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Makapansgat suids and *Metridiochoerus*

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Fossil suid material from Member 3 of the Makapansgat Formation was described as *Potamochoeroides shawi* but some authors have regarded it as an early stage of the *Metridiochoerus andrewsi* lineage. There is no complete cranium so a new reconstruction has been based on combining the data from a number of partial specimens. Comparison with *Metridiochoerus andrewsi* is difficult as there are reasons to suspect that the so-called 'male' and 'female' crania from Koobi Fora could be specifically distinct. An undescribed cranium from the Omo Shungura Formation is morphologically similar to the 'male' and is attributed to *Metridiochoerus jacksoni.* Comparison with the reconstructed Makapansgat suid indicates that the latter already shows an early stage in the distinctive architecture of the *M. jacksoni* cranium, as well as some resemblances in dental features. Accordingly it is suggested that the Makapansgat suid be designated as M*etridiochoerus shawi.* A few teeth from Member B11 of the Shungura Formation, with an age close to 2.95 Ma, are placed provisionally as *M.* cf. *shawi*; previously described molars referred to an early *Notochoerus scotti* are probably from a similar level. While this is suggestive, correlation is not firmly established.

Keywords: suid, *Potamochoeroides, Metridiochoerus,* Makapansgat, Shungura Formation, Koobi Fora Formation, Plio-Pleistocene, Africa.

INTRODUCTION

The Makapansgat Limeworks cave deposits have yielded substantial quantities of fossil remains of Plio-Pleistocene vertebrates, including important specimens ascribed to *Australopithecus africanus.* The deposits represent the consolidated infillings of a large cave system that was developed in the regional dolomitic limestone, The early phase of deposition was subaqueous and resulted in the building of layers of speleothem ('travertine') several metres thick on the floor, walls and roof of the cavern. This high grade calcium carbonate attracted the attention of miners in the 1920s and early 1930s and was removed with the curious result of leaving the former cave fillings as a roof above the galleries that now provide access to the site.

The stratigraphy of the clastic sediments above the travertine is rendered complicated by the existence of several depositories but the sequence of events has been ably reconstructed by Latham, Herries and Kuykendall (2003). Although it is not possible to trace each horizon across the entire area, the 'Classic Section' on the west side provides a useful reference frame and the nomenclature proposed by Partridge (1979, 2000) is still convenient.

The basal speleothem (Member 1) is followed by horizontally stratified red sandy and silty sediments (Member 2). Above this is Member 3, consisting largely of bones and bone fragments in a matrix of grey silty sand, heavily calcified and from 50 cm to as much as 2 m thick. Commonly referred to as 'the grey breccia', this is by far the major source of fossil material. Overlying the bone bed is a thick deposit of pinkish sandy material, sometimes stratified and occasionally rich in clasts of dolomitic material (Member 4); it has yielded a few fossils, notably cercopithecoids but also one specimen of *Australopithecus africanus.*

The purer calcite limestone was removed by the miners and burnt in a kiln on the northwest side of the caves. Any rock that was not pure limestone was discarded and dumped near the kilns, fortunately including blocks and pieces of the grey breccia. Under the direction of Alun Hughes and James Kitching in the 1940s and 1950s the dump material was examined and sorted so that the fossils could be extracted from the easily-recognized grey breccia. Many thousands of bones and teeth were recovered from these dumps whereas only a handful of specimens have been recovered *in situ* from small excavations carried out by Ron Clarke in the 1970s and Jeff McKee in the 1990s. However, the material is so characteristic in appearance that there is little doubt about its derivation from Member 3.

DESCRIPTION

Suid remains

The first account of suids from Makapansgat was given by Maureen Dale (1948) in a brief paper describing two species that she named *Pronotochoerus shawi* and *Potamochoeroides hypsodon.* The type specimen of the latter was a right maxillary fragment with the third molar slightly damaged; the matrix shows that it came from a pinkish deposit. The type specimen of *Pronotochoerus shawi* was a right mandibular ramus from the grey breccia, with lower P3–M3, and it was compared with the material from Omo described by Leakey (1943) as *Pronotochoerus jacksoni.* Subsequently more material was recovered from the grey breccia and one additional specimen from the pink deposit. In 1958, Ewer described the total collection, referring Dale's two species both to *Potamochoeroides* with the species *shawi* having page priority, but she retained the two specific names. Cooke & Wilkinson (1978) considered them conspecific as *Potamochoeroides shawi.* Harris & White (1979) placed the Makapan suid in the genus *Metridiochoerus* as representing Stage I in what they regarded as the *Metridiochoerus andrewsi* lineage, based on the evolution of the third molars. All the cranial material from Makapansgat was re-examined and described by Bender (1992). He constructed a cladogram that he considered as demonstrating the apparent affinity of *Potamochoeroides shawi* with *Potamochoerus porcus* and a

lack of affinity with *Metridiochoerus andrewsi* as represented by the fine material from Koobi Fora. This conclusion needs to be reconsidered.

The cranium

There is no complete cranium in the Makapansgat suid collections, the most complete specimen being M1391 which comprises much of the frontal, nasal and maxillary areas and part of the parietals. The snout is broken and the canine flanges and premaxilla are lost, but the palate is almost complete to the back of the third molars. The whole of the occiput is missing and the zygomatic arches are lost. It has been illustrated by Ewer (1958, pl. 2) and by Bender (1992, figs 2 & 3). The specimen shows that there was originally a full set of cheek teeth belonging to a mature animal (Wear Stage 6 of Kullmer, 1999).

Other portions of crania make it possible to effect a reasonably good reconstruction of the cranium, except for the zygomatic arches. M588 is the ventral portion of an occiput and may actually have belonged to M1391. M2062 preserves the braincase behind the nasal/frontal suture, as well as part of the maxilla with an erupting UM2 that shows this to be a young animal. It has been described briefly and well illustrated by Bender (1992, figs 4, 5 & 9). Because of the age difference this specimen cannot simply be integrated with with M1391 but can be used to infer that the braincase was gently arched but not unduly elevated and the orbits rose almost to the roof; the pterygoids protrude ventrally. The morphology of this young cranium accords with the features seen in M305, which preserves the dorsal surface of the frontals from the lachrymal foramina to the occipital crest, as well as part of the parietals and the orbits. Ewer (1958, fig. 2) illustrated the right orbit and lachrymal based on M2062 and M304, showing that the lachrymal was short as in *Potamochoerus.* M2262 is a substantial piece of the braincase from the lachrymal foramina to the occipital condyles but lacking the supraoccipital area and the ventral part of the braincase. Parts of the zygomatic process of the squamosal are preserved, as well as some of the inner surface of the eye sockets. The lower part of the occiput is well preserved, with the foramen magnum, the condyles and the upper part of the paraoccipital proceses, the bullae, the ear region and the basioccipital. The basicranium is also well preserved in M588. Unfortunately the form of the zygomatic arches is unknown, although the maxillary root is seen in the best specimen with the palate (M1391) and seems to resemble the smooth outward sweep of the arch seen in *Hylochoerus* rather than the abrupt lateral projection found in *Potamochoerus.* It also suggests that the zygoma was fairly broad below the orbits. Putting all these pieces together results in the restoration shown in Fig. 1.

The cheek teeth are well preserved in the palate (M1391) and show that the full complement of premolars was present in a mature adult, although only the root impressions of UP1 and UP2 are preserved. UP2 is intact in two other specimens, M321 with UP2–M3, and M353 with UP2–4. The UP3 and UP4 occur together in six other specimens and, although somewhat like these teeth in *Potamochoerus* and *Sus,* are not very close to either but perhaps more like *Sus.* The UP3 has only three roots instead of four. The UM1 is reduced to a stump and UM2 shows the very characteristic *Metridiochoerus* pattern of a rim of enamel enclosing a tract of dentine with scattered 'lakes' of enamel. The teeth are illustrated here in Fig. 2A. In the UM3 there is a distinct gap between the first and second lateral pillars on the buccal side and the lingual pillars have flattened external walls and are rather poorly 'paired' with the buccal pillars. The trigon has only the usual two pairs of lobate lateral pillars and the talon consists of a variable number of smaller, more rounded, pillars that are not obviously paired. Bender (1992) distinguished three groupings in the talon: Group 1 has a single median cusp and 3–4 surrounding styles; Group 2 has 2 medians and 3–5 styles; Group 3 has 3 medians and 5–8 styles. The maximum crown height in the third molars is rarely greater than the anterior basal breadth, the Hypsodonty Index, 100H/B, being close to 120–130 in both uppers and lowers as the lower teeth are narrower than the uppers.

Lower dentitions or partial dentitions are represented in the collections, the best specimen being M2081, which is a mandible with the left ramus broken off behind the LM3 and broken also through the right LM2 (Fig. 2C). The symphysis is virtually intact with the bases of both canines remaining. The anterior border of the symphysis is only gently curved, unlike the projecting central part of the symphysis in the bush pig. There are sockets for six evenly spaced incisors, apparently like those of the bush pig but perhaps a little smaller. The symphysis is not as long as in the bush pig and lacks the small shelf at the back of the symphysis as well as the marked constriction behind the canines that are rather characteristic of *Potamochoerus.* The full premolar series was present. The socket for P1 lies a short way behind the canine, midway to P2. The third molars are in fairly early wear (WS 5 of Kullmer) but M1 is already worn to a featureless tract of dentine. The first lateral pillar on the lingual side of the talonid is larger than that on the buccal side which, however, is in the position to form a third pair of laterals on the crown.

Also shown in Fig. 2D are occlusal and lingual views of the dentition of the original Type of *P. shawi* (M302), which does not appear to have been illustrated since the drawing given with the type description but which unfortunately distorts and elongates the back of the LM3. The lower third molar of the original type of *Potamochoeroides hypsodon* is also illustrated here for comparison (Fig. 2E), as well as a third molar of the extant *Potamochoerus porcus* (Fig. 2F). Dale (1948) recognized the resemblances between the Makapansgat material and the Shungura species *'Pronotochoerus' jacksoni,* now regarded as *Metridiochoerus jacksoni.*

***Metridiochoerus* from Koobi Fora**

After he had listed all the specimens from Makapansgat and described the morphological features of the more complete ones, Bender (1992) tried to evaluate the anatomical features by comparison with actual crania of *Potamochoerus* and *Phacochoerus.* He attempted to include *Metridiochoerus* in his analyses but, not having access to

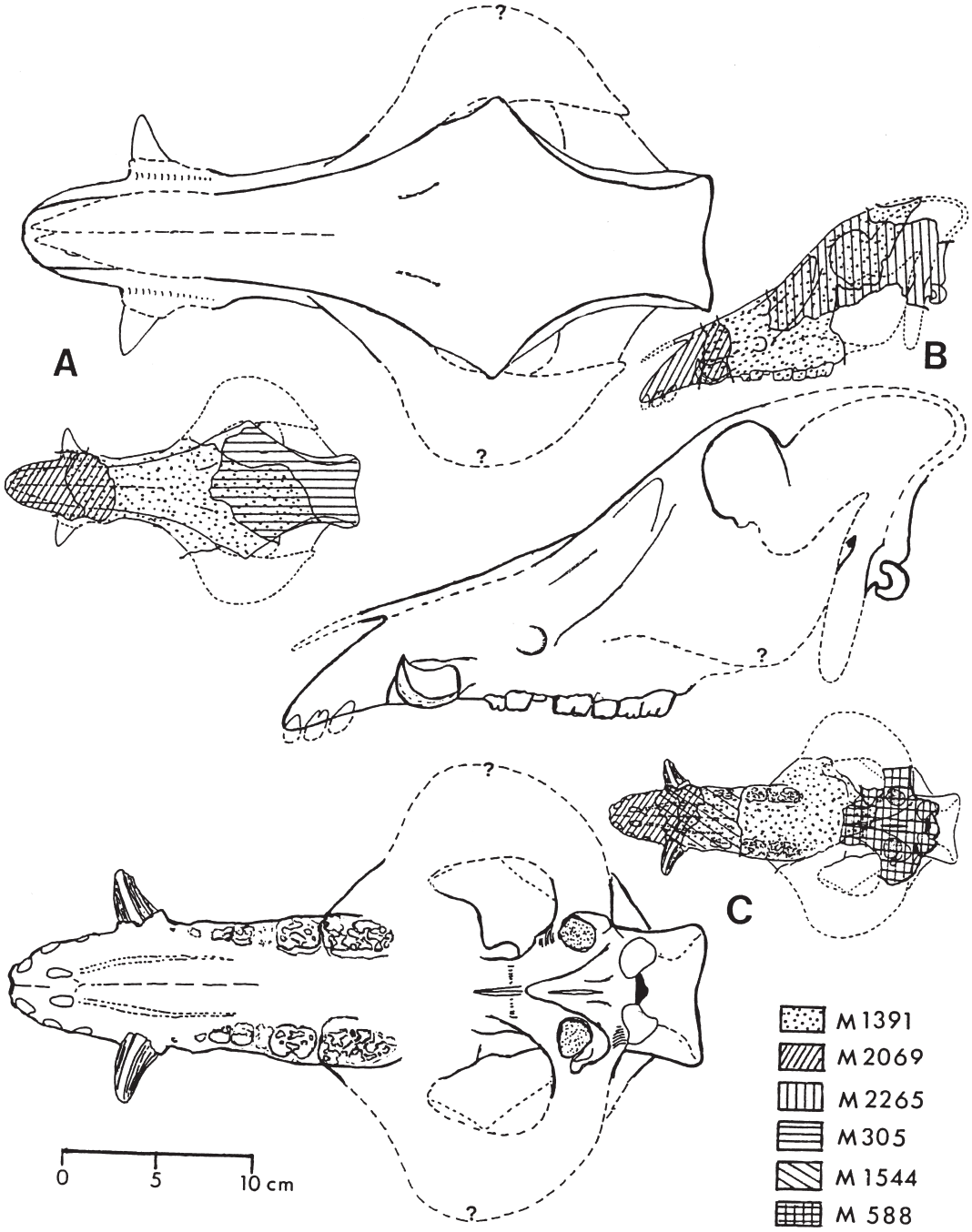


Figure 1. Reconstruction of the cranium of *'Potamochoeroides' shawi* from Makapansgat Member 3, showing the outlines of the specimens used in the synthesis. The form of the zygomatic arches is not known. Isolated canines are potamochoerine but more robust.

the East African material, his concept of *Metridiochoerus* rested largely on the published accounts and illustrations given by White & Harris (1977), Harris & White (1979) and Harris (1983). These authors considered that the two types of crania from Koobi Fora attributed to *Metridiochoerus andrewsi* represented sexual dimorphism with large zygomatic protuberances in the males but none in the females. Two rather poor specimens were reported to have come from the *Notochoerus scotti* zone (below the KBS tuff) while the others are said to be from the *Metridiochoerus andrewsi* zone, above the KBS tuff and thus to occur within a fairly limited time span. The best specimen is an almost complete cranium, KNM ER 228, with some damage to the canine flanges but with well preserved molars and providing a fine model for the 'female' morphology (Harris & White 1979, pl. 13, mislabelled as ER 223). The most complete of the 'male' crania is KNM ER 1210, which has only slight damage in the basicranial area and has lost the front of the nasals and the premaxilla. Very similar but with more damage to the occiput is KNM ER 1644, illustrated by Harris & White (1979) in Plate 14 but mislabelled as KNM ER 1210.

Figure 3 compares the dorsal aspects of hemicrania of the 'female' (A) and the 'male' (C), aligned on the infraorbital foramina. The vertex length of ER 1210 is close to 495 mm, compared with 557 in ER 228, while the corresponding figures for the basilar length are 380 mm and 464 mm, respectively. These differences in size are the exact converse of what is usual in the living suids in which the male is consistently larger than the female. This does

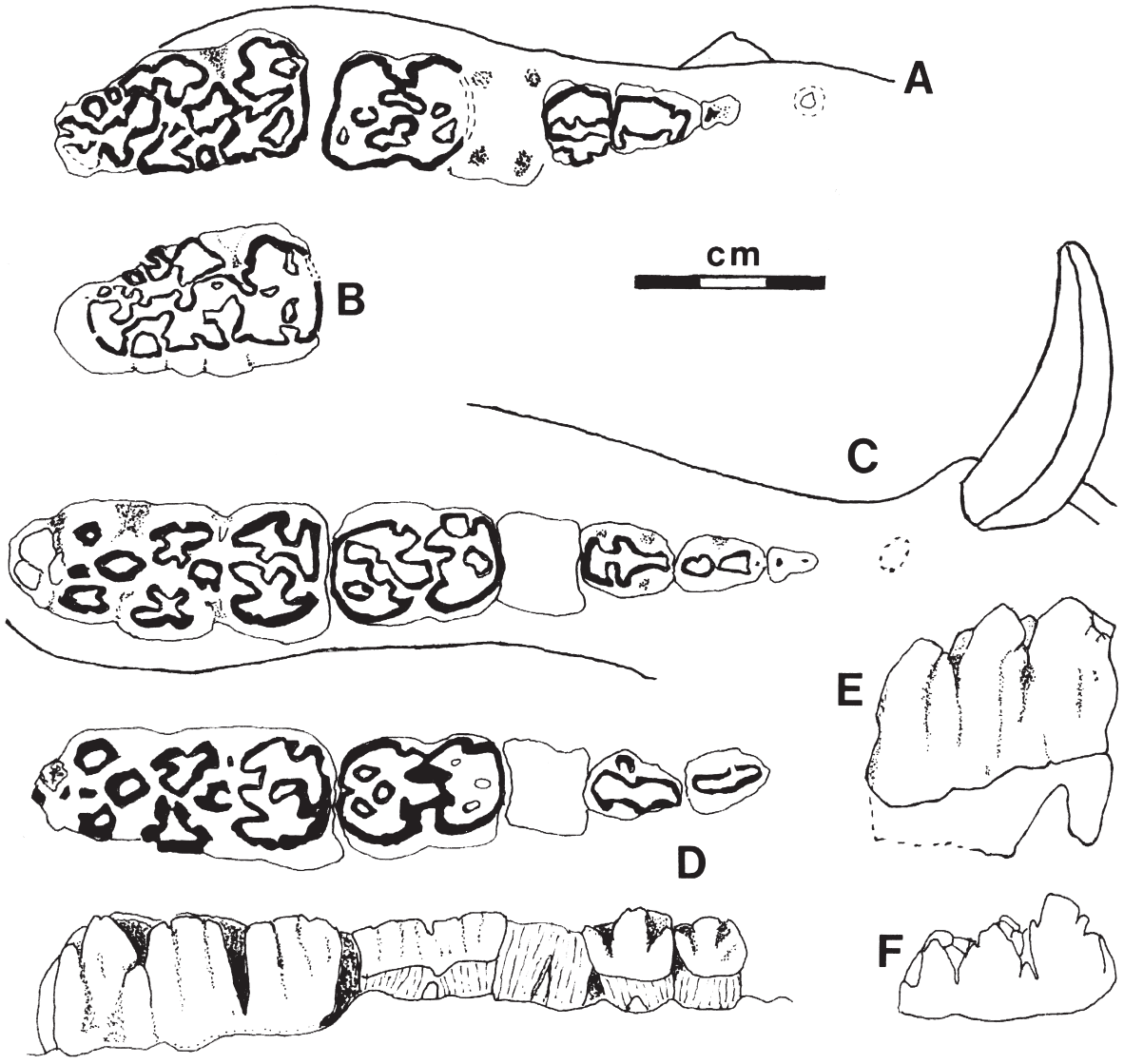


Figure 2. **A**, Occlusal view of RUP3-M3 of *'Potamochoeroides' shawi* in the palate M1391 from Makapansgat. **B**, Occlusal view of crown of RUM3, L1-459, from Member B11 in the Omo Shungura Formation and attributed to *'P.' shawi*. **C**, Occlusal view of LLP1-M3 in a mandible M2081 of *'P.' shawi* from Makapansgat. **D**, Occlusal and inner lateral (lingual) views of LLP3-M3 in incomplete mandibular ramus M302, the type specimen of the species *'shawi'* from Makapansgat. **E**, Lingual view of RUM3 in a maxillary fragment, M303, from Makapansgat, originally the Type of *Potamochoeroides hypsodon*, now absorbed into *P. shawi*. **F**, Lingual view of RUM3 of extant *Potamochoerus porcus*.

not accord with the attractive but simplistic interpretation of mere sexual dimorphism and the possibility that they may be different but related species should be considered.

In the living Suidae, sexual dimorphism is apparent in the upper canines, which are usually significantly larger and more robust in the male than in the female, although in *Hylochoerus* and *Phacochoerus* the female canines are relatively big. However, the morphology of the canines and the general form of the canine flanges are broadly similar in males and females. In the 'males' of *Metridiochoerus* from Koobi Fora the canine flanges are rather like those in the warthog, emerging fairly abruptly from the maxilla at about the same angle or are directed even a little more laterally (Fig. 3C,D). The outer part of the flange is elevated and separated from the main part of the maxilla by a fairly deep parallel groove, much as in *Hylochoerus.* The canine socket is oval with the long axis almost parallel to the palatal plane and shows that the canine was flattened with a broad shallow groove on the dorsal surface and a slightly smaller groove on the ventral surface, very much as in *Phacochoerus.* The nasals widen above the canine flanges and become narrow again above the infraorbital foramen. In the 'female' form the nasals remain narrow and parallel sided. In this form the canine flanges are unusual in that they jut outwards just in front of, or at, the infraorbital foramina. The root portion of the canine is almost parallel to the long axis of the skull and the roots extend so far back that they partly obstruct the nasal passages (Fig. 3A,B). The sockets have a trefoil shape and look rather like an ace of clubs upside down. The two dorsally situated lobes are separated by a fairly shallow groove; the anterior, or medial, groove is also shallow but the posterior groove is deeper. Canines with this morphology exist and are stout and strongly curved, with a slight spiral twist that results in the tips pointing a little upwards and inwards, much as in *Hylochoerus.* These differences in the canines are greater than might be expected with mere sexual dimorphism.

The molars in ER 228 are very similar to the teeth from Kagua, well illustrated by Leakey (1958, pl. 8). Of the

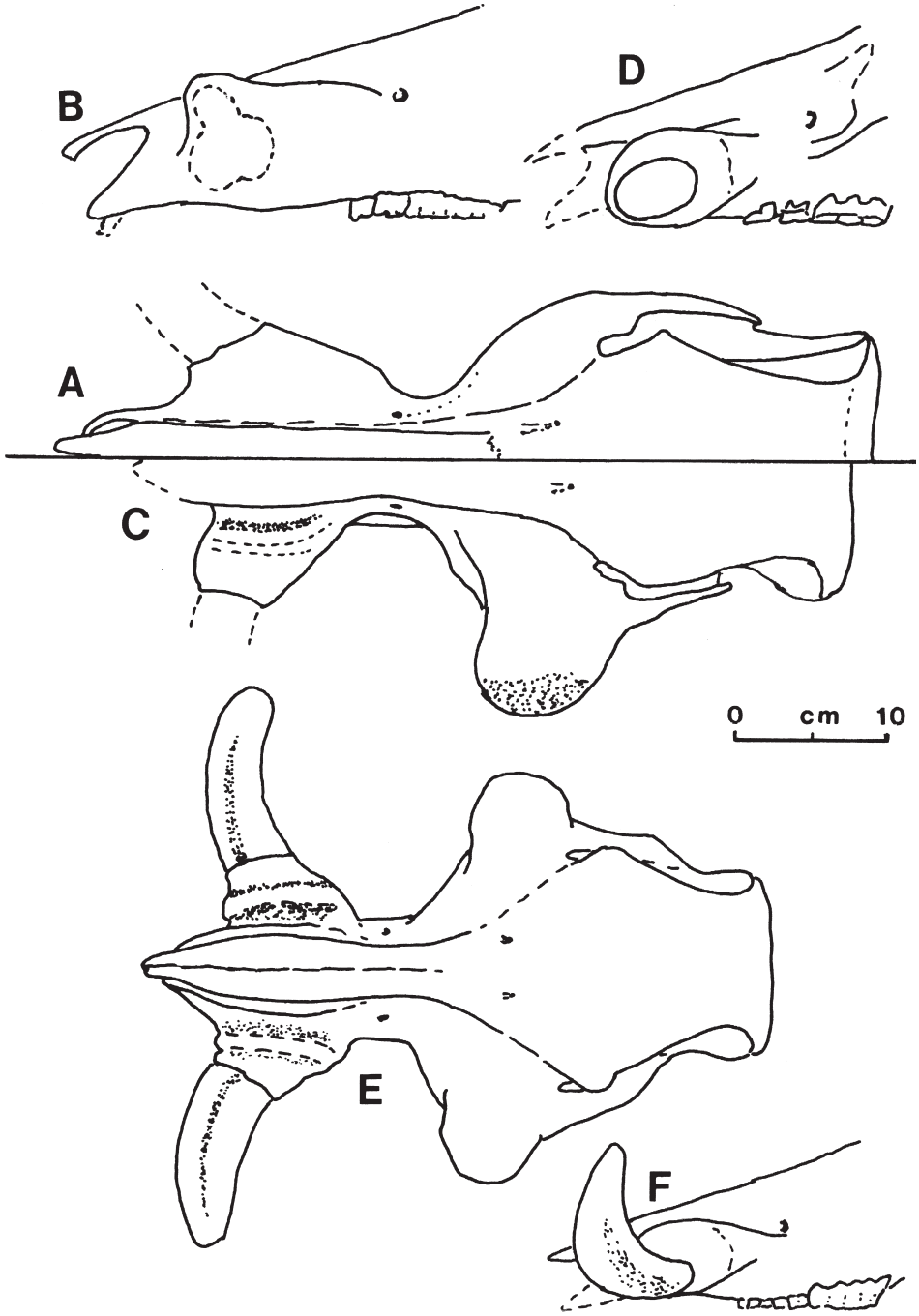


Figure 3. **A**, Dorsal view of hemicranium and **B**, lateral view of canine flange in KNM ER228 from Koobi Fora, supposedly female of *Metridiochoerus andrewsi*. **C** and **D** are similar views of KNM ER1210 from Koobi Fora, supposedly male of *M. andrewsi*. **E**, Dorsal view of cranium O6-332 from lower Member G in the Shungura Formation, attributed to *M. jacksoni*. **F**, lateral view of canine flange of O6-332.

premolars UP4 alone was apparently present in life; only the roots remain but they show that it was a fairly small tooth, later to be shed. Both ER 1210 and ER 1644 were old individuals as the third molars are worn to a border of enamel enclosing a tract of dentine with a number of elongate 'lakes' oriented diagonally across the crown. Despite the advanced age of these two animals, the stumps of moderate sized third and fourth premolars are still present, in contrast to the condition seen in ER 228. These two premolars are very similar to those in the Makapansgat suid but with greater development of the cusps on the lingual side. Even though the 'males' may have come from the lower part of the KBS unit and the 'females' from the upper part, it would be difficult to attribute these morphological difference simply to a time factor; specific separation appears more likely than sexual dimorphism.

Metridiochoerus from the Shungura Formation

In a preliminary assessment of the Suidae from the Lake Rudolf (= Turkana) Basin, Cooke (1976) recognized two species of *Metridiochoerus, M. jacksoni* and *M. andrewsi* and presented scatter diagrams showing the length/breadth relationships in the third molars of the samples from the Omo Shungura Formation and the East Rudolf Koobi Fora Formation, some of which came from below the KBS tuff. The age ranges sampled are respectively 3.0–1.9 Ma and 2.0–1.6 Ma. The Omo material was referred to *M. jacksoni*

Table 1. Statistics for metridiochoerine third molars from various horizons in the Koobi Fora Formation, the Shungura Formation and Makapansgat. *n* = sample size; S.D. = standard deviation; min = minimum; max = maximum; mean = mean; HI = Hypsodonty Index = 100 × height/breadth (maximum in sample). Measurements in mm.

			Upper third molars								
Formation	Unit or 'zone'	*n*	Length				Breadth				HI
			Min	Max	Mean	S.D.	Min	Max	Mean	S.D.	
Koobi Fora	*M. andrewsi*	30	50.2	82.3	65.38	6.50	21.1	30.9	25.75	2.33	257
	N. scotti	12	51.9	76.0	59.78	6.29	24.6	28.9	25.98	1.22	206
Shungura	G up	1			53.8				24.5		143
	G lr	14	44.8	54.5	50.80	2.87	22.3	29.9	25.34	2.08	152
	F	3	44.1	56.8	51.57	5.32	24.1	26.2	25.27	0.87	131
	E	4	45.8	48.0	46.67	0.94	24.5	26.5	25.58	0.95	122
	D	5	47.2	53.0	50.40	2.06	24.0	28.7	26.96	1.64	119+
	C	6	42.5	48.1	45.58	2.00	23.0	24.7	23.73	0.61	126
	B11	1			39.5				22.8		68+
Makapansgat		24	40.0	50.5	45.28	3.01	21.0	26.8	23.75	1.56	121
			Lower third molars								
Formation	Unit or 'zone'	*n*	Length				Breadth				HI
			Min	Max	Mean	S.D.	Min	Max	Mean	S.D.	
Koobi Fora	*M. andrewsi*	32	56.5	84.3	66.32	10.92	18.2	24.8	20.13	3.94	328
	N. scotti	5	53.0	64.5	58.78	4.44	19.0	25.0	22.86	2.43	184
Shungura	G up	3	51.5	64.0	60.60	3.26	18.8	22.0	20.20	1.64	191+
	G lr	18	46.0	64.4	56.99	5.00	18.0	24.9	20.99	2.17	209
	F	4	50.6	62.2	56.33	5.24	17.8	23.2	20.95	2.61	172
	E	6	49.0	58.0	53.73	2.89	20.5	23.5	22.43	1.21	181+
	D	2	45.0	59.0	52.00	7.00	19.2	22.5	20.85	1.65	173
	C	5	44.3	57.9	49.92	6.36	18.3	22.5	19.46	1.53	166
Makapansgat		24	39.2	54.8	46.92	3.99	19.3	23.4	20.66	1.11	130

(formerly *Pronotochoerus jacksoni*) and the bulk of the Koobi Fora material to *M. andrewsi.* Morphologically, the molars of *M. jacksoni* and *M. andrewsi* differ in the relative development of the talon, which is shorter than the trigon in *M. jacksoni* and longer in *M. andrewsi* with additional laterals. The lateral pillars are distinctly separated almost to the base of the crown in *M. jacksoni* but in *M. andrewsi* are in closer mutual contact for much of their height and become confluent near the base of the crown. The height of the crown is equal to or less that the basal length in upper third molars of *M. jacksoni* but greater in *M. andrewsi.* A better measure is the Hypsodonty Index, 100H/B, which is below 150 in *M. jacksoni* upper molars, or 200 in the lowers, while in *M. andrewsi* the corresponding figures are 200 in the uppers and more than 300 in the lowers. The premolars are reduced but *M. jacksoni* retains a functional UP3 in the adult, which is lacking or shed early in *M. andrewsi.*

Unfortunately the only upper third molar shown as coming from Member B in Cooke's 1976 scatter diagrams was L1-113. Harris & White (1979) concluded that the specimen had been mislabelled and astutely recognized it as the antemere of a specimen from Member G. (Although mislabelling is fortunately rare, an upper third molar, O158 was illustrated by Harris & White (1979) in their figs 82 & 83 as from Member B but this locality is recorded by De Heinzelin (1983) as Member C8 or lower C9.) The only upper third molar certainly from Member B11 is L1-459, illustrated by Harris & White (1979) in their fig. 84; it is redrawn here as Fig. 2B for comparison with the corresponding molar in the Makapansgat palate M1391, which is strikingly similar. There is some overlap in the size ranges of the third molars from the Shungura and Koobi Fora formations, as was indicated in Cooke (1993, fig. 3). It is suspected that some of the specimens from the lower part of the Koobi Fora Formation (*'Notochoerus scotti'* zone) may belong to *Metridiochoerus jacksoni.* Table 1 sets out the statistical data separately for the material assigned by Harris (1983) to the *'N. scotti'* and *'M. andrews*i' zones, respectively, as well as for the different Members of the Shungura Formation and for Makapansgat. These data are presented graphically in Fig. 4

Cranial material is rare in the Shungura Formation but there are two good crania in Member G. From the base of this unit is O6-332 and from the top of G is O29-2098, belonging to an individual not yet quite mature. O6-332 is almost complete except for slight dorsoventral compression. It is morphologically very similar to ER 1210, although a little shorter (basilar length 360 mm compared with 380 mm) and has a relatively narrower occipital crest (124 mm compared with 163 mm). The parietal area is wide and flat, or even slightly concave, and the rims of the orbits are swollen and elevated just above the parietal surface, The zygomatic arches are expanded and carry thimble-shaped protuberances, the overall bizygomatic breadth being 279 mm as compared with 324 mm in ER 1210, so that the proportions are essentially similar in the smaller cranium, as is seen in Fig. 3E,F. The canine flanges resemble those of *Hylochoerus* and the canines are

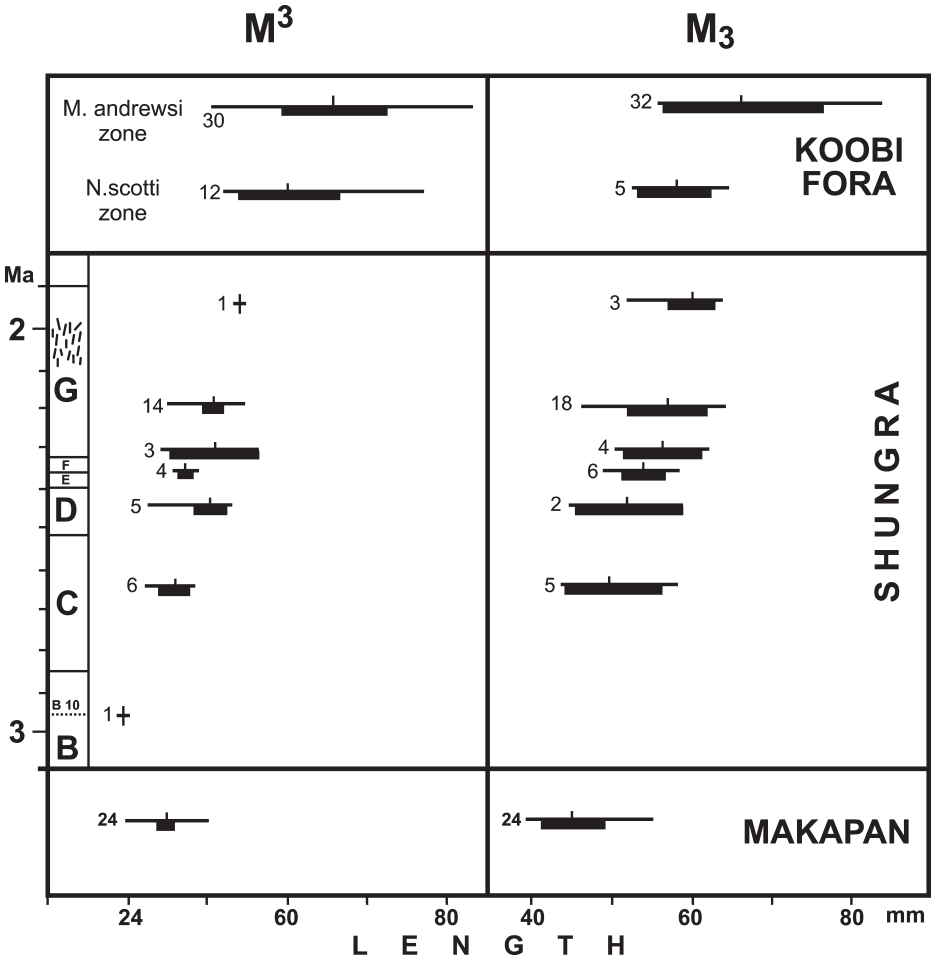


Figure 4. Statistics for third molars referred to *Metridiochoerus jacksoni* from various horizons in the Shungura Formation and comparative figures for metridiochoerine third molars from the Koobi Fora Formation and for Makapansgat Member 3. The figure is sample size, the bar shows range with the heavy bar one standard deviation either side of the mean.

preserved on both sides, very like the tusks of *Phacochoerus* but stubbier and having ribbed enamel on the ventral surface. The palate is damaged but the right UM2 and UM3 are well preserved while on the left side there is a good UM3, a stump of UM1 and intact UP3 and UP4. The teeth are illustrated in Fig. 5A,B, in which the left premolars (C) have been reversed in the occlusal view and transposed to their appropriate positions on the right side to illustrate the appearance of the whole series. The dimensions of the RUM3 are: basal length, 52.8 mm, basal breadth 27.0 mm, and maximum height 31.0+ mm, giving a Hypsodonty Index of 115+. These measurements fit well with the range of other molars from the Shungura Formation attributed to *Metridiochoerus jacksoni* and lie near the bottom of the range for the Koobi Fora sample (see Cooke 1993). Accordingly, this cranium may be taken as representative of *M. jacksoni.* The type specimen of this species is a left lower third molar, M 17083, in the collections of the Natural History Museum, London, and is illustrated here in Fig. 5 in occlusal (G), lingual (H) and buccal (I) aspects.

There are several good mandibles in the Shungura collections that show the retention of both LP3 and LP4, although only LP4 is present in one of the mandibles from the higher levels (Omo 1967 'Type Area Upper'). A good dentition from Member C, O3-126, is illustrated in Fig. 5D and is very similar to the Type specimen in structure but a little less worn. The LP4's are a little smaller and less rectangular than in the bush pig. They have a posterior cingulum and a stout main cone with ridges on either side that produce a cruciform island with wear , sometimes resembling a bird in flight (Fig. 5E,F). The two persistent foveae behind the 'wings' become lakes in more advanced wear. A similar structure is found in the LP4 of the Makapansgat suid (Fig. 2C) and is sufficiently unusual to be of diagnostic value.

Mandibles

The morphology of the mandibles from several different horizons is outlined in Fig. 6 as a series of comparative drawings. *Potamochoerus porcus* is on the left. Next is the Makapan mandible M2081 (with some restoration from M301), which exhibits a wider and shorter symphysis than in *P. porcus* and is not as constricted behind the canines; it also lacks the small shelf at the back of the symphysis which is very characteristic of the bush pig. The Omo mandible O3-126 is shaped rather like the Makapansgat jaw but has a slightly longer diastema behind the canines and also lacks the two anterior premolars. Compared with O3-126 from Member C, the fine jaw that was collected in 1967 from the 'Type Area Upper' (probably Member G but possibly even from Member H) shows greater elongation of the front of the jaw, made more obvious by the fact that the back of the symphysis lies well in front of the anterior

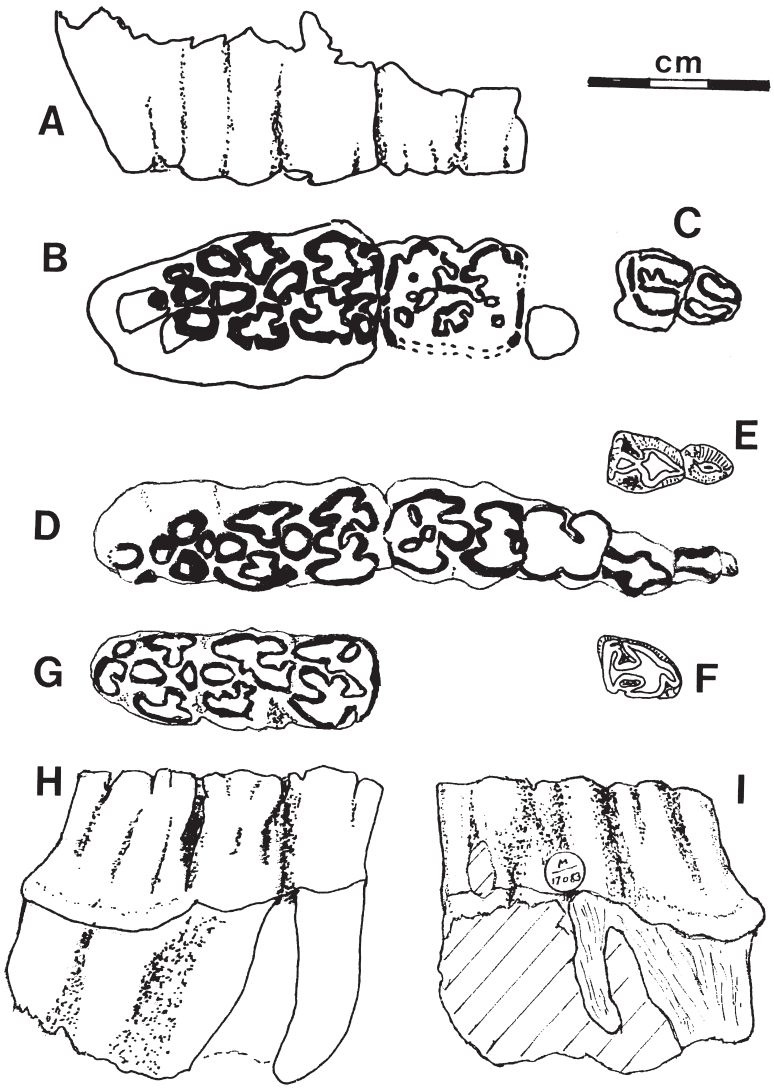


Figure 5. **A**, Outer lateral sketch of UM2-3 in cranium attributed to *Metridiochoerus jacksoni.* O6-332 from lower Member G in the Omo Shungura Formation. **B**, Occlusal view of RUM2-3 shown in A. **C** shows the LUP3-4, drawn reversed and transposed to complete the appearance of the whole series of cheek teeth. **D**, Occlusal view of LLP3-M3 in mandible O3-126 from Member C2 in the Shungura Formation, attributed to *M. jacksoni.* **E**, **F**, Other specimens of LP3 and LP4 from the Shungura Formation to illustrate wear patterns in *M. jacksoni.* **G**, **H**, **I**, Occlusal, lingual and buccal views of LLM3 of the Type of *Pronotochoerus jacksoni* from an uncertain horizon in the Shungura Formation, Natural History Museum, London, M17083.

premolar. The diastema between the canine and the LP4 is substantially increased. Figure 6 also includes one of the most complete mandibles from Koobi Fora, KNM ER222, although the teeth are damaged. The symphysis is long and spatulate. The canine is stout and only gently curved and does not curve back into the body of the ramus but is implanted in the corner of the symphysis and flares upward and outward (Cooke & Maglio 1972, fig. 4). Other mandibles from higher in the Koobi Fora sequence tend to be still more massive. By comparison with Omo 1967, the greater length of the LM3 from Koobi Fora is apparent, with three good pairs of laterals and an incipient fourth pair. In summary, the Makapansgat mandible is morphologically more like the Omo mandible from the lower part of the Shungura Formation than it is like either the mandible of *P. porcus* or that of the Koobi Fora *Metridiochoerus.*

DISCUSSION

In view of the fact that *Potamochoerus* has a very poor fossil record even in the later Pleistocene, it may have been naive to assume that a three million year old ancestor was sufficiently like the extant bush pig for comparison to be meaningful. Specimens from Pliocene deposits that were originally referred to *P. porcus* have subsequently come to be regarded as belonging to *Kolpochoerus afarensis* which, however, may itself be ancestral to *Potamochoerus* (see White 1995, p. 181). In view of the similarity of *K. afarensis* to the bush pig, it may still be reasonable, with caution, to use the living form as a proxy for the ancestor.

The molars of *K. afarensis* are smaller than those of the living bush pig and have thicker enamel and less folding. There are also resemblances in the molars of *K. afarensis* to those of *Metridiochoerus jacksoni* in which the pillars are less bunodont but not yet fully columnar. The Makapansgat material appears to represent one of the members of this early differentiation and mis-assignment of particular specimens within the overall complex is possible. The cranial fragments of the Makapan suid conform to the morphology of a fairly basic suid and *Potamochoerus porcus* provided a somewhat better comparison than *Sus*, which

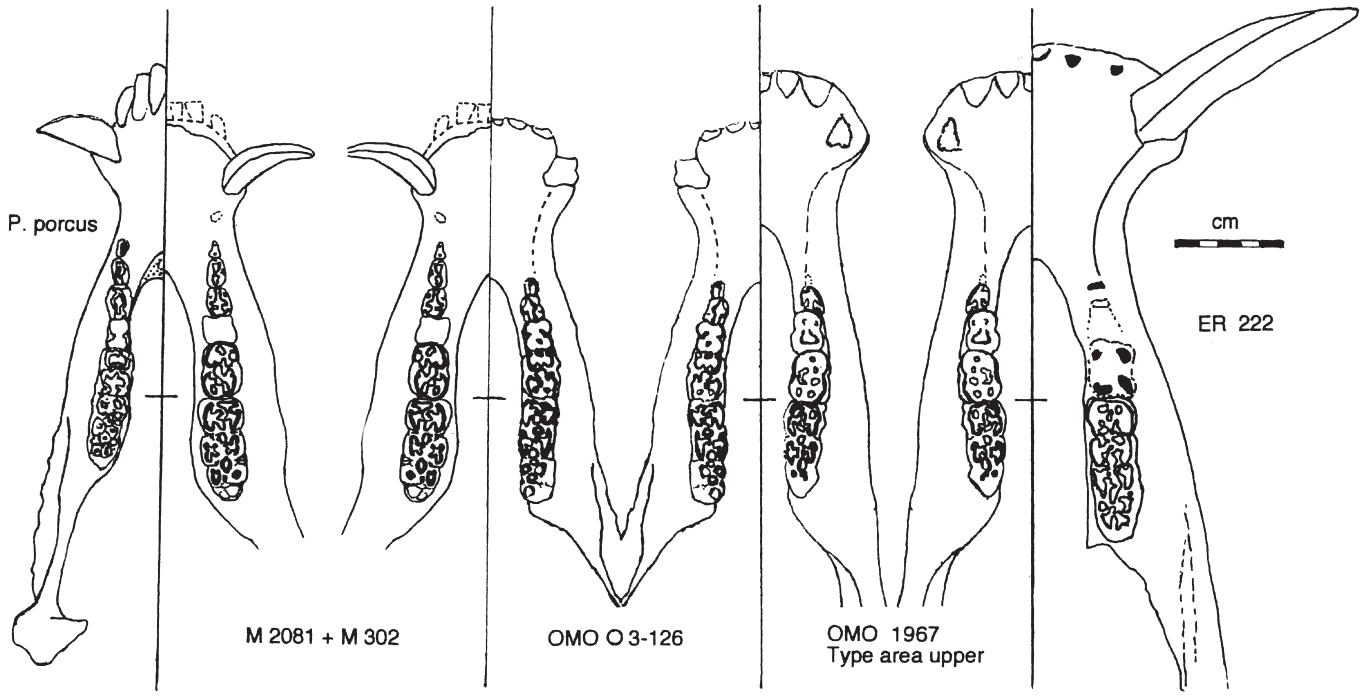


Figure 6. Comparative occlusal views of mandibles, aligned on the M2/M3 boundary. The species represented are, from left to right: extant *Potamochoerus porcus*; Makapansgat *'P.' shawi,* M2081/M302; *Metridiochoerus jacksoni* O3-126 from Member C2 of the Shungura Formation; *M. jacksoni* Omo 1967 from Member G or H of the Shungura Formation; and *M. andrewsi* KNM ER222 from the *M. andrewsi* zone of the Koobi Fora Formation.

led to the designation *Potamochoeroides*. However, the new reconstruction of the Makapansgat cranium provides a slightly different picture.

Figure 7 shows in bold outline the reconstructed cranium of the Makapansgat *Potamochoeroides shawi* compared with (A) *Potamochoerus porcus* and (B) with the Omo cranium O6-332 attributed to *Metridiochoerus jacksoni.* The crania have been aligned on the front of the third molar. Relative to the bush pig, the Makapansgat cranium shows distinct elevation of the occipital condyles and some elevation of the parietal area and orbits as well as backward extension of the braincase and occiput. These features are more developed in the Omo cranium and are characteristic of *Metridiochoerus,* becoming more exaggerated in the Koobi Fora 'female' material and reaching an extreme in *M. compactus.* Thus by comparison with a bush pig, the Makapansgat cranium already shows evidence of the characteristic features of *Metridiochoerus* that are not seen in *Potamochoerus porcus.*

What may be regarded as an important defining characteristic of the cheek teeth of *Metridiochoerus* is the precocious wear on the first and second molars so that by the time the back of the third molar comes into wear, the first molar is reduced to a tract of dentine or is already a mere stump. At this stage the second molars are largely dentine with scattered 'lakes' of enamel. more marked in the upper than in the lower molars. This trend is already apparent in the Makapansgat suid whose cheek teeth are very similar to those attributed to *M. jacksoni* (see Figs 2 & 4). The Omo third molars are a little higher crowned with a Hypsodonty Index of up to 150 in the uppers and up to 200 in the lower third molars as compared with close to 120–130 for both uppers and lowers in the Makapansgat sample. The Makapansgat suid had a complete premolar dentition, although the first premolars may be shed early. *M. jacksoni* retains a functional UP3 in the adult although in some of the later lower dentitions only LP4 is retained. The morphology of both upper and lower P4s is very similar in both the Makapansgat suid and in *M. jacksoni.*

As may be seen in Fig. 4, *M. jacksoni* is a fairly stable species through Shungura Members C to G, showing only a slight increase in the length, most apparent in the lower molars. The solitary upper third molar from Member B (L1-459) is shorter than the later specimens and the enamel pattern is strikingly similar to the corresponding tooth in the Makapansgat palate, M1391 (Fig. 2) and could conveniently be designated *Metridiochoerus* cf. *shawi.* The age of this specimen is close to 2.95 Ma, which would accord with other estimates of the age of Makapansgat Member 3. Although a single specimen would provide a dubious basis for correlation, it may offer a reasonable indication of the age. The only other suid from Member 3 is a *Notochoerus,* represented by a pair of robust lower third molars originally referred by Ewer (1958) to *N. euilus.* In 1993 Cooke referred these mandibles, together with a more recently discovered incomplete lower third molar, to *Notochoerus scotti.* It was pointed out that *N. scotti* was represented by robust specimens in he lowest levels, tending to become narrower and higher crowned in the younger levels and that the Makapansgat specimens accorded best with the samples from Members B and C. Although the evidence is far from conclusive, the two suid species both suggest an age about equivalent to that of Shungura Members B and C.

In the light of this re-analysis of the data, it seems desirable to abandon the genus *Potamochoeroides* and to designate the Makapansgat suid *Metridiochoerus shawi* as an early stage in the evolution of the *Metridiochoerus* complex but

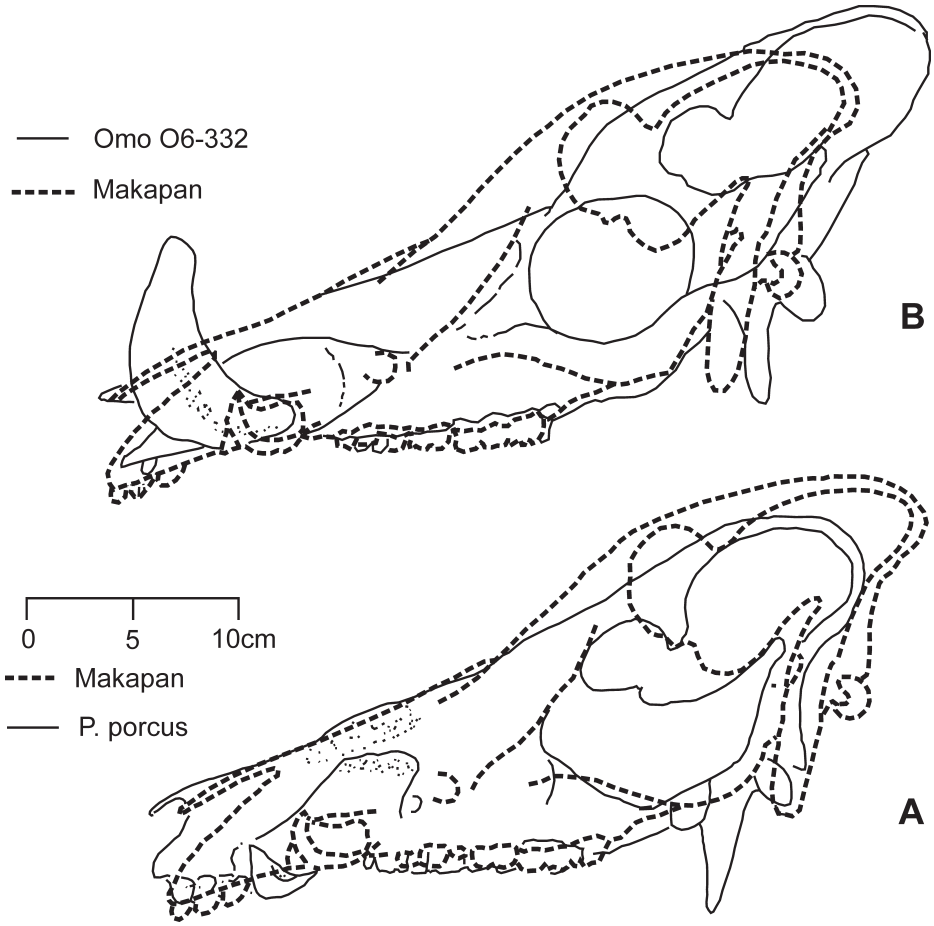


Figure 7. Comparative lateral views of the reconstructed cranium of the Makapansgat suid *'P.' shawi* in bold outline and, in light lines. **A**, Adult male of *Potamochoerus porcus* and **B**, undescribed male cranium, O6-332, attributed to *Metridiochoerus jacksoni* from the Omo Shungura Formation Member G1.

distinguished from *M. jacksoni* by the retention of the anterior premolars, the hypsodonty of the molars, and the different canines.

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