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UNDESCRIBED SUID REMAINS FROM BOLT'S FARM AND OTHER TRANSVAAL CAVE DEPOSITS

by

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ABSTRACT

Although individual suid specimens from other sites have been described, only Makapansgat has been treated comprehensively, but much new material has come to light in the past three decades. The University of California African Expedition worked several sites of different ages at Bolt's Farm and the material recovered includes a virtually complete, slightly compressed, skull of *Phacochoerus modestus* (= *P. antiquus* Broom 1948) from Pit 3, associated with *Antidorcas recki*, and also several cranial and dental fragments from Pit 14 that belong to the typical Makapansgat *Potamochoeroides shawi*. Bolt's Farm was the source of a cranial specimen described by Broom as "*Notochoerus meadows*i" (= *Metridiochoerus andrewsi*); other specimens referred to this taxon and described by Shaw as from "Sterkfontein Lime Works" more probably came from Bolt's Farm as well. Broom's cranium and a pair of mandibles have closer resemblances to *Metridiochoerus jacksoni* of East Africa. Swartkrans has yielded both described and undescribed material referred to *Phacochoerus modestus* and to *Metridiochoerus*. Discounting Shaw's material, only one small specimen has come from the Sterkfontein Type Site, a mandible fragment of a juvenile with an incompletely formed third molar in alveolus but it can be matched remarkably closely with a specimen from Makapansgat and there is very little doubt that it belongs to *Potamochoeroides shawi*. An undescribed third molar from the pink breccia at Makapansgat is comparable with early *Notochoerus scotti* from East Africa. The status of *Notochoerus capensis* is reconsidered.

KEY WORDS: Suidae, Plio-Pleistocene.

INTRODUCTION

Curiously, although a number of individual specimens of suids have been described from the Transvaal cave breccias, Makapansgat is the only site to have been treated as a whole (Ewer, 1958), but a good deal of additional material has come to light during the past three decades. The Makapansgat suids have been reconsidered recently by Bender (1992). Accordingly, the present account will concentrate on some interesting or important specimens from the other Transvaal cave breccias that seem to warrant description or reconsideration.

BOLT'S FARM

"Notochoerus meadowsi" *material*

In 1948 Broom gave a very brief description of a partial cranium from Bolt's Farm (TM BF 1; Figure 1) which he referred to *Notochoerus meadowsi* and he included drawings of the upper second molars but did not illustrate the specimen itself. This scanty account was amplified by Ewer (1956) who provided measurements of the teeth and figured one of the associated canines; she followed Cooke (1949) in his (incorrect) designation as *Tapinochoerus meadowsi*, now generally regarded as a synonym of *Metridiochoerus andrewsi*. Later Broom recovered two incomplete lower third molars from Bolt's Farm (TM BF 2) but the matrix is slightly different. There is also in the Transvaal Museum a pair of undescribed mandibular rami (here called "X" and "Y") with fully formed but unworn third molars. The matrix of these mandibles is extremely like that of Broom's cranium from Bolt's Farm and, as the dental age is similar, it is highly probable that they were found at Bolt's farm after the original discoveries and likely that they belonged to the same individual, so are regarded as part of TM BF 1.

Subsequent to Broom's description of the cranium, Shaw (1938, 1939) described some teeth from "the Sterkfontein Lime Works" which he thought established that *Notochoerus meadowsi* was a synomym of *Notochoerus capensis*, a view that Ewer (1956) rejected. Shaw originally had at his disposal two lower third molars ("A" and "B") and one upper third molar ("C") but in his 1939 paper added an additional damaged upper third molar ("D") that might be the mate of "C". His specimens are now in the Bernard Price Institute for Palaeontological Research and are numbered as follows: A - BPI M 8913; C - M 8912; D-M 8914; specimen B has apparently been lost. The matrix is not like that of the Sterkfontein Type Site and, as the term "Sterkfontein" was at that time used very loosely, it is probable that they came also from Bolt's Farm or possibly even from Swartkrans. The specimens are illustrated in Figure 2. Revised measurements are set out in Table 1.

Figure 1. Partial cranium of immature individual from Bolt's Farm, TM BF 1. A, left lateral view showing unerupted LM_3. B, palatal aspect with little worn second molars, and occclusal view of detached RM^3. C, inner lateral view of RM^3, showing section line. D is a dorsal view of the sectioned surface of the crown displaying the complex enamel pattern typical of *Metridiochoerus*. 43% natural size.

TABLE 1

Measurements (mm) on *Metridiochoerus* from Bolt's Farm

NUMBER	TOOTH	LENGTH		BREADTH	HEIGHT
		occlusal	basal		
TM BF 1	LM^2	35.5	26.5e	22.2	20+/19+
	RM^2	35.1	26 e	20 e	24+/29+
(unerupted)	LM^3		59 e	21 e	53e/?/?/?
(unerupted)	RM^3		58 e	21.5e	55/57.5/50/39
left upper canine		+84+		max.42.5/min.34	
right upper canine		+130+		max.45.0/min.31.5	
TM BF 2	LM_3		(+54) 70e	21.0	-/62.5/65+/68e/56e
'A' M 8913	LM_3		78.8	22.8	50+/57/62/56/10
on sectioned surface			69.6	21.7	
'B'*	M_3		(77)	(20)	-/-/(66)/-/-
'C' M 8912	LM^3		+54+ (66e)	30.5	51/60.5/62.5
on sectioned surface			61.8	30	
'D' M 8914	RM^3		63e	22+ (30e)	44+/52.6/63.3/64
TM BF 1 'X'	RP_4		11.1	7.8	10.4+
	RM_1		17.4	13e	9.0+
(cracked)	RM_2	31.6	22 e	16.7	17+/18+
(damaged)	RM_3		57 e	16 e	45.9/43/34e
diastema	$C\text{-}P_4$	37.5			
lower canine		med.17.2/ post.10.2e/ lat.14e			
TM BF 1 'Y'	LM_3		58.5	17 e	49/50.2/46.7/38.6/31.

*measurements given by Shaw 1938
e = estimated measurement; med = medial; post = posterior; lat = lateral; max = maximum; min = minimum; heights are given on succesive lateral pillars, starting at the front of the crown.

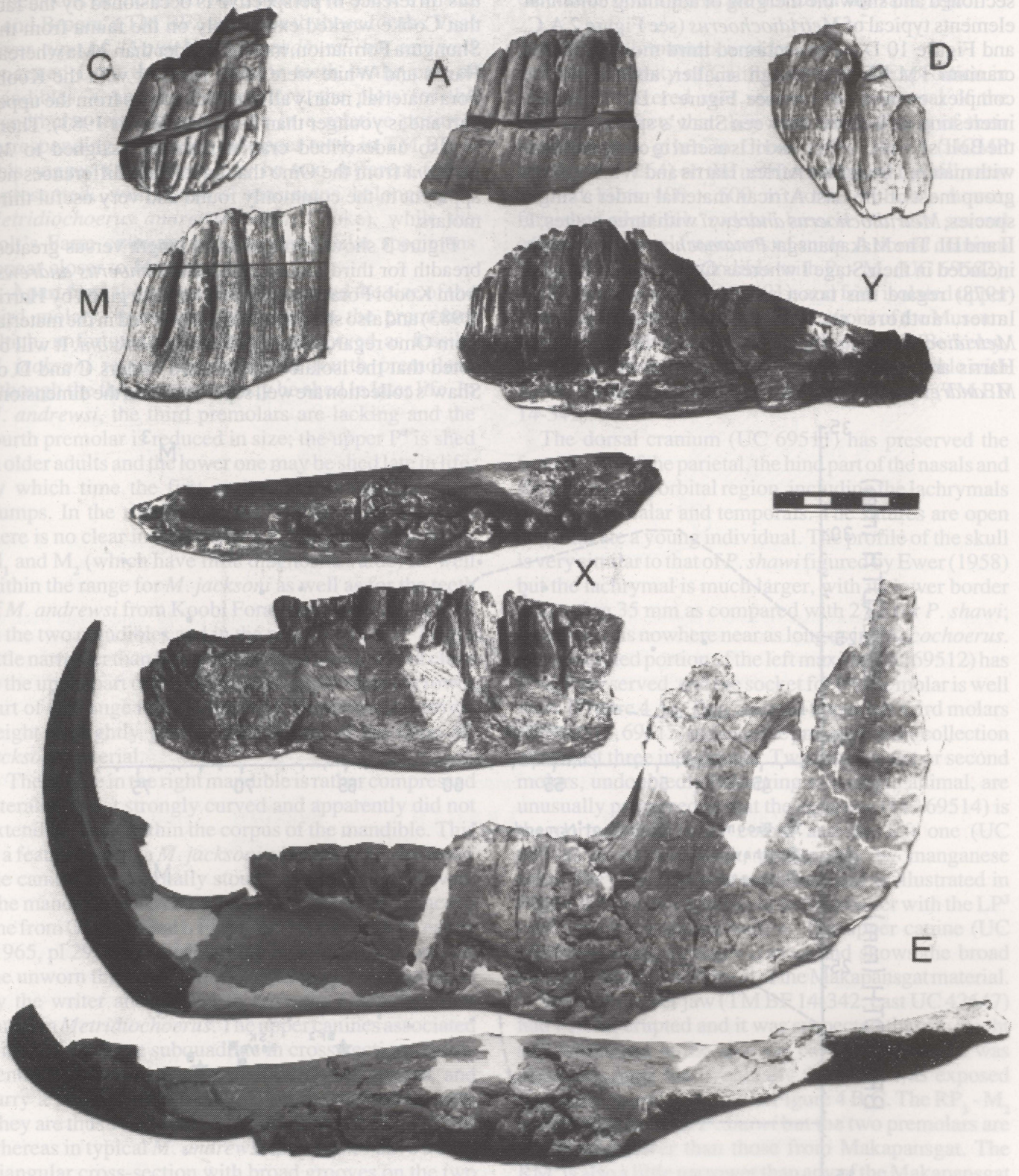

Figure 2. A, C and D are specimens from Shaw's collection (Shaw's specimen B is lost). A is an LM_3 (BPI M 8913). C is an LM^3 (M 8912) of which the enamel pattern on the sectioned surface is shown in Figure 10 D. D is a RM_3 (M 8914). For comparison, M is the RM^3 from the Vaal River that was originally the type of *Notochoerus meadowsi* (sectioned surface shown in Figure 10 C). X and Y are the hemimandibles in the Transvaal Museum believed to belong with Broom's cranium TM BF 1 (see Figure 1). "Y" is shown in inner lateral aspect and its mate "X" in occlusal and inner lateral views. For comparison, E is a specimen from Olduvai Bed I, FLK N1 335, attributed to *Metridiochoerus jacksoni*. One half natural size.

Shaw's lower M_3 ("A") and upper M^3 ("C") were sectioned and show the merging of adjoining columnar elements typical of *Metridiochoerus* (see Figure 2 A,C, and Figure 10 D). The sectioned third molar from the cranium TM BF 1, although smaller, also shows the complex enamel pattern (see Figure 1 D). There are interesting differences between Shaw's specimens and the Bolt's Farm cranium and it is useful to compare them with material from East Africa. Harris and White (1979) group most of the East African material under a single species, *Metridiochoerus andrewsi* with three stages, I, II and III. The Makapansgat *Potamochoeroides shawi* is included in their Stage I whereas Cooke and Wilkinson (1978) regard this taxon as generically distinct. The latter authors recognize a distinct species, *Metridiochoerus jacksoni*, for most of the material in Harris and White's Stage II and restrict the usage of *M. andrewsi* to Stage III, although including some material from Stage II (see Cooke 1985). At least in part this difference in perspective is occasioned by the fact that Cooke worked extensively on the fauna from the Shungura Formation, most of it older than 2 Ma whereas Harris and White were more familiar with the Koobi Fora material, nearly all of which comes from the upper part and is younger than 2 Ma (see Harris 1983). There is also undescribed cranial material assigned to *M. jacksoni* from the Omo that underlines differences not apparent in the commonly found and very useful third molars.

Figure 3 shows plots of basal length versus greatest breadth for third molars of *Metridiochoerus andrewsi* from Koobi Fora, based mainly on data given by Harris (1983) and also shows the range observed in the material from Omo regarded by Cooke as *M. jacksoni*. It will be noted that the isolated upper third molars C and D of Shaw's collection are well separated from the dimensions

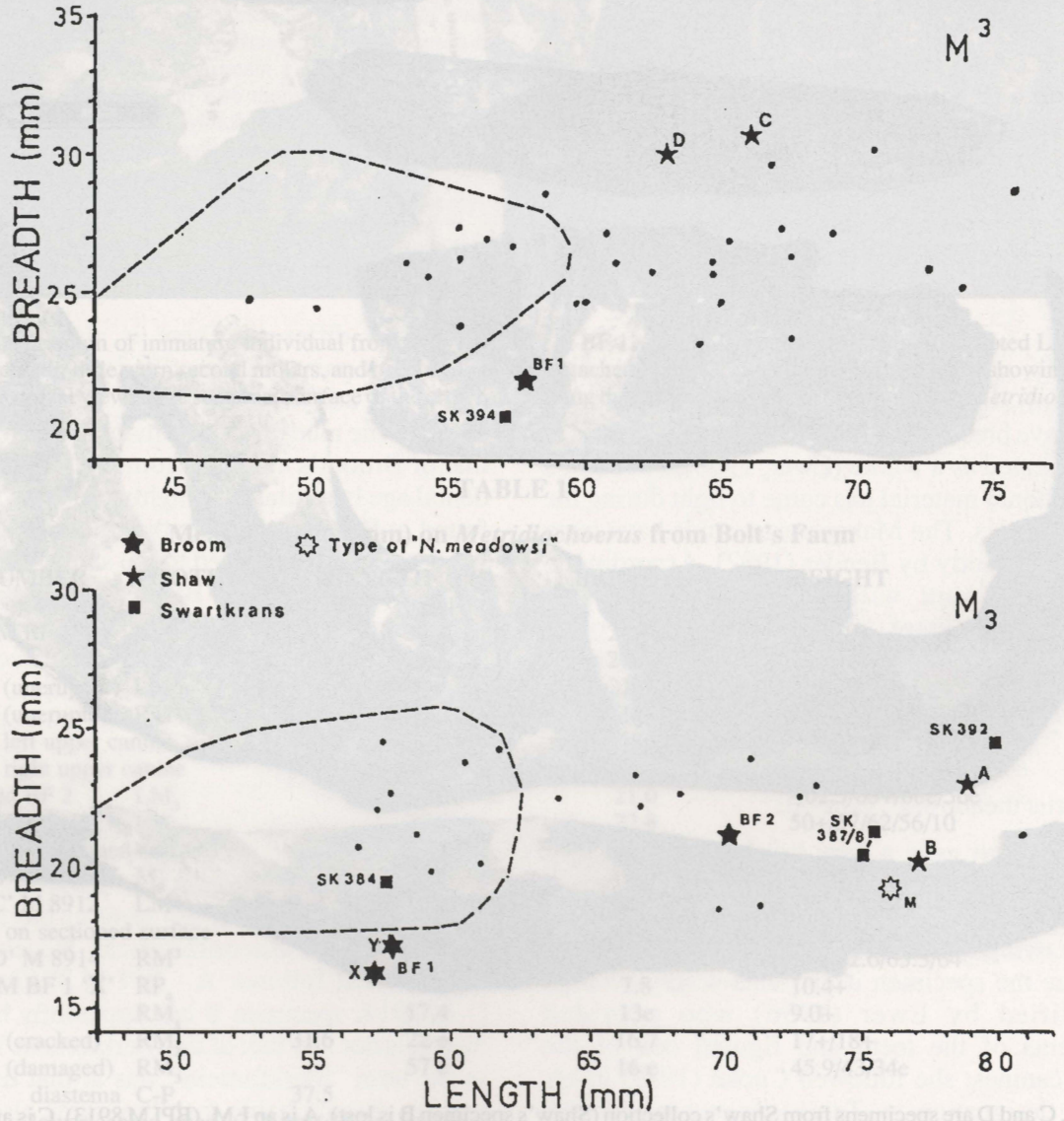

Figure 3. Length-breadth plots for specimens from Koobi Fora, shown by dots, attributed to *Metridiochoerus andrewsi* by Harris (1983). The dashed line encloses the field of variation for material from Omo ragarded by Cooke (unpublished) as *Metridiochoerus jacksoni*. Shaws third molars, A, B, C, D, are indicated by stars, as also are Broom's specimens TM BF 1 and TM BF 2 from Bolt's Farm. Five specimens from Swartkrans are also included. M is the original type of *Notochoerus meadowsi*.

of the teeth in Broom's cranium TM BF 1. Likewise, the dimensions of the lower third molars in Shaw's A and B and Broom's TM BF2 are close to those for the Vaal River type of "*Notochoerus meadowsi*" but are well separated from the plots for the teeth in the pair of mandibles X and Y. Furthermore, the plots for the mandibular teeth X and Y are in a relative position corresponding to that for the upper teeth in TM BF 1. This suggests that there may be two different forms represented, with Shaw's specimens belonging to *Metridiochoerus andrewsi* (*sensu* Cooke), while the Bolt's Farm cranium and the mandibular specimens appear closer to *M. jacksoni*.

Apart from the cranial differences and the size of the third molars, there are differences in the premolars which, unfortunately, are rarely preserved as fossils. *M. jacksoni* retains the third and fourth premolars, although the third premolar may be shed in later life. In *M. andrewsi*, the third premolars are lacking and the fourth premolar is reduced in size; the upper P^4 is shed in older adults and the lower one may be shed late in life, by which time the first molars are reduced to mere stumps. In the right mandible "X", P_4 is retained but there is no clear indication of a P_3 having been present. M_1 and M_2 (which have little diagnostic value) lie well within the range for *M. jacksoni* as well as for the teeth of *M. andrewsi* from Koobi Fora. The third molars both in the two mandibles and in the cranium TM BF 1 are a little narrower than in the East African material but close to the upper part of the range of *M. jacksoni* or the lower part of the range for *M. andrewsi*. However, the crown height is slightly greater than in any of the Omo *M. jacksoni* material.

The canine in the right mandible is rather compressed laterally, is not strongly curved and apparently did not extend far back within the corpus of the mandible. This is a feature noted in *M. jacksoni* whereas in *M. andrewsi* the canines are normally stouter and even less curved. The mandible of TM BF 1 has a striking resemblance to one from Olduvai Bed I, FLK N1 335, figured by Leakey (1965, pl 29) who ascribed it to *Notochoerus* cf *euilus*; the unworn third molar of this specimen was sectioned by the writer and proved to have the enamel pattern found in *Metridiochoerus*. The upper canines associated with TM BF 1 are subquadrate in cross-section, dorso-ventrally flattened with a shallow dorsal groove, and carry a band of ribbed enamel on the ventral surface. They are thus very similar to the canines of *M. jacksoni* whereas in typical *M. andrewsi* the canines have a sub-triangular cross-section with broad grooves on the two lateral surfaces as well as dorsally so that at the alveolar margin the cross-section is almost a trefoil shape. It is thus difficult to be certain of the status of TM BF 1 and the (associated?) mandibles as there are resemblances both to *M. andrewsi* and *M. jacksoni* but on balance it may be best to refer it to *Metridiochoerus* cf *jacksoni*. *M. jacksoni* and *M. andrewsi* occur together at Omo in Member G and in Olduvai Bed I, of similar age (c.2 Ma). It must also be borne in mind that the many pockets of breccia at Bolt's Farm are not all of the same age.

Remains of Potomochoeroides shawi

The University of California African Expedition in 1947-48 recovered suid remains from several of the different pockets that they excavated; a map of their localities was given in Cooke 1991. Pit 14 (UCMP locality V 67264) on the northern flank of the hill, near the old kilns 400 - 500 m north of Bolt's house, furnished plentiful "rodent" breccia but also several cranial and dental fragments of suids. A dorsal cranium (UC 69511), a left mandible with P_3 - M_1 (UC 69582), a left upper canine (UC 89491), and four isolated upper teeth (UC 69513-16) are in the collections of the Museum of Paleontology at the University of California, Berkeley, but the most interesting specimen, a right mandible with P_3-M_3, was donated to the Transvaal Museum (TM BF 14-342).

The dorsal cranium (UC 69511) has preserved the frontal, part of the parietal, the hind part of the nasals and the bones of the orbital region, including the lachrymals but not the malar and temporals. The sutures are open and indicate a young individual. The profile of the skull is very similar to that of *P. shawi* figured by Ewer (1958) but the lachrymal is much larger, with its lower border measuring 35 mm as compared with 27.5 for *P. shawi*; however, it is nowhere near as long as in *Phacochoerus*. An associated portion of the left maxilla (UC 69512) has P^3 - M^1 preserved, and the socket for P^2; the molar is well worn (Figure 4 A). Two isolated upper left third molars (UC 69513, 69515) indicate the presence in the collection of at least three individuals. Two unworn upper second molars, undoubtedly belonging to a single animal, are unusually preserved in that the right one (UC 69514) is the normal dark ivory colour and the left one (UC 69516) is stained black, presumably by manganese salts. The right one was sectioned and is illustrated in Figure 4 A, but reversed so as to fit in better with the LP^3 - M^1 which are shown with it. The upper canine (UC 89491) is stout, strongly curved and shows the broad ventral enamel band typical of the Makapansgat material.

The right lower jaw (TM BF 14-342; cast UC 42647) had P_3 - M_2 erupted and it was suspected that M_3 might still be present in the alveolar cavity. The matrix was extremely hard but eventually the tooth was exposed successfully and is shown in Figure 4 B,C. The RP_3 - M_2 are close to those of *P. shawi* but the two premolars are slightly narrower than those from Makapansgat. The RM_3 is also a little narrower than any of the Makapansgat specimens, perhaps because it is still incompletely formed, and it also differs slightly in lying at the upper limit for crown height. The form of the columns is a little different and it seems probable that it represents a variety later and more evolved that the typical *P. shawi* of Makapansgat. It is unfortunate that no upper third molar is available from this locality. The dimensions of all these specimens are listed in Table 2.

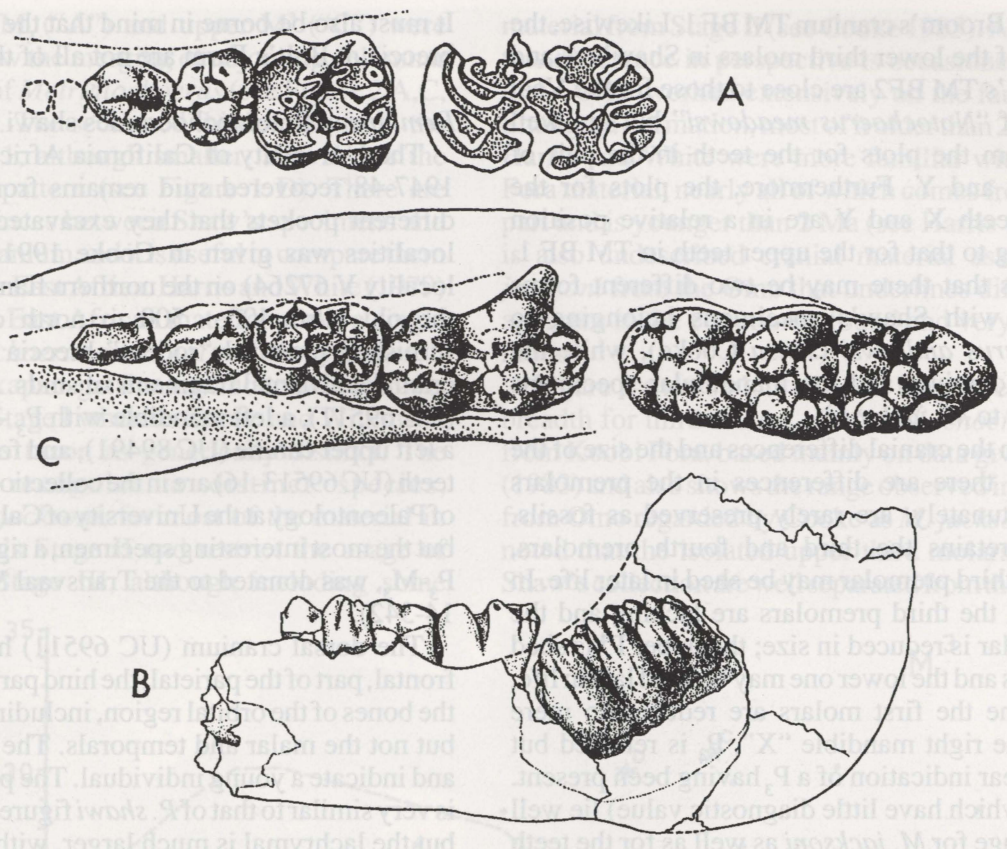

Figure 4. A shows occlusal views of a portion of left maxilla (UC 69512) from Pit 14, Bolt's Farm with LP^3-M^1 in moderate wear; the sectioned surface of an isolated RM^2 is added but reversed for better comparison (Natural size). B is an inner lateral view of a partial mandible, TM BF 14-342, from the same locality, with the unerupted RM_3 exposed after removal of the bone (One half natural size). C gives occlusal views of the teeth in the mandible (Natural size). All are referred to *Potamochoeroides shawi*.

TABLE 2

Dimensions (mm) of teeth from Pit 14, Bolt's Farm referred to *Potamochoeroides shawi*

	NUMBER	TOOTH	LENGTH occ.	LENGTH bas.	LENGTH max.	BREADTH occ.	BREADTH bas.	HEIGHT
Upper dentitions								
Loose:	UC 69513	LP^3	10.5	11.0	11.1	7.5	9.5	9.5
	UC 69515	LP^3	12.0	12.1	12.5	7.0	10.5	11.0
Maxilla:	UC 69512	LP^3	10.5	10.5	12.0	7.0	10.5	11.0
		LP^4	11.0	10.5	11.0	12.0	13.0	11.5+
		LM^1	18.5	16.0	18.5	14.5	17.0	6.0+
Loose:	UC 69516	LM^2	28 e	22.0	31.0	14 e	22.0	22.0
	UC 69514	RM^2	28 e	21.0	32.0	14 e	21.0	22.0
Mandible								
	TM BF 14-342	RP_3	11.0	10.0	11.0	4.0	5.5	10.0+
		RP_4	12.0	12.0	13.0	4.5	9.0	14.0+
		RM_1	17.0	15.0	17.0	11.0	12.5	6.5+
		RM_2	24.5	20.0	27.0	11.0	15.5	18.5+
	unerupted	RM_3	40.0	47.5	47.5	13.5	17.0	29.0/20.5

occ = occlusal; bas = basal; max = maximum; e = estimated measurement

Skull of Phacochoerus modestus

Pit 3 of the University of California's workings lay very close to the old lime kilns. There was much loose fill containing various living taxa and two crude stone-age cores in chert and quartzite. The solid breccia yielded much rodent material and some 70 fragmentary remains of mammals including several specimens of *Antidorcas recki*, a fine skull of *Crossarchus*, *Suricata suricatta*, hyaena, *Procavia transvaalensis*, and an almost complete, laterally compressed skull of *Phacochoerus modestus*. The suid skull has been presented to the Transvaal Museum (TM BF 3-335).

The skull is remarkably complete, although somewhat compressed, and still has the axis and atlas vertebrae

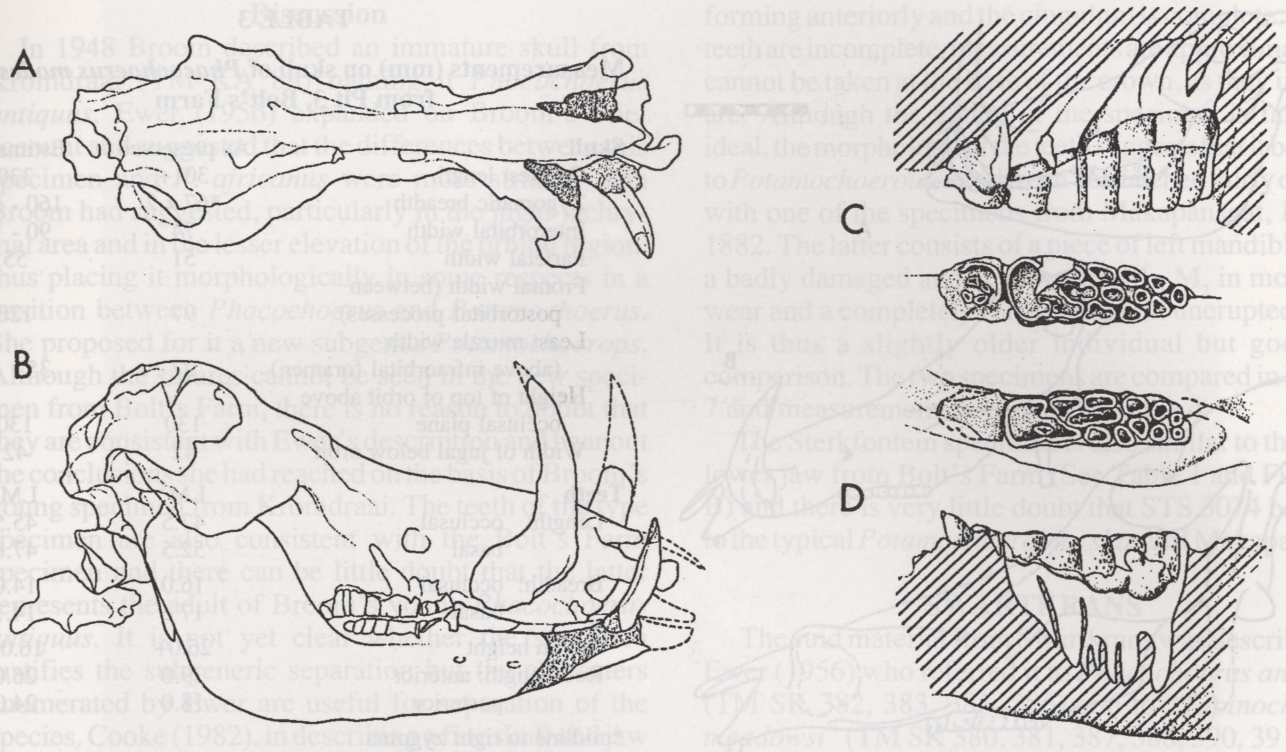

Figure 5. A, B, dorsal and right lateral views of skull of *Phacochoerus modestus* from Pit 3, Bolt's farm (TM BF 3-335), one quarter natural size. C shows the buccal and occlusal aspects of the RM^{2-3}, and D the lingual and occlusal aspects of the RM_{2-3} but C is reversed in drawing for better comparison with the lowers. One half natural size.

associated with it. It is smaller that the normal adult living *Potamochoerus* or *Phacochoerus* and, although a mature adult, in general form resembles an immature individual of the latter genus. On the left side the zygomatic arch is lost, together with part of the ascending ramus of the mandible. Viewed from below, the mandibular rami are seen to be almost parallel and it is clear that only a moderate amount of lateral compression has taken place. This is seen also in the dorsal view of the skull shown in Figure 5. However, the degree of compression is not extreme and from measurements on the rami it is possible to arrive at a reasonable estimate of its extent. The lower jaw has been shifted forward slightly as a result of some compression on the back of the cranium. The right upper canine has been bent slightly forward. A restored drawing is shown in Figure 6, the restoration being based on an estimate of the degree of compression of the palate, which is known in other specimens. The dimensions of the skull, as preserved, are given in Table 3, together with estimates of the dimensions based on the restorations.

Although the skull is *Phacochoerus*-like in general appearance, it will be seen from the reconstructions in Figure 6 that there are also important differences. The back part of the skull is not as elevated as in *P. africanus* and the orbits do not rise above the general surface of the fronto-parietal surface, although they are flush with it. The rest of the zygoma is considerably elevated above the level of the infraorbital foramen, as in *Phacochoerus*; however, as the orbits are not as high above the palatal plane, the zygomatic arch is not as broad and plate-like as in the warthog. The ascending ramus of the mandible is also not as long as in *Phacochoerus*, and the mandible is relatively thinner anteriorly and less spatulate. The canines have the general shape of those of the warthog but are relatively less robust, although this may be to some extent a sexual tendency and the fossil may be a female. The surface of the canines is damaged but there does not seem to be any enamel covering. The occipital region, though damaged, does not show the distortions exhibited in *P. africanus* but resembles the occiput of *Potamochoerus*; however, the supraoccipital projects farther posteriorly and gives the appearance of having been rotated backwards about a line through the ear region so as to provide additional leverage for the neck muscles. The auditory bullae are very similar to those of *Phacochoerus* but are smaller and more pointed; the paroccipital process is very long, reaching almost to the occlusal plane. From the dorsal aspect, it seems that the zygomatic arches do not flare out as much as in *P. africanus* and resemble superficially – but not structurally - the contour seen in *Hylochoerus*. The fronto-parietal region is not as much shortened as in the warthog, but is relatively shorter than in the bushpig; it is also relatively broader than in either, though not nearly as wide as in the forest hog. Compared with the East African material of *Metridiochoerus andrewsi*, the skull differs markedly in the braincase, which in that form is long and rises well above the orbits as a continuation of the sloping profile (Figure 6). In the Bolt's Farm specimen the braincase is shorter and there is an abrupt change of slope at the orbits so that the

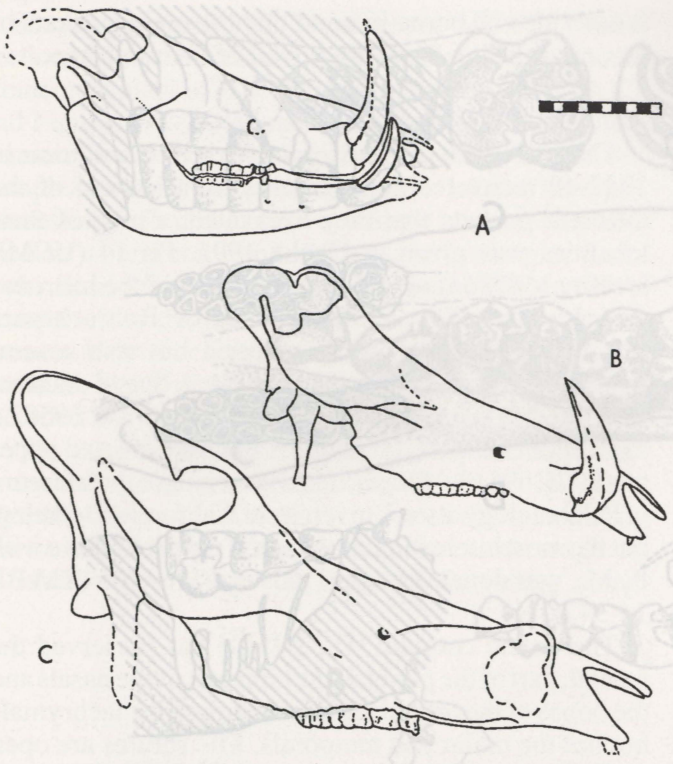

Figure 6. A reconstruction of the *Phacochoerus modestus* skull, TM BF 3-335, from Bolt's Farm in comparison with crania of *Phacochoerus africanus* (B) and female *Metridiochoerus andrewsi* KNM ER 228, from Koobi Fora (C).

neurocranium is essentially horizontal, as also is the parietal surface with the rim of the orbit flush with it. The essential cranial morphology thus clearly justifies the generic status of the Bolt's Farm fossil as *Phacochoerus*.

The mandible is not as much thickened in the vicinity of M_3 as in the living *P. africanus*, nor is the symphysis as wide and spatulate as in the recent warthogs. The anterior tip of the lower jaw is missing so that the incisors cannot be seen but there are traces of the ends of deep alveoli which might suggest that the teeth were larger than those of *P. africanus*. The lower canines are set in the jaw very much as in the warthog. The outer (lateral) surface is flat and was apparently covered with thin enamel while the inner (medial) surface is rounded, also with thin enamel, and the posterior face is narrow and gently rounded.

Dentition

Most unfortunately, the matrix proved to be extremely hard and the bone very soft so that cleaning was an arduous task and it is impossible to distinguish the sutures. With great difficulty a block of the left lower jaw was detached with LM_{2-3} in it and the bone and matrix were removed to expose the crown pattern and root system on the lingual side. The crown pattern of LM^{2-3} was also exposed and the maxillary bone and matrix were removed to show the upper root system on the buccal side. The crown patterns of these teeth are shown in Figure 5, but the drawing of the upper molar has been reversed so as to approximate the lingual aspect and facilitate comparison of the teeth. Their dimensions are included in Table 3.

TABLE 3

Measurements (mm) on skull of *Phacochoerus modestus* from Pit 3, Bolt's Farm

Skull	As preserved	Estimated
Greatest length	301+	330
Zygomatic breadth	*67 x 2	160 - 170
Interorbital width	74	90 - 100
Parietal width	51	55
Frontal width (between postorbital processes)	97	120
Least muzzle width (above infraorbital foramen)	27	35 - 40
Height of top of orbit above occlusal plane	130	130
Width of jugal below orbit	42	42
Teeth	LM^3	LM_3
Length: occlusal	47.5	45.5
basal	52.5	47.8
Breadth: occlusal	16.0	14.0
basal	17 e	14.7
Crown height	26.0+	16.0+
Root length: anterior	39.0	26.0
posterior	18.0	24.0

*midline to right zygoma
e = estimated measurement

The teeth are essentially phacochoerine in structure and pattern although retaining some resemblance to the basic ancestral form. The second molars are still present, though worn to stumps, and are thus retained rather longer than is the case with *P. africanus*, although the shedding of the earlier teeth is in keeping with the *Phacochoerus* succession in general. It is clear that these teeth belong to an old individual, thus eliminating any possibility that the peculiarities of skull structure are the result of immaturity. Comparable roots in third molars are seen in the Suidae from East Africa described by Leakey (1958) as *Pronotochoerus jacksoni*, *P. nyanzae* and *Notochoerus compactus* but are not usually seen in the living *Phacochoerus africanus* because the anterior root forms early in this species and the front of the tooth is already shed before the last columns close. Even in the recently extinct *Phacochoerus aethiopicus*, in which root formation is delayed until after the last pillars reach the grinding surface, the roots are never as strongly developed as in the fossil. There are also other dental characters that differ from those in modern *Phacochoerus*, notably:- the number of pairs of lateral columns is 5 in the upper M^3, 6 in the lower M_3, compared with 6 or more in the warthog; the enamel is thicker in the fossil; the columns are larger, less pillar-like and better separated laterally; the median columns are larger, particularly in the upper molar and are lacking in the back part of the lower molar; the crown is relatively short, especially for so old an individual.

Discussion

In 1948 Broom described an immature skull from Kromdraai (TM KA 89) naming it *Phacochoerus antiquus*. Ewer (1956) expanded on Broom's brief account and suggested that the differences between this specimen and *P. africanus* were more striking than Broom had suggested, particularly in the jugal-lachrymal area and in the lesser elevation of the orbital region, thus placing it morphologically in some respects in a position between *Phacochoerus* and *Potamochoerus*. She proposed for it a new subgenus *Potamochoerops*. Although the sutures cannot be seen in the new specimen from Bolt's Farm, there is no reason to doubt that they are consistent with Ewer's description and bear out the conclusions she had reached on the basis of Broom's young specimen from Kromdraai. The teeth of the type specimen are also consistent with the Bolt's Farm specimen and there can be little doubt that the latter represents the adult of Broom's young *Phacochoerus antiquus*. It is not yet clear whether the specimen justifies the subgeneric separation but the characters enumerated by Ewer are useful for separation of the species. Cooke (1982), in describing a fine skull and jaw from Olduvai Bed II suggested that Broom's species was a synonym of the Van Hoepens' (1932) *Tapinochoerus modestus* but considered that the species should be placed in the genus *Phacochoerus* on cranial characters rather than in *Metridiochoerus* as Harris and White (1979) suggested primarily on dental resemblances. The name "*modestus*" has priority over "*africanus*". *Phacochoerus modestus* is also a significant element in the Swartkrans fauna and is known at Olduvai not only by the fine skull from Bed 1 but by teeth that range up to Bed IV.

STERKFONTEIN

Discounting the possibility that some of Shaw's material did come from Sterkfontein, only one suid specimen has been recovered certainly from the breccia of the type site. It is a damaged fragment of the left mandible of a juvenile (TM STS 3074). It has the back of LM_1, the upper part of the crown of a little worn LM_2 and the front part of a developing LM_3, still in alveolus and incompletely formed. The bone has been cleaned away to expose the crown of M_3, which has good roots forming anteriorly and the cingulum is complete. As the teeth are incomplete, measurements are approximate and cannot be taken at the base of the crown, as they usually are. Although the nature of the specimen is far from ideal, the morphology of the teeth suggests that it belongs to *Potamochoeroides* and it can be matched fairly closely with one of the specimens from Makapansgat, BPI M 1882. The latter consists of a piece of left mandible with a badly damaged and very worn LM_1, M_2 in moderate wear and a completely formed but still unerupted LM_3. It is thus a slightly older individual but good for comparison. The two specimens are compared in Figure 7 and measurements are given in Table 4.

The Sterkfontein specimen is also similar to the right lower jaw from Bolt's Farm (See Table 1 and Figure 4 B) and there is very little doubt that STS 3074 belongs to the typical *Potamochoeroides shawi* of Makapansgat.

SWARTKRANS

The suid material from Swartkrans was described by Ewer (1956) who referred it to *Phacochoerus antiquus* (TM SK 382, 383, 385, 386) and to "*Tapinochoerus meadowsi*" (TM SK 380, 381, 387, 388, 390, 391, 392, 394). She gave measurements for these specimens, illustrated a few and gave an excellent account of the main features of the anatomy and of the dentitions. Since then a fair amount of new material has been recovered but most of it is fragmentary and adds litle to Ewer's account. However, there are a few items that deserve comment and, as Ewer's published measurements were incomplete, some new measurements are given here.

Phacochoerus modestus (= *antiquus*). The only good mature mandible is still TM SK 382, described and measured by Ewer, but it now transpires that the LM_3 cited by her as SK ? 383 fits on to the LM_2 so that the complete specimen now has the right lower canine, RP_4, RM_{1-2} and LM_{1-3}. Two isolated upper second molars, SK 385 (RM^2) and SK 386 (LM^2) were found in association with the mandible and almost certainly belong with it so that all Ewer's material probably came from a single individual. A new specimen, SK 5989, is a partial mandible with RM_1 and RM_2 very similar to those in the earlier specimen but the crowns are somewhat longer. The best upper dentition is a new specimen SK 4005,

TABLE 4

Measurements (mm) on juvenile mandible from Sterkfontein Type Site compared with juvenile *Potamochoeroides shawi* from Makapansgat

		STS 3074			M 1882		
		LM_1	LM_2	LM_3	LM_1	LM_2	LM_3
Length:	occlusal	+10 (18e)	22.8	34.0+	16.5 (17e)	26.5	37 e
	basal	-	22 e	-	-	22.4	48.0
Breadth:	occlusal	-	10.9	16 e	-	14.0	15.0
	basal	10.8	13.0(14e)	19 e	11.5 e	16.8	19.8
Height		+6+	+6+	16/+13	4+	12.5+/15+	27.5

e = estimated measurement; + = incomplete

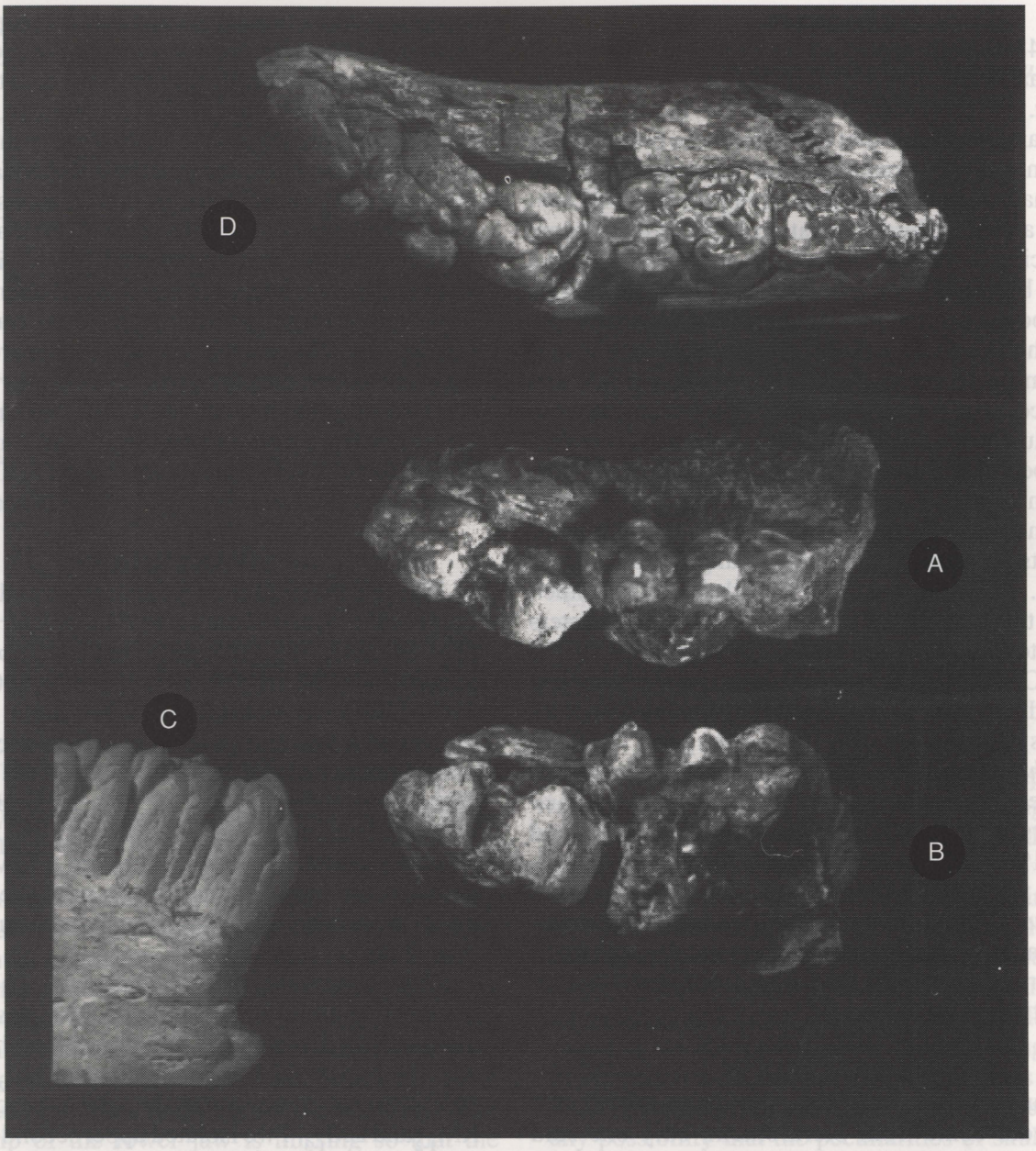

Figure 7. A, B, occlusal and inner lateral views of left mandible fragment of juvenile from Sterkfontein Type Site, TM STS 3074. For comparison, C is a lateral view of the unerupted M_3 from Bolt's Farm (shown in Figure 4B) and D is a somewhat older juvenile of *Potamochoeroides shawi* from Makapansgat (BPI M 1882). Natural size.

comprising a palate with M^{2-3} on both sides and the roots for RP^4 and RM^1. The breadth across the mandible is 67 mm and the breadth of the palate close to 32 mm. The palatal notch is only 18 mm wide which is less than in most comparable living warthog specimens available for comparison. On the right side the root of the zygoma can be seen beginning above the front of M^3 whereas in the living form it is usually a little farther forward, above the middle of M^2. The infraorbital foramen is also farther back in the fossil, lying above the M^1/M^2 boundary instead of above the P^4/M^1 contact. The LM^3 is not fully in wear but roots are forming anteriorly, and there is a strong lateral bulge on the second root. There are four pairs of lateral pillars, the fourth one being divided on the external side, plus a talon pillar. The thicker enamel and simpler pattern of the teeth pointed out by Ewer are apparent. A juvenile maxilla fragment, SK 14131, has the Rdm^{3-4} and RM^1 and is very similar to Broom's type of *P. antiquus* from Kromdraai. SK 6030 is a piece of maxilla with the left M^2 still erupting and it could belong with SK 14131. There is also another incompletely formed RM^3, SK 2359, a little larger than Ewer's SK 385. There are some other fragments that may represent *P. modestus*, including a number of specimens with the prefix SKX from Members 3 and 5 and one problematical RM^3, SKX 1926/7 from Member 2. All the other specimens are from Member 2 and this taxon has not been recorded from Member 1. Measurements are given in Table 5 and are plotted in Figure 8.

Metridiochoerus andrewsi is represented by the Swartkrans specimens described by Ewer (1956) under *Tapinochoerus meadowsi* but there is very little useful

TABLE 5

Measurements (mm) on specimens from Swartkrans Member 2 assigned to *Phacochoerus modestus*

	TOOTH	LENGTH	BREADTH	HEIGHT
TM SK 382	RP_4	9.6	6.4	6.5+
	RM_1	11.5	9.4	2.0+
	RM_2	20 e	13.0	18.5
	LM_3	52 e	14.0	42.5+/42.5+/48+/42/39
TM SK 385	RM^2	22.0	15.7	14+/15+
TM SK 386	LM^2	-	13.2	13+
TM SK 5989	RM_1	17.1	9.5	7.0+/7.5+
	RM_2	23.5 e	10 e+	21 e
TM SK 4005	RM^2	23.1	14+	11+/12+
	LM^2	22.5 e	12 e	13.5+
	RM^3	45 e	12+	?/30+
	LM^3	47.6	16 e	41+/41+/52/47
TM SK 14131	Rdm^3	8.9	6.9	3.0+
	Rdm^4	12.8	9.4	3.3+/3.5+
	RM^1	19.8	10.9	10 e+/10 e+
TM SK 6030	LM^2	17.6	11.8	31.5/31

e = estimated measurement; + = incomplete

TABLE 6

Measurements (mm) on specimens from Swartkrans Member 1 assigned to *Metridiochoerus*

	TOOTH	LENGTH	BREADTH	HEIGHT
MMK 3940 (Vaal river; type of *Notochoerus meadowsi*)	LM_3	76.5	18.5	54+/59+/66.5+/64/52
TM SK 387	LM_3	75 e	20.2	50+/61+/68+/69/63
TM SK 387	RM_3	75.5	21.0	53+/62.5+/64.5+/69/59
TM SK 392/2380	RM_3	80.8	24.2	8+/11.5+/11+/12+/13.5+
TM SK 384	LM_3	57.5	19.3	46+/55.5/54/45
TM SK 394	RM^3	37.5+ (57 e)	20.5	20+/22+/22+/-
	LM^3	41.5+ (57 e)	20 e	24+/26+/28+/-

e = estimated measurement; + = incomplete; MMK = MacGregor Museum, Kimberley

additional material in the later collections. The best of Ewer's specimens were a pair of lower third molars SK 387 (LM_3) and SK 388 (RM_3); the former was illustrated by Ewer (1956: Pl.2 Figures 3, 4) and its twin, SK 388, had been sectioned by Broom, who figured the enamel pattern of the cut surface (Broom 1948: Figure 18E) as *N. meadowsi*, but without any mention of its catalogue number or source. Through the courtesy of the McGregor Museum, Kimberley, the original type specimen of *Notochoerus meadowsi* from the Vaal River gravels was sectioned by the present writer and the two specimens and their enamel patterns are shown in Figure 10 C, E. The resemblances are clear but the section of the Vaal River specimen is higher up the crown and does not yet show as much fusion between adjoining columns as in the Swartkrans specimen. The dimensions are very similar and also close to Shaw's specimens A and B, thought to be from Bolt's Farm. Ewer's SK 392, a very worn incomplete third molar joins on to SK 2380 and the complete tooth is probably a lower right third molar rather than an upper left M^3 as Ewer had thought. The dimensions are given in Table 5 and the teeth are included in the plots in Figure 3.

A left M_3, Sk 384 is decidedly smaller that the teeth considered above and was originally thought to be *Phacochoerus modestus*. However, it is larger than any of the other material of this taxon and when sectioned showed the merging of columns usually associated with *Metridiochoerus*. Unlike all the specimens of *Phacochoerus modestus*, it was found in Member 1. The damaged skull fragment SK 394 was also included by Ewer (1956) with the other *Tapinochoerus meadowsi* material. It is a curious specimen with the back two thirds of the left M^3 in a piece of maxilla but the front two thirds of the right M^3 was moved back and lies at right angles to the other tooth. However, because the two pieces overlap, it is possible to use them to restore each other and thus make possible good estimates of their dimensions; they prove to be very close in size to the third molars of Broom's skull TM BF 1 from Bolt's Farm.

Accordingly, these Swartkrans specimens from Member 1 repeat the apparent association between TM BF 1 and the mandibles X and Y. Accordingly it is considered best to designate them also as *Metridiochoerus* cf *jacksoni*.

KROMDRAAI

Very little suid material has come from Kromdraai. The only significant specimen is the immature skull with lower jaws, TM KA 89 that Broom (1948) made the type of *Phacochoerus antiquus* and which Ewer (1956)

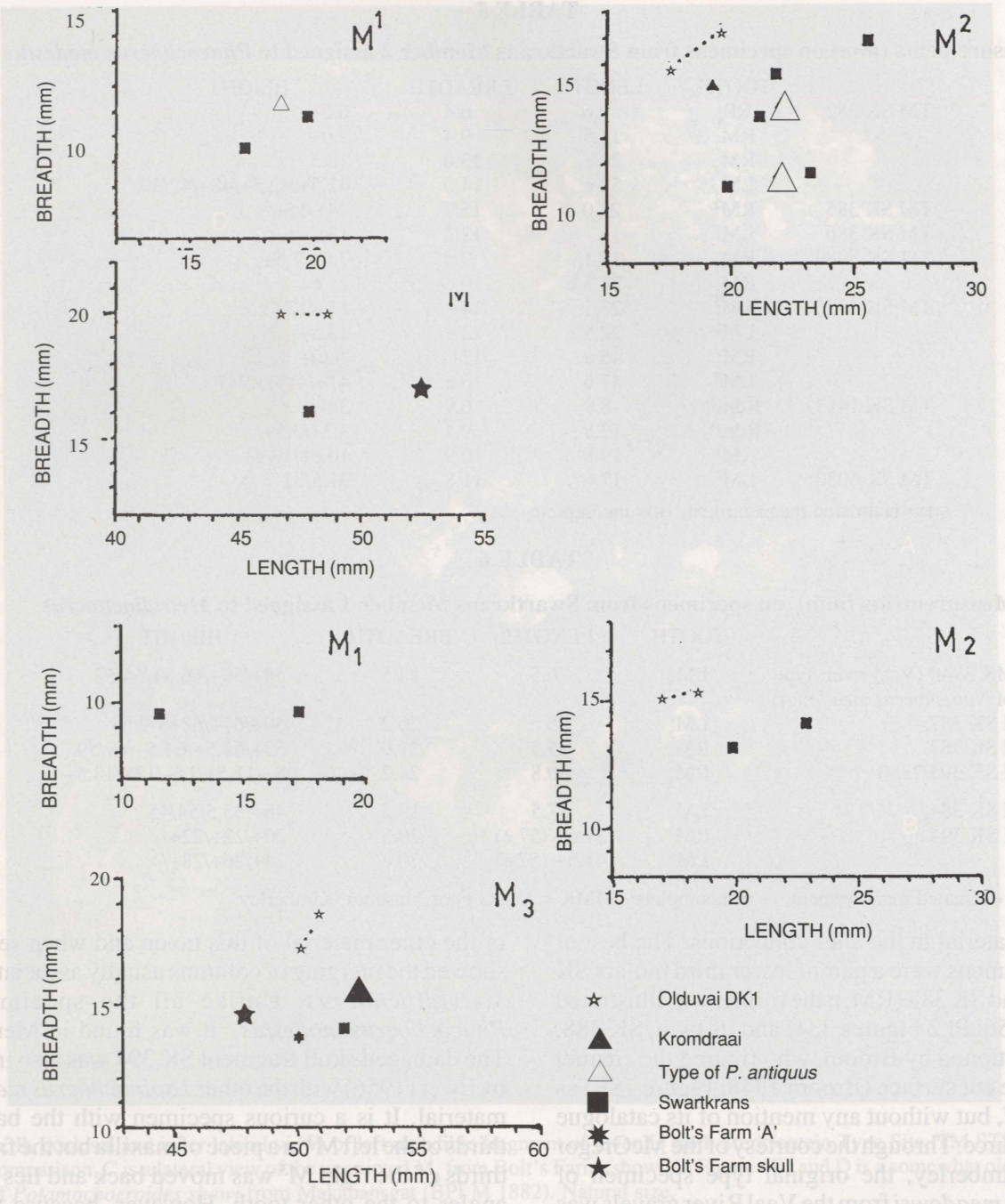

Figure 8. Length-breadth plots for upper and lower molars attributed to *Phacochoerus modestus*; measurements are given in Table 5.

described in greater detail. Ewer mentioned a lower third molar "K2 90", clearly also *Phacochoerus modestus*. Otherwise there are only scraps of a third molar, KA 1192, that might be from a *Metridiochoerus*. These are all from Kromdraai A and the only specimen from Kromdraai B is an unerupted RM^2, TM KB 3276 from layer 3, very similar to SK 385 and referred to *Phacochoerus modestus*. There are also some scraps of a juvenile cranium from Kromdraai B.

MAKAPANSGAT

The suids from Makapansgat were very well described by Ewer (1958) and were reconsidered by Bender (1992), who has incorporated the later discoveries into his account and deals mainly with *Potamochoeroides shawi*. However, there are some aspects of the *Notochoerus* material that warrant further discussion here in the light of information gained by study of the extensive collections made in East Africa since 1967. When Ewer wrote her insightful account, the only *Notochoerus* material known comprised Broom's (1925) incomplete upper third molar from the Vaal river gravels - the type specimen of *Notochoerus capensis* - some partial lower molars from Kaiso described by Hopwood (1926) as *Hylochoerus euilus*, the Laetoli specimens referred to *H. euilus* and

*Notochoerus serengetensis** by Dietrich (1942), the two good third molars and nine fragments from Shungura, Omo, named *Gerontochoerus scotti* by Leakey (1943) and a few specimens, also from the Omo, referred by Arambourg (1947) to *Notochoerus capensis*.

The best of Ewer's specimens were a partial mandibular ramus BPI M 2025 with the left M_3, slightly damaged anteriorly, and M 2031, a right M_3 lacking the anterior one and a half pairs of pillars. Specimen M 2079 subsequently proved to be the missing part of the right M_3 and the tooth is now intact, but has been re-numbered M 2077. Although M 2025 was figured by Ewer (1958: Pl.5, figures a, b), M 2077 is now more complete and also has the remains of right M_2, worn to featureless dentine, so is worth illustrating here (Figure 9 A,B, 10 A). It has five well developed pairs of laterals, a weak sixth pair and three small terminal pillars. The dimensions are given in Table 7, together with comparative measurements for the types of "*Gerontochoerus*" *scotti* and *Notochoerus capensis*. Ewer described the Makapansgat *Notochoerus* as *N. (Gerontochoerus) euilus*, thus recognizing in part the affinity with Leakey's Omo specimens. However, it has also been referred to *N. capensis*, although at one time Cooke and Maglio (1972) suggested that it is inseparable from *N. scotti*.

The completion of the right M_3, M 2077, shows that the dentition was in a fairly advanced stage of wear although the sixth pair of laterals is almost unworn. While it is difficult to be sure of the original crown height this was certainly not less than 45 mm and unlikely to have been much more than 50 mm. Fortunately an almost complete right M_3 in very early wear has since been found, BPI M 8275, which has a crown height not less than, but close to 52 mm (Figure 9 C). There are five pairs of lateral pillars and it is probable that a weak sixth pair and a terminal pillar have been lost at the back, so the basic structure was the same as in M 2077. The antero-internal pillar shows the characteristic X-shaped enamel island while the antero-external pillar is mushroom shaped or resembles a squashed 3. The second pair of pillars approximates the usual H-shape. The pillars are wide laterally and are almost in mutual contact for most of their height. The tooth has been sectioned 12 mm below the present wear surface anteriorly and 19 mm below the little worn 3rd pillar. The sectioned surface shows that the axial portion of the buccal and lingual enamel islands have merged to form an anterior complex and the remaining enamel islands assume the usual H-shape with the medial lobe smaller than the outer one and linked more and more towards the front in the successive pairs on the talon (see Figure 10 B). Roots are well formed on the anterior two pairs of pillars, exceeding 20 mm in length. A single elongate open root is formed on the talonid. There are also two other specimens that show the height of the crown. M 1922 is the central part of a left M^3, and M 8352 is a piece of maxilla with the central part of its mate. The maximum measurable breadth of M 1922 is 28.6 mm and of M 8352 is 27 mm while the heights of the unworn pillars are respectively 54 and 51 mm.

The new specimen, M 8275, is a little smaller and narrower than the massive tooth, M 2077, but it shows the same morphological characters, which it also shares with the "2nd syntype" of Leakey's *Gerontochoerus scotti*. Indeed, the closely apressed elongate laterals with rather flattened outer walls that are sometimes grooved externally, is one of the important features that distinguishes *Notochoerus scotti* from *N. euilus*, in which the laterals tend to have curved outer walls and the columns are tapered from their bases towards the crown. The inner enamel is a little thinner in *N. scotti* that in *N. euilus* and there is a heavier coating of cementum. Although there is a wide range of variation within both *N. euilus* and *N. scotti*, these morphological differences are usually apparent even when dimensions overlap. Furthermore, *N. scotti* tends to be more hyposodont, *N. euilus* seldom exceeding a crown height of 45 mm for unworn pillars and very rarely reaching 50 mm whereas *N. scotti* rarely falls below 45 mm and is usually more than 50 mm.

Figure 11 shows plots of length versus breadth for samples of *N. euilus* and *N. scotti* from the Omo sequence (Cooke, unpublished) and from Koobi Fora (based on measurements in Harris 1983). On these diagrams are plotted the specific data for the "type" (#1) and "2nd syntype" (#4) of *N. scotti* as well as for the three Makapansgat specimens, M 2025 (#5), M 2077 (#6) and M 8275 (#7). The plots show that specimen M 2025 (#7) lies close to the mean value for the Omo sample of *N. scotti* and this confirms the inferences made from the morphological characters. The two Makapansgat mandibular teeth are as long as a number of the Omo teeth but are appreciably wider. It is of interest to record that the most robust representatives of *N. scotti* in the Omo sequence are from the earlier horizons; from Member D up there is a tendency to add additional pillars on the talon and the talonid, accompanied by tighter contact between the laterals, rather than by increase in length, and also by narrowing of the crown and a consequent increase in the hypsodonty index. A badly weathered mandible (L1-64) from level B 11 in the upper part of Shungura Member B has the broken remnants of the very worn third molars, with five pairs of laterals lingually, six buccally, a basal length of 100.5 mm and a breadth estimated at 26.5 mm. There are several other specimens of *N. scotti* from the same locality, none quite as large as L1-64 and they occur alongside typical *N. euilus* teeth. It seems clear that the Makapansgat *Notochoerus* is not *N. euilus* and there does not seem to be any good reason to regard it as anything other than a robust *N. scotti*, perhaps from a

*clearly from deposits later than the Laetolil Beds and now referable to *Stylochoerus compactus*

stage roughly equivalent to the upper part of Member B at Omo.

This raises the question of why this material should not be regarded as *N. capensis*, as has been widely proposed by several authors in the past (including the present writer!). The type specimen, which belongs to the Port Elizabeth Museum and numbered PE 1436/3, is currently in the Bernard Price Institute for Palaeontological Research. It is an upper right third molar, broken anteriorly and lacking an unknown amount from the front. The crown is in a moderately early stage of wear as the hindmost pillars are only slightly abraded. Broom (1925) regarded it as a lower molar and restored it with an additional pair of laterals at the front (Figure 12 A; Figure 11, 2). In 1939 Shaw challenged this reconstruction and suggested that the tooth was broken through the anterior pair of laterals and that only the anterior cingulum complex was lost. Shaw possibly reduced the antero posterior length of the laterals unduly and the present writer has prepared a new possible restoration of the shortened crown (Figure 12 B; Figure 11, 3). This would make the original crown the possessor of only four pairs of laterals and a terminal pillar. Although the lateral pillars on the lingual side are wide and the anterior ones parallel sided, on the buccal side all the pillars have a strong upward taper from the base, as

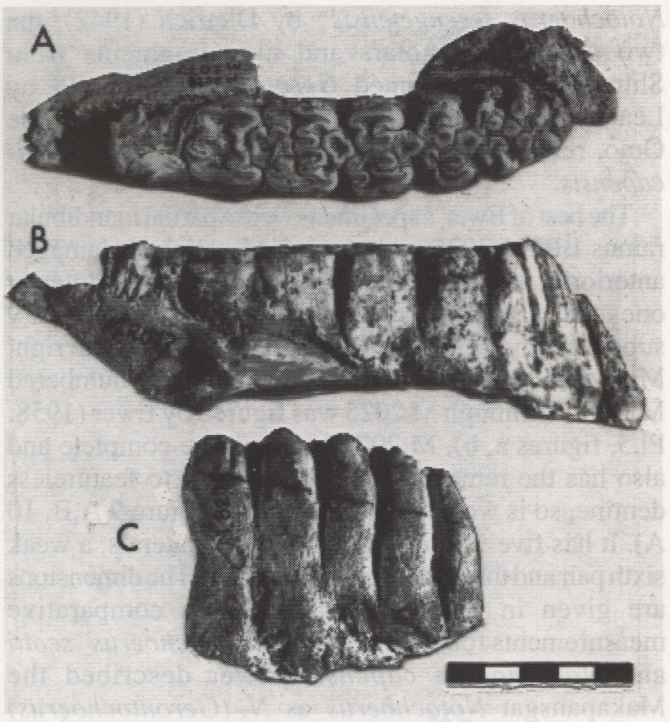

Figure 9. A,B, occlusal and inner lateral views of moderately well worn RM2-3, BPI M 2077, from Makapansgat. C is a lingual view of an incomplete RM3, BPI M 8275, from Makapansgat and regarded as inseparable from *Notochoerus scotti* of East Africa. 47% natural size.

TABLE 7

Measurements (mm) on *Notochoerus* third molars from Makapansgat, East Africa and the Vaal River

#	ORIGINAL SPECIES REF.	CATALOGUE NUMBER	TOOTH	LENGTH	BREADTH	HEIGHT
5	*"N. euilus"*	BPI M 2025	LM_3	107.0	27.3	22+/22+/25+/31+/35+/40+
6	*"N. euilus"*	BPI M 2077	RM_3	113.5	27.5	23+/23+/31+/34.5+/38.5+/42.5+
7	New	BPI M 8275	RM_3	83.8+ (98 e)	25.3	36.6+/41.3+/46.7+/51.6+/?
1	*"G. scotti"* TYPE	KNM OS 5	RM^3	83	30.0	22.5+/26.5+/39+/42+/52
4	*"G. scotti"* 2nd Syntype	KNM Omo 2	LM_3 (88 e)	82 +	24.0	14+/17+/22+/28+/32+
2	*N. capensis* TYPE	PE 1436/3	RM^3	65 + (81 e Broom)	30.0	-/25+/31+/38+/45+
3				(72 e Cooke)		25+/31+/38+/45+
8	*"N. euilus"*	OMO B 225A	RM^3	77.0	33.2	26+/31+/36+/38.5/35.5

= plot number in Figure 11; e = estimated; + = incomplete

is usual in *N. euilus*. A feature of the type specimen is the strong secondary folding in the enamel islands and in the central islands. The stellate shape of the enamel figures in early wear and then changes with increased abrasion as illustrated by Cooke and Coryndon (1970, Figures 11, 12) in connection with the type and associated material of *N. euilus* from Kaiso. There thus seems to be at least a good possibility that *N. capensis* is a variant of *N. euilus*. There is, in fact, a striking resemblance to an upper right third molar (numbered B 225) of *N. euilus* from the Usno Formation, shown in Figure 12 C, for comparison with the *N. capensis* type and for which dimensions are included in Table 7. There are also close similarities to teeth from Laetoli described by Dietrich (1942), notably Vo 330 figured in his Pl.17, Figure 136, which is reproduced here in Figure 12 D. Although it is still difficult to be completely certain, there seems to be at least a good probability that *N. capensis* is a variant of *N. euilus*, even if Broom's restoration was correct. As *N. capensis* is the genotypes species, it is suggested that until further evidence is available, this species name be used in future only for the type specimen itself.

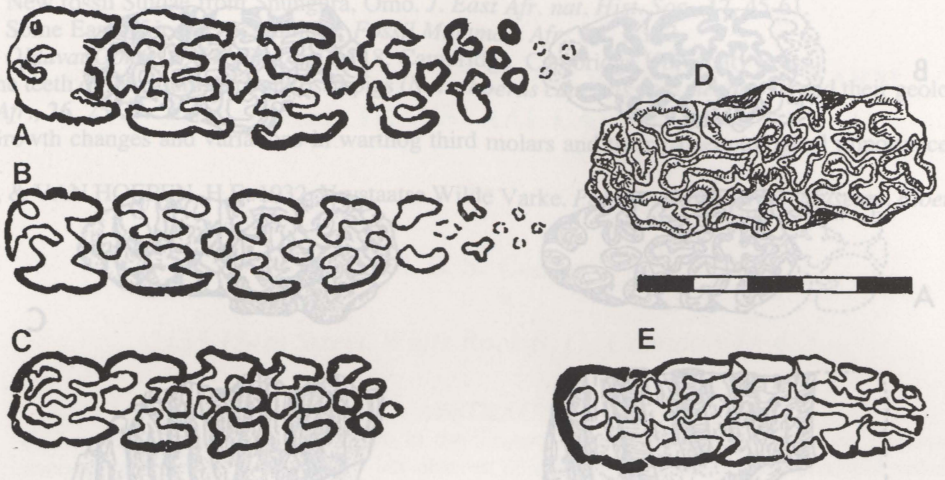

Figure 10: A, drawing of enamel pattern of RM_3, BPI M 2077, in the partial mandible from Makapansgat shown in Figure 9 A, B.B is a drawing of the sectioned surface of the RM_3, BPI M 8275, shown in Figure 9 C.C is a drawing of the sectioned surface of the RM_3, MMK 3940, from the Vaal River (see also Figure 2 D), originally the type of *Notocherus meadowsi* Broom, showing the early stages of fusion of the elements seen in *Metridiochoerus*.D is a drawing, by Shaw, of the enamel pattern on the sectioned surface of the upper LM^3 of his specimen "C", regarded here as *M. andrewsi*.E shows the complicated enamel pattern in an RM_3, TM SK 388, from Swartkrans Member 1, also placed in *M. andrewsi*.All 70% natural size.

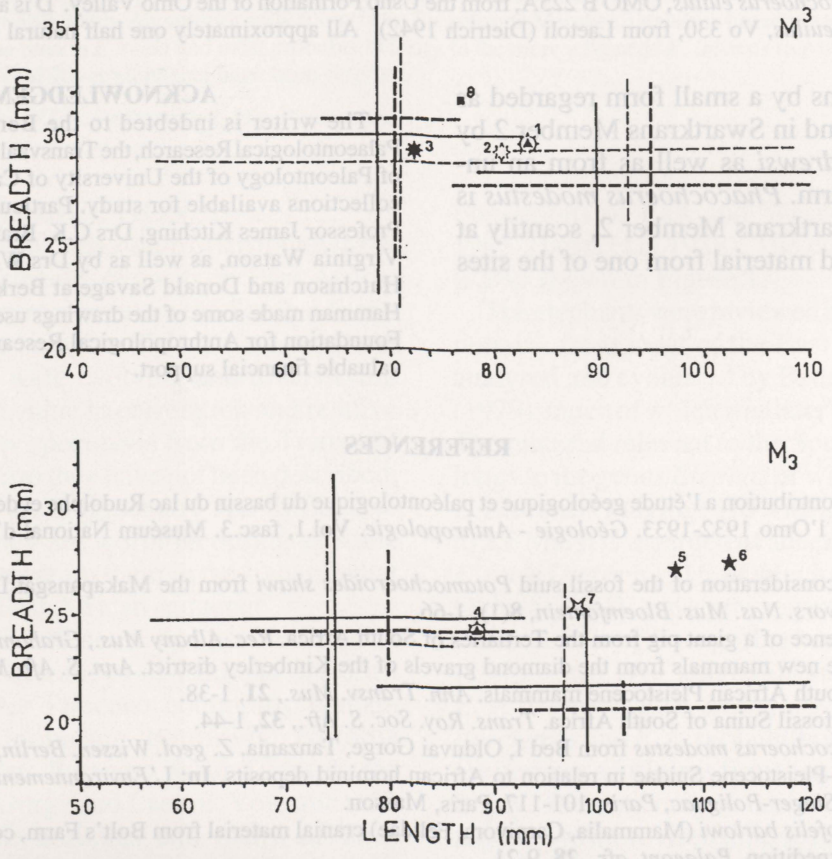

Figure 11. Length-breadth plots for upper and lower third molars of *Notochoerus*. Full lines show observed ranges and means for all sites, given by Harris and White (1979); the light broken line is for material from the Omo (Cooke, unpublished) and the heavy broken line is for Koobi Fora specimens (from data in Harris, 1983). *N. euilus* is on the left and *N. scotti* on the right. The key to the numbers of the specimens plotted individually is given in Table 7.

CONCLUSION

The Makapansgat deposit contains plentiful remains of *Potamochoeroides shawi* which is apparently represented also in one of the pockets from Bolt's Farm and at the Sterkfontein Type Site. The large notochoere from Makapansgat appears to be inseparable from early *Notochoerus scotti* of East Africa, but this taxon is not at present known from other sites in South Africa. The type of *N. capensis* may well be a synonym of *N. euilus* of East Africa and it seems desirable to restrict use of this specific name to the type specimen only. *Metridiochoerus* is represented at Bolt's Farm and in

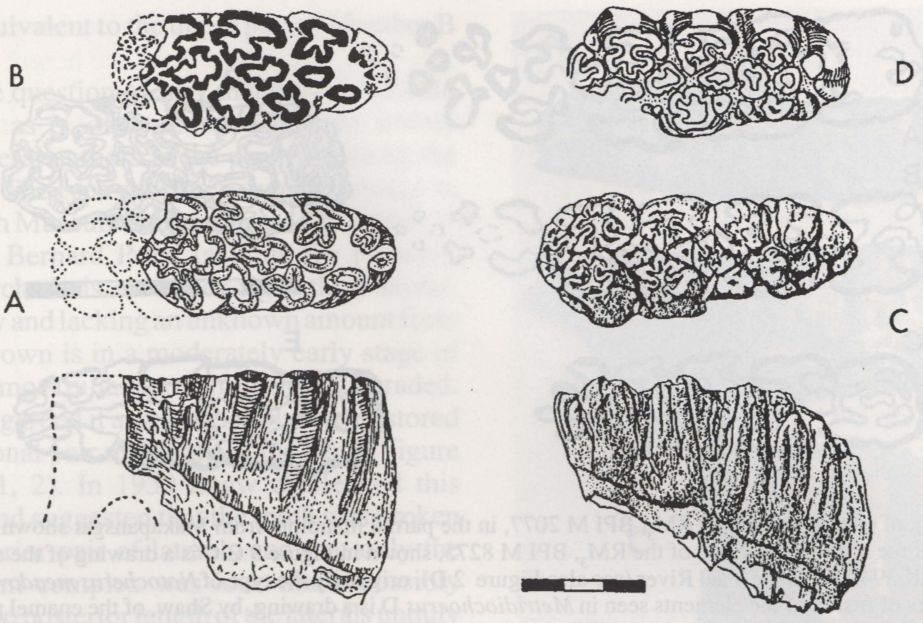

Figure 12. A, crown pattern and innner lateral view of RM^3 of the type of *Notochoerus capensis*, PE 1426/3, as reconstructed by Broom in 1925. B is a shortened reconstruction following the suggestion of Shaw (1939). C shows inner lateral and and occlusal aspects of an RM^3 of *Notochoerus euilus*, OMO B 225A, from the Usno Formation of the Omo Valley. D is an occlusal view of an RM^3 of *Notochoerus euilus*, Vo 330, from Laetoli (Dietrich 1942). All approximately one half natural size.

Member 1 at Swartkrans by a small form regarded as possibly *M. jacksoni*, and in Swartkrans Member 2 by the larger form *M. andrewsi* as well as from an unknown site at Bolt's Farm. *Phacochoerus modestus* is well represented in Swartkrans Member 2, scantily at Kromdraai, and by good material from one of the sites at Bolt's Farm.

ACKNOWLEDGEMENTS

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