination of the wax model.

The model failed in a few instances where there was minimal difference between the densities of the bone and the matrix, so that the CT scan was unable to differentiate between them, and this failure was consequently reflected in the model. It was not possible, for instance, to glean any new information on the small and very thin (<1 mm thick) scleral plates from the orbits, because they were interpreted as amorphous fused blobs. The scleral plates are wedge-shaped, paper-thin, flat plates of bone, each approximately 9 mm in width and 6 mm deep, and in QG165 they lay in two loose piles; in the model, each pile was interpreted as a single entity. One possible means of overcoming this limitation would be to digitally reprocess the scleral plates with a different HU value and then prototype them on their own. This limitation in discrimination did not, however, apply to other small but more robust elements, such as teeth. Using the model, it was possible to locate and count all the teeth preserved in the left dentary, even though several of them could not be seen in the original specimen.

CONCLUSIONS

The use of CT scans that can be transferred into digital format in order to build accurate three-dimensional models through rapid prototyping is a potentially powerful tool in the analysis and reconstruction of fossil skeletons (Torres *et al.* 2003). In the case of QG165, the physical preparation necessary to expose all the required details of skull construction would inevitably have resulted in damage to or destruction of many of the critical structures. The wax model obviated the need to take such risks. Combining direct observation of the original fossil with study of the wax model grown from the CT scan data allowed critical areas of the partially disarticulated skull to be reconstructed with confidence, from which a definitive identification of the taxon under study could be made, which in turn helped to resolve a long-standing taxonomic dispute (Bristowe 2004). With the rapid advance of these technologies there are exciting prospects ahead for the development of ever more useful non-destructive, even non-invasive, investigative techniques in many fields, not least in palaeontology.

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On the use of percussion cartridges to extract fossils from hard breccia

A.G. Latham[1*] **& T.C. Crawford**[2]

[1]*Archaeology Department, Hartley Building, Liverpool University, L69 3GS Liverpool, U.K.*

[2]*Anthropology Department, Washington University, Missouri, MO63110, U.S.A.*

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The use of percussion cartridges (caps) affords a simple, quick, controlled and safe way to remove pieces of hard breccia from around fossils or to remove breccia pieces that contain fossil material. We have demonstrated its use over two field seasons to remove pieces of breccia containing quite small animal bones and it is as good as, or better than, the use of jackhammer drills and other methods. Safety procedures are simple but must be strictly followed at all times.

Keywords: Makapansgat, percussion cartridges, breccia, fossils.

INTRODUCTION

Traditional methods of extracting fossil material from hard breccias, especially in the hominid-bearing caves of South Africa, have involved the initial use of a jackhammer to prepare a hole into which a small quantity of charge is placed, or the use of a straight plaster charge (Mason 1988) or, more frequently, metal wedges. The pieces of rock are further reduced, away from the site, using hammers, chisels, punches and acetic acid baths, in the usual way. Explosives are now seldom used because of their overall destructiveness. This is because, in addition to the destruction of archaeological or palaeontological material, fossils, bones, tools and flakes may become disassociated from each other and from their context. Modern excavation methods on archaeological sites in the last twenty years, in general, have become much more elaborate and painstaking and so the use of explosives has largely been discontinued. Jackhammer drills are effective with the use of wedges, but they are heavy and noisy and, for most excavations, they require two or more people to operate. Also drilling becomes quickly more difficult as the approach face becomes steeper and the terrain becomes rougher. Percussion cartridges are used in the construction industry and, since about 1990, have been adopted by cavers in Europe and the U.S.A. to widen narrow cave passages. We investigated their possible effectiveness on newly exposed breccias at the australopithecine site at Makapansgat and the results are presented here.

APPARATUS AND METHODS

Figure 1 shows the basic arrangement required to drill and cap 8 mm diameter holes in hard breccia. The apparatus consists of an electric drill with hammer facility, an 8 mm × 30 cm long bit, an anvil made of brass or mild steel rod that is at least 2.5 kg (5 lb) in weight with an 8 mm hole drilled centrally, several 8 mm screwed rods about 30 cm long (about 1 ft), each sharpened at one end to a V-shape to act as a firing pin, about 30 cm square (1 ft square) mat of heavy rubber (for example, a piece cut from an old conveyor belt), goggles, helmet and gloves and a box of Hilti™ cartridges (black is strongest). Ear protectors are optional (see later). The operator also requires a >2.5 kg (about 5 lb) lump hammer and various metal chisels.

An 8 mm hole is drilled to a depth of between six and nine inches such that the percussion of one or two cartridges placed at the base of the hole heaves or cracks pieces of rock breccia away from a free face. Cracked pieces can then be removed with hammer and chisel and the resulting pieces of rock are documented, taken away and treated as usual for any fossil material.

It is possible to use a 24-V hammer drill powered from its own re-chargeable batteries to make the holes in the rock. Depending on the amount of drilling, the two batteries that come supplied with such a drill can normally be used to prepare from five to eight holes before the batteries need to be re-charged. It is normally expected, however, that a drill will be powered from a nearby generator, in which case, as many holes can be prepared as necessary for the day's work.

Experience shows that the optimum depth for a hole is from six to nine inches depending to some extent on the

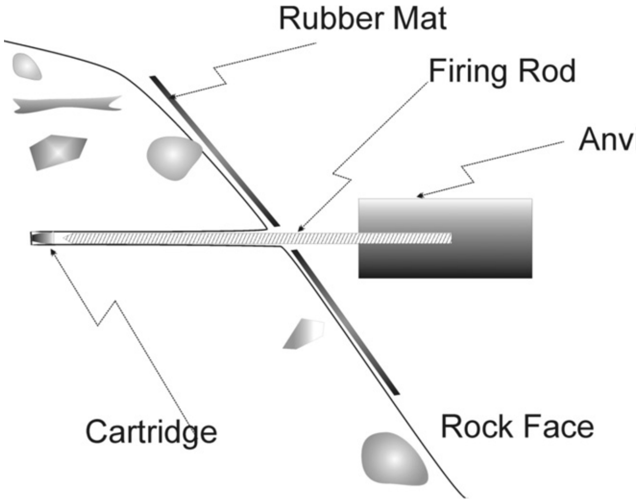

Figure 1. Ready for firing the cartridge. The position of the drill hole, cartridge, rubber mat, firing pin and anvil, ready for hammer strike into fossil-bearing hard breccia.

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

proximity of a second free face, such as a root hole or unconsolidated ground. Each hole is reamed and cleaned out with the bit in order that the cartridges will slide to the base of the hole with minimum of resistance. Each hole therefore needs to be cleaned of rock powder and the easiest way to do that it to use a small piece of plastic tubing (two to three ft long) and blow down it. The hole may also be cleaned with the bit as it is brought in and out of the hole. The blunt end of the screwed firing rod can also be inserted into the hole in order to assist in further cleaning and to ascertain the actual depth of the hole.

Next, wearing goggles, helmet and gloves, one cartridge is place into the hole, point first and the blunt end of the rod is used to push it to the end. Note that if there is resistance to the movement of the cartridge, and it has not gone the whole way then the following procedure must be followed for safety. It is very unlikely that the cartridge will detonate as it is inserted into the hole but it must be assumed that this could happen. First the mat must be placed over the rod and made flush to the face (Fig. 1). The anvil must be placed over the free end (the V-shaped end) of the rod in order to assist in sending the cartridge to the far end of the hole, and it may be lightly tapped with the hammer to sink the cartridge.

The rod is then extracted and turned round so that the V-shaped end points down the hole as the firing pin. The mat must be placed over the rod flush to the face, and the anvil placed over the rod. The anvil is then struck with the hammer to detonate the cartridge(s). The mat prevents small rock from flying back toward the operator, and it is for this reason that the hole must be greater than six inches in depth. The percussions are not strong enough to lift larger pieces. If the anvil is loose over the rod then a single loop of tape (or paper) can be wrapped over the end of the rod before the anvil is placed over it.

If necessary, two cartridges may be use to good effect but it is inadvisable to use three cartridges. Obviously, all safety precautions must be followed including the use of goggles, helmet and gloves, safety boots and, particularly, the anvil.

OBSERVATIONS AND NOTES

The danger of the technique arises mainly from the firing pin (rod) coming out of the hole at high speed. The reason that the 8 mm rod is screw threaded is that the threads act as a binder in the hole so offering some resistance to the percussion from the detonation, that is, to prevent the rod flying out of the hole. But it is known that the threads do not always offer enough resistance on their own to the detonation. It is, therefore, *imperative* that when either the blunt end or the V-shaped end of the screwed rod comes into contact with the cartridge in the hole, the mat is placed over the rod flush to the face and the anvil is placed over the free end of the rod. The anvil not only acts as the striking surface through to the rod but also absorbs any momentum that the rod acquires from the detonation. The rod does not have enough mass of its own to absorb the detonation and instead it can become a missile. Hence the anvil must be used at all times when the rod is against the cartridge. The authors know of three accidents, to 2002 worldwide, with this technique when, in each case, the rod was used *without the anvil.*

The anvil is held by its sides quite safely when the top is struck. If the anvil is struck at arms length from some distance away without it being steadied, the blow is not likely to be as 'clean' on the top surface of the anvil, and experience shows that the rod soon becomes bent and unusable. It is also not advisable to make rods that are too long since they may bend too much under the weight of the anvil when the rod and hole are not vertical.

Eventually, after a few holes have been detonated the screwed rod will become bent anyway. Hence for a day's session of drilling, it is usual to make up four or five lengths of rod. An angle grinder can be used for cutting up a 2 m length of rod, into the required pieces and to grind a V-shaped end on each. Burrs need to be removed so that the rod slides easily into the hole by either rod end. Unless the rod can be made dead straight again on a workbench it is usual to jettison bent rods.

In some arrangements, the rod is actually screwed into the anvil, which adds the extra precaution that the anvil and rod do not get separated. The disadvantage is that the screwed threads tend to become damaged which necessitates more maintenance. So as each rod becomes too bent to insert into the next hole it is unscrewed from the anvil and a new rod is inserted.

It occasionally happens that the end of the hole becomes over widened slightly due to the drilling procedure, especially if the bit is made to linger at its maximum depth; the cartridges also have rims and the result of both of these factors means that, sometimes, the cartridge may become skewed at the end of the hole. The result is that the cartridge may not detonate immediately upon being struck by the firing pin through the anvil. It should not be necessary to strike the anvil so hard as to bend the screwed rod. It is better to take the rod out an inch or so and rotate it to between 45° and 90° and reinsert it so that the V catches a new position on the rim of the cartridge. Occasionally it may be necessary to do this a second or a third time.

If the rock face containing the fossils is of sufficient bulk then it is better not to place the hole into the mass of the rock body but to drill the hole about parallel to a second face. In that way the rock is shattered or cracked off from the other free face. If the hole is too shallow (less than six inches) then rock tends to be blown off the top of the drilled face. This is the reason for having the heavy mat.

The technique should not be used in breccia that is too soft, has holes or has soft (uncemented) pockets in it. Cartridges may either be lost in unconsolidated breccia which means that they have to be fished out carefully by breaking up the rock the long way round (obviously, for safety reasons, they cannot be left in), or the caps may detonate uselessly (see later).

Hilti™ cartridges come in strengths, yellow, red and black (strongest). We have used all three strengths and found it is safe to use two blacks cartridges together in drill holes greater than 6 inches deep. The cartridges are supplied separated from one another in plastic holders in boxes of 100.

RESULTS

Dr Kuykendall and Jeff McKee cleared the surface of deposits comprising Member 2 and layers below Member 2, above the so-called Original Ancient Entrance of the Limeworks in 2001, in preparation for *in situ* sampling. In the 2003 field season, we tried the capping technique on the cemented breccia of Member 2 with the following results; the first author, who had used this technique in caves in the U.K., was the 'capjack', and the second author took over later in the field season. Fossil-bearing pieces from the harder parts of the breccia were removed as effectively as, and more easily than, could be removed by a jackhammer that was being used at the same time. On two occasions, however, we drilled into pockets of less well-cemented breccia with no result. In one case we made a new hole near to the first and fired the rock so that the original cartridge was eventually retrieved intact. In the second case, we began to extract the cartridge by making a series of drill holes and breaking up the rock with hammer and chisel away from the cartridge. We then found that the cartridge had in fact fired but the sound had been muffled by the unconsolidated rock. Despite these two 'dud' holes, we made good, controlled progress, frequently using old tree root-holes as the free face. In the 2004 field season, we confined our use of the technique more to the highly cemented sediments and calcites below Member 2 on which, we found, the technique was ideally suited. The second author was the capjack. There were no misfires or pockets of softer material and control was sufficiently good that we were able to extract an articulated skeleton of a small bovid with little damage. Because of the disposition of the face, one or two of our holes were drilled at quite steep angles. We ran into trouble drilling one layer of this Member when the drill bit hit clasts of detrital silica. It was then necessary to re-site the hole and try again. The detonations did not produce lots of small pieces but a few large ones. We subsequently examined the country rock again to see if new cracks had opened up so as to usefully place and direct the next hole.

Ear protectors may be used but occasionally some detonations may not be heard. It is necessary, of course, to know that all firings have actually occurred, and therefore we did not use ear protectors and we have suffered no discomfort.

CONCLUSIONS AND RECOMMENDATIONS

In two field seasons at the Limeworks, Makapansgat, we have successfully demonstrated the use of percussion cartridges to remove lumps of hard breccia, containing fossils, under controlled, safe, conditions and with minimum damage to the fossils. The capping technique can be used in places where it would be impossible or difficult for other techniques to be used, such as in the interiors of caves (as, for example, in the lower reaches of Gladysvale, Gauteng, South Africa), on vertical walls or in confined spaces. We do not recommend the technique be used in situations where there is a chance that the cartridge holes may end up in soft material. Directors of excavations who intend to use the technique should not allow undergraduate students or junior persons to 'have a go'. As some situations may require extra judgement involving considerations of safety, it is recommended that the capjack be sufficiently senior at the excavation and that he or she be in charge of the capping equipment (drills, bits, anvil, rods, mat and cartridges) both in its use, transport and storage.

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STYLE GUIDE FOR AUTHORS — REVISED 2003

GENERAL

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The Editor
Palaeontologia africana
Bernard Price Institute for Palaeontological Research
University of the Witwatersrand
Private Bag 3
WITS 2050
South Africa
Telephone: [+27-11] 717-6682
Fax: [27-11] 403-1423
E-mail: bamfordm@geosciences.wits.ac.za

Submission of a manuscript for publication will be taken to indicate that the material is original and has not been submitted for publication elsewhere.

Authors wishing to reserve copyright to themselves should stipulate this at the time of submission of a manuscript.

PREPARATION AND SUBMISSION OF MANUSCRIPTS

Manuscripts

Manuscripts should be typewritten in English on one side of A4 size paper in double spacing throughout and with margins at least 25 mm wide all round. All pages must be numbered consecutively in the top margin (central), beginning with page 1 on the title page.

Three copies of each manuscript plus illustrations are required by the Editor. In addition, authors are asked to submit a copy of the text on disk (preferably on a DOS formatted 1.44 MB, 3.5 inch diskette, or composed in MS ‘Word’ or ‘WordPerfect’, or saved in ‘Rich Text Format’). We are unable to accept files on disks formatted for MAC-OS.

Layout

Except in the case of short communications, manuscripts should normally be divided into appropriate conventional sections set out in the following order: title, abstract, introduction, body of text (subdivided as appropriate), acknowledgements, references.

Title

The title should be concise and should reflect the contents clearly. Names of new biological taxa proposed in the manuscript should not be included in the title. If the title is long a suitable abbreviated running title must be provided.

The title must be followed on a separate line by the authors’ name/s and institutional address/es (the e-mail address of the first-named author should also be included if possible). In multi-authored contributions, the institutional address of each individual must be linked to the relevant name using superscript numbers.

Abstract

An informative abstract not exceeding 300 words must be provided.

Keywords

At least three keywords should be provided immediately after the abstract.

Introduction and main text

The manuscript should be divided as appropriate into conventional sections (e.g. Introduction, Materials and Methods, Results, Discussion, References, etc).

Acknowledgements

Authors should include only those acknowledgements that are truly warranted.

References

References are listed at the end of the manuscript, beginning on a new page. Under this heading, authors must list only published works that have been cited in the text.

Unpublished works, even those that are ‘in press’, must not be included unless full bibliographic details can be provided, including pagination. However, formal theses and dissertations, even though unpublished, may be listed provided full details are supplied; this must include reference to the institution where the master copy is lodged. Work that is ‘in preparation’ and ‘personal communications’ may be referred to in the text, but must not be included in the list of references.

The list of references must be arranged alphabetically, then chronologically, according to the layout of the examples below. Leave one blank line between each reference, and do not indent or otherwise format each entry. The layout sequence is:

(i) Author’s name(s) and initials (in uppercase only). In the case of multi-authored manuscripts, successive authors’ names should be separated by commas, with an ampersand (&) between the penultimate and last name;
(ii) Year of publication (not in brackets). If more than one paper by the same author is listed for the same year, successive entries must be designated by placing the letters a, b, c, etc., after the year of publication;
(iii) Full title of paper. Use capitals only for the first letter and for proper names. Generic and specific names must be italicized, unless such names themselves fall within an italicized title, in which case the names should be in regular (non-italic) script. If your equipment is unable to produce italics, please underline those words that should be italicized;
(iv) Full (*unabbreviated)* title of journal, book or other source, in italics. Book titles should be followed by the edition (if other than the first), the place of publication and the name of the publisher.
(v) Volume specification of journal: i.e. series (if applicable), volume number (in bold), part number (if any) in brackets, pagination (first and last page).

Examples of reference citations (to save space, the blank line between successive entries has been omitted):

ANDERSON, H.M. 1976. *A revision of the genus* Dicroidium *from the Molteno Formation.* Unpublished Ph.D. thesis, University of the Witwatersrand, Johannesburg.
ANDERSON, H.M. & ANDERSON, J.M. 1970. A preliminary review of the biostratigraphy of the uppermost Permian, Triassic and lowermost Jurassic of Gondwanaland. *Palaeontologia africana* **13**, 1–22.
CROMPTON, A.W. 1962. On the dentition and tooth replacement in two bauriamorph reptiles. *Annals of the South African Museum* **46**(9), 231–255.
HOPSON, J.A. & BARGHUSEN, H.R. 1986. An analysis of therapsid relationships. **In**:Hotton, N., MacLean, P.D., Roth, J.J. & Roth, E.C. (eds), *The Ecology and Biology of Mammal-like Reptiles,* 159–168. Washington, Smithsonian Institution Press.
ROMER, A.S. 1966. *Vertebrate Palaeontology* (3rd edn). Chicago, University of Chicago Press.
ROMER, A.S. 1973. Permian reptiles. **In**: Hallam, A. (ed.), *Atlas of Palaeobiogeography,* 159–168. Amsterdam, Elsevier.
VAN DER MERWE, N.J., LEE-THORP, J.A., THACKERAY, J.F., HALL-MARTIN, A., KRUGER, F.J., COETZEE, H., BELL, R.H.V., & LINDEQUE, M. 1990. Source-area determination of elephant ivory by isotopic analysis. *Nature* **346**, 744–746.

Reference citations in the text should give the name of the author and the date on each occasion, and substitutes such as *op. cit., loc. cit.* should not be used, e.g. ‘Smith & Jones (1943) suggested that ...’, ‘... extinction rates (Smith & Jones 1972) and other factors ...’. In the text, successive references by the same author should be separated by commas, and those of different authors by semi-colons: (Brain 1990, 1991; Hughes 1961; Smith & Jones 1972).

Headings

Three orders of headings are used.

FIRST ORDER, printed in bold capitals and left-aligned.
Second order, printed in bold upper and lower case and left-aligned.
Third order, printed in upper and lower case italics and left-aligned.

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

Tables

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

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

Illustrations

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

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

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

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

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

Good quality digital images in TIF and EPS format (at least 800 dpi for photographs and 1200 dpi for line drawings) may also be accepted. They may be submitted on PC-format disks or CD-ROM.

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

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

Numerical data

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

ACCEPTANCE OF PAPERS

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

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

REPRINTS

Fifty reprints will be supplied free of charge to the sole or senior author, who must see to an equitable distribution if more than one author is concerned.