

**A RECONSIDERATION OF THE FOSSIL SUIDAE OF THE MAKAPANGAT LIMESTONES,
POTGIETERSBURG, NORTHERN TRANSVAAL.**

Patrick Alan Bader

**A dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in
fulfilment of the requirements for the degree of M.Sc.**

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DECLARATION

I hereby certify that this dissertation is my own work, unless otherwise stated in the text, and that it has not been submitted to any other university for degree purposes.

Signed:

A Bender

26th day of March, 1990.

TO MY FAMILY

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ABSTRACT

The present study examines all the fully prepared Makapansgat Limeworks fossil suid specimens. Thirty undescribed and three uncatalogued specimens were added to the previously described collection. The cranial morphology of these suids is compared to the extant southern African Suidae, *Potamochoerus porcus* (bushpig) and *Phacochoerus aethiopicus* (warthog), and other relevant extant and fossil genera. A system of measurements was used to facilitate the description and analysis of the Limeworks fossils and in the comparisons with the other suids.

The taxonomy and phylogeny of the Limeworks species *Potamochoeroides shawi* is revised. It is shown to be distinct from *Metridiochoerus andrewsi*. A cladogram illustrating the relationships between specific Plio-Pleistocene African suid genera is presented, and it is concluded that *Potamochoeroides* is more primitive and therefore possibly older than previously thought. Since *Potamochoeroides* and the Makapansgat hominid remains occur in the same geological unit, it is suggested that *Australopithecus africanus*, may also be older than previously considered.

The palaeoecology and taphonomy of the Limeworks Suidae is examined and discussed. Indications are that the suids were brought into the cave mainly by predators, including hyaenas, felids and the hominid *Australopithecus africanus*.

" In an old hut with a tin roof on a university campus in Johannesburg, a magician presides over a room full of bones. Row upon row of mandibles, femurs, loose teeth, and horn cores lie on shelves and trestle tables, are neatly arranged in drawers, or overflow into wooden boxes on the floor. There are tens of thousands of skeletal fragments, all neatly numbered - the remains of more antelope, pig, and giraffe than anyone has seen together since the time of the great migrations. The bones are surprisingly heavy. Each has lain so long beneath the earth that all its cells have been replaced by calcite or silica. Soil stuff has seeped into the tissue, keeping its precise shape, but taking its place, turning it into limestone. They're all fossils, rows of bone turned to stone by time. "(Watson 1982, p6).

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CHAPTER 1. INTRODUCTION

The prepared Makapansgat Limeworks fossil suid collection consists of two extinct species, *Potamochoeroides shawi* Dale 1948, and *Notochoerus capensis* Broom 1925, with the former species erected on this collection. The two suid species were mostly found in the extremely fossil rich Member 3 (grey breccia), within the dolomitic Makapansgat Limeworks cavern, situated some nineteen kilometres E.N.E. of Potgietersrus in the Northern Transvaal. Previous research (Dale 1948; Ewer 1958a; Cooke and Wilkinson 1978; Harris and White 1979) dealt only with a part of the collection. This study is thus the first to deal with all the fully prepared specimens.

The suids, particularly the Plio-Pleistocene African Suidae, to which the Limeworks species belong, have been extremely important in East African hominid research (Cooke 1978). Fossil remains, specifically teeth, occur in large numbers at most of the well known East African hominid sites (Cooke and Ewer 1972; Cooke 1978). These remains have been extensively used for biostratigraphical correlation between various East African hominid sites, and for relative faunal dating of the East African hominids (White and Harris 1977; Cooke 1978). The importance of the Makapansgat Limeworks Suidae becomes apparent when it is realised that both species can be compared to East African species, and thus a relative age of approximately 2.6 myr has been postulated for the Limeworks hominids (White, Johanson and Kimbel 1981). However, this comparison has been a "bone of contention" among a number of researchers (White and Harris 1977; Cooke 1978; Cooke and Wilkinson 1978; Harris and White 1979) in that the taxonomic and phylogenetic position of *Potamochoeroides shawi* is uncertain.

The present study revises and updates the taxonomy and the phylogenetic relationships of *Potamochoeroides shawi*, particularly in the context of the East African *Metridiochoerus andrewsi* material. Close examination of all the prepared *Potamochoeroides* specimens revealed a number of previously unmentioned anatomical features, which appear to alter the interpreted phylogenetic

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position of this species. The taphonomy and palaeoecology of the Limeworks suid collection was examined within the context of the fossil-fauna as a whole. Previous study of the abovementioned aspects have been important in the evaluation of the extent and habit of *Australopithecus africanus* (Dart 1957; Prain 1981; Maguire, Pemberton and Collet 1980). The minimum number of individuals (MNI) and the relative age profiles were also examined with regard to the taphonomy of the Limeworks suids.

1.1 THE LIMeworks FOSSIL SITE AND ITS SIGNIFICANCE

The site at present consists of the remnant of a large dolomite cavern, and the basal section of its infill. The infill, known as the Makapansgat Formation (Maier 1973), is up to twenty five metres thick and consists of travertines, mudstones and breccias (Maguire, Schrenk and Stanistreet 1985). This deposit has been previously mined for its massive travertine layers, which are approximately 98% pure carbonate. The name 'Makapansgat Limeworks' refers to the mining operations (Maguire *et al.* 1985), which drew attention to fossil bones within the breccia waste dumps. These dumps have yielded several dozen specimens assigned to *Australopithecus africanus* (Dart 1965), and a rich Plio-Pleistocene vertebrate fauna consisting of some 250 000 specimens. Microfaunal evidence indicates that Makapansgat is older than the Krugersdorp australopithecine sites (Pocock 1987), which makes Member 3 (grey breccia) yielding *Australopithecus africanus* remains, the oldest hominid bearing deposit in southern Africa (Partridge 1979; McFadden and Brock 1984; Turner 1984).

1.2 LOCATION AND SITUATION

The Makapansgat Limeworks fossil site is situated in the Makapansgat valley, to the east and below the Makapan Strydpoort Plateau, within the Strydpoort Mountains. It is approximately nineteen kilometres E.N.E. of Potgietersrus in the Northern Transvaal (Fig.1). The exact location is 24°12'S,

28° 57'E, and the elevation 1 460m above sea level. The Limeworks extend over an area of roughly 1.5ha, within the 1km² area of the valley (Maguire 1976; Cadman 1985) (Fig.1).

1.3 GEOLOGY OF THE VALLEY

The rocks which form the Makapansgat valley lie within the Transvaal Supergroup. The Eastern margin, or valley head, is composed of Black Reef Quartzite which is the basal member of this Supergroup. The hills surrounding the cliffs consist of the same quartzites. The Limeworks itself, and the hills to the east are composed of dolomite of the Malmani Subgroup. Tectonic movement, possibly related to the N-S trended faults at the valley head, has resulted in fracturing and folding in the dolomite and quartzites. The resultant structural weaknesses were probably important in controlling cave formation. Shales and quartzites of the Pretoria Group occur where the valley widens towards the flats in the Potgietersrus area. Apart from the cave and other superficial deposits, no other geological groups appear within the Makapansgat valley. Thus the hiatus from the Transvaal Supergroup to the cave deposits covers a time span of approximately 2 250 myr (Button 1973; Greer 1982).

1.4 GEOMORPHOLOGY OF THE VALLEY

The Potgietersrus area, and indeed most of the Northern Transvaal, was covered by a mantle of Karoo Sequence sediments of late Triassic or early Jurassic age. On this cover developed the present drainage systems (King 1951). The Limeworks are situated below the Afrikaner erosion surface, within the first post-African erosion cycle (during which cave openings within the valley occurred), and the later Plio-Pleistocene cycle, which began about 2myr ago (King 1951).

1.5 CAVE GEOLOGY AND STRATIGRAPHY OF THE MAKAPANGSAT LIMeworks

The stratigraphy and geology of the Limeworks has been discussed and reviewed by a number of researchers in the last thirty three years (i.e. Wells and Cooke 1957; Brain 1958; Partridge 1979; Schrenk 1984; Maguire *et al.* 1985) (Fig.2). It is important to note that all of the lithological succession schemes outlined in Fig.2, are generalised, and therefore often do not adequately document the geology and stratigraphy within the various depositories.

Cave geology involves two opposing processes. The first is erosion, including mainly solution of the dolomite, which formed the original solution cavity and hence the cavern structure. The second process is deposition, including chemical precipitation. Both processes can occur simultaneously and interchangeably. The deposition process has been largely responsible for the Makapansgat Limeworks breccia deposit, from which most of the fossil fauna was recovered.

The term Makapansgat Formation (Maier 1973) has been adopted in the formal lithostratigraphy of South Africa for the Limeworks Breccia deposit (SACS 1980). The system of Members, proposed by Partridge (1979) does not conform to the codes of stratigraphic nomenclature, and therefore is not formally registered (Maguire *et al.* 1985). However, this system is widely used and thus, for convenience, it is referred to. The Makapansgat Formation includes the complete cave-fill lithostratigraphy. A number of lithologically distinct horizons are present (Fig.2) although some overlapping of units does occur. These include:

Travertine (in contact with the dolomite host rock) (Member 1).

Red calcified mud (often rich in fossil microfauna) and contaminated travertine (Member 2).

Grey fossil-rich cemented marl or grey breccia (Member 3). Coarse pink breccia, highly calcified, with weathered dolomite blocks (Member 4).

Coarser sandy breccia with gravel bands (Member 5).

Within the Limeworks complex, there are four separate depositories where red calcified mud (Member 2), and associated other layers are present (Maguire *et al.* 1980). These are: The Main Quarry depository and the Cone Mouth depository to the west of a central floor high, and the Chimney depository and Rodent Corner depository to the east (Fig.3).

Some of the contact relationships are conformable, especially between adjacent members. However, because of the complex nature of the four separated depositories and the complex nature of cave deposition, whereby older deposits frequently overly younger, the present stratigraphy generally represents an oversimplification (Maguire *et al.* 1980). It is thus considered that informal unit names should be given to lithostratigraphic subdivisions of the Makapansgat Formation, within the four depositories (Maguire *et al.* 1980). The stratigraphy is often not applicable to faunal studies due to the paucity of *in situ* fossil remains, which makes it difficult to establish provenience.

1.6 SCENARIO FOR THE LIMeworks CAVE FORMATION

The cavern was probably formed below the water table, with later enlargement by erosion along lines of weakness. Travertine, sometimes contaminated by residual cavern earth, was then deposited, with the cavern subsequently isolated above the water table. Links by aven or solution cavity, were later established with the surface, resulting in the deposition of Phase I breccia (Members 3 and 4) (Brain 1958). Roof collapse was followed by the deposition of phase II (Member 5) breccia (Brain 1958), with a period of erosion bringing the scenario up to the present stage.

1.7 PRESENT AND PAST CLIMATE AND ENVIRONMENTS

The Makapansgat valley is situated in the summer seasonal rainfall belt of southern Africa (Peters and Maguire 1981). Vegetation in the valley is extremely varied, with over 800 identified plant species

(Cadman 1985). Acocks (1975) recognised two vegetation types in the area, namely: north-east mountain sourveld and tropical bush and savanna. However there is a complex mixture of a number of different micro-environments caused by the sudden changes in altitude, and the rich alkaline soils derived from the dolomites. Thus the flora ranges from sub-tropical evergreen forest near the river and under the cliff face at the end of the valley, to higher altitude communities of *Erica* floras typical of the temperate Cape region.

Butzer (1980) and Turner (1980) postulated a wetter climate than at present, during the deposition of Members 2 (red calcified muds) and 3 (grey breccias). Levinson (1985) and Pocock (1985) indicated that the climate was similar to the present day, possibly with wetter and drier periods. Cadman and Rayner (1989) suggest major fluctuations in climate and vegetation during these times.

Palynological studies (Cadman 1985) indicated that the vegetation was similar to the present. There appear to have been more forest trees and similar numbers of bushveld trees of rocky and moist habitats. Indications are that there were a similar number of grasses to the present.

1.8 TAPHONOMY, PALAEOFAUNA AND PALAEOECOLOGY OF THE LIMESWORKS

The Limesworks fossil faunal assemblage is composed mainly of the more resistant skeletal elements. This is to be expected, whatever the accumulating agent may have been. Dart (1957) analysed 7 159 faunal specimens from Member 3 (grey breccia) and found that 91.7% were bovid, 4% non-bovid ungulates, including the suids, and 4.3% other animals. He then postulated that hominids had been mainly responsible for the grey breccia bone accumulation. More recently, studies (Brain 1981; Maguire et al. 1980) have shown that hyaenas accumulate bones at their breeding lairs, and indications are that, if the lairs are in caves which have served as bone accumulation sites for thousands of years, then the accumulation could be massive. The combination of water current action and gravity has been acknowledged as a notable possible concentrator of bone specimens (Maguire et al. 1980). The

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abovementioned studies indicate that other carnivores could also be responsible for the bone accumulation. Ewer (1958a) on the basis of a relative age profile of *Potamochoeroides shawi*, postulated that carnivores, in general, could have been responsible for the suid accumulation.

The Limeworks fauna is largely derived from approximately 40 000 tons of discarded breccia blocks outside the limeworks, of which ninety five tons was bone bearing; thirty five tons of grey and sixty tons of pink/red breccia. All in all, over 250 000 bone specimens have been recovered, including 360 identifiable skull remains, 3 276 identified post cranial bones and some 12 928 bone flakes (Dart 1957; Kitching pers. comm.).

A total of 572 cranial suid specimens, have been recovered from the Member 3 (grey) and Member 4 (pink) breccias, but mainly from the former. The collection is composed predominantly of teeth. The presence of *Potamochoeroides shawi* and *Notochoerus arvensis* appears to indicate that grassland and open woodland/forest was present in the vicinity of the Limeworks (Ewer 1958a; Cooke and Wilkinson 1978).

Various cranial and post cranial fragments of *Australopithecus africanus* have been recovered, particularly from Member 3 (grey breccia) (Dart 1965); a pelvic specimen was recovered from a block containing a *Potamochoeroides shawi* and a *Makapania broomi* specimen. These specimens were within a half a metre of one another (Kitching pers. comm.). *Australopithecus* specimens have also been recovered from Member 4 (pink breccia), many of them from the Cercopithecoid dump (refer to Fig. 3) (Dart 1965).

At least 500 cercopithecoid specimens have been recovered, comprising five species: *Cercopithecus williamsi*, *Parapapio jonesi*, *P. broomi*, *P. whitei* and *Simopithecus darti* (Freedman 1970; Maier 1970; Eisenhart 1974).

Carnivores, although not numerous, are important as contributors to the Lineworks fossil faunal assemblage. Two hyaena species have been recovered from the grey breccia, *Crocota cf. brevirostris* and *Hyaena hyaena makapani*. *Crocota crocota*, the spotted hyaena, is found in Member 4 (pink breccia) (Toerien 1952; Randall 1981). Other carnivores include one specimen of *Cynictia sp.*, and a single specimen each of *Canis sp.* and *Vulpes sp.* There are two or three small Felinae specimens and twelve specimens of the sabre-toothed cat comprising two species, namely *Dinofelis barlowi* and *Homotherium cf. nestianus* (Ewer 1956; Collings, Cruikshank, Maguire and Randall 1976). Two species of extinct porcupine *Xenohystrix crassidens* and *Hystrix makapanensis* have been recorded (Greenwood 1955). The specimens are all of mature adults, found in close association with numerous remains of large mammals. There is evidence that the porcupines were bone collectors (Collings et al. 1976; Maguire 1976).

The Bovidae, studied by Wells and Cooke (1957) and Vrba (1977; 1980; 1987a), are represented by no fewer than eighteen species, indicating a complex varied physiographic setting. The bovid collection includes a number of species closely related to extant species, as well as a number of extinct species. The fauna is dominated by four species, *Redunca darti*, *Phenotragus vanhoepeni*, *Makapania broomi* and *Gorgon taurinus*, with the first three species unique to the Lineworks. There are also high proportions of the tribes Alcelaphini and Antilopini which, in terms of species numbers and numbers of individuals, indicate open grasslands and lower minimum temperatures and/or lower rainfall (Vrba 1980, Greenacre and Vrba 1984).

The Lineworks is locally very rich in microfaunal remains. The majority of the small fossil mammals seem to have been part of owl pellets, or regurgitations which disintegrated after deposition (Levinson 1985). The most important rodent collections have been recovered from the back of the Exit Quarry Member 2 (red mud) (refer to Fig.3), in situ Member 4 (pink breccia) from Rodent corner, and nearby dumps from the same locality [De Graaff (1960) and Pocock (1987) give faunal lists and details]. Other faunal elements include, fossil rhinoceros remains (Hooijer 1959), Giraffidae (specimens indicate a

large giraffid, similar to extinct *Sivatheres* of Asia and East Africa (Wells and Cooke 1947), a subspecies of hippopotamus (Kitching 1951), and remains of *Chalicotheres* (George 1950). Invertebrate remains are; numerous blow-fly pupal casts, more abundant in Member 4 than in Member 3, and a juvenile centipede, *Scalopendra cf. mortisans* found in a calcite lens from Member 3 (Kitching 1980).

1.9 DATING OF THE MAKAPANGGAT LIMESWORKS

The Limesworks has not been successfully dated using radiometric methods, or any other absolute method (White *et al.* 1981). Palaeomagnetic analysis has been attempted, suggesting an age of 2.9-3.32myr for the pink and grey breccias (McFadden, Brock and Partridge 1979). A geomorphological estimate dates the cave opening at 3.7myr (Partridge 1973).

Biostratigraphy appears to provide a more reliable means of dating. Extensive documentation of mammalian palaeofaunas within a well-dated stratigraphy in East Africa, allows for relatively accurate biostratigraphic placement of the Limesworks pink and grey breccias (Cooke 1978; Harris and White 1979; White *et al.* 1981; Turner 1984). Member 3 (grey breccia) is of particular importance to this study, as most of the faunal dating research has been concentrated on this unit. White *et al.* (1981), dated *Australopithecus africanus* within the Limesworks grey breccias at 2.4 - 2.6myr, which postdates *Australopithecus afarensis* by some 0.5myr. A *Potamochoeroides* specimen has been found associated with an *Australopithecus africanus* specimen within Member 3 (Kitching pers. comm.) (refer to section 1.8), indicating that *Potamochoeroides* and *Australopithecus* coexisted. The carnivores (Collings *et al.* 1976) and the cercopithecoids (*sensu* White *et al.* 1981), place the age of Members 3 and 4 at 2myr-3myr. More recent carnivore research (Turner 1984), estimated Member 3 at 3myr. Bovid studies also suggest a 2-3myr age for Members 3 and 4, with the latter date more acceptable (Vrba 1976, 1977). Vrba (1987a) later confirmed an age of 2.5-3myr. Bovids of the tribe hippotragini seem to indicate that Member 3 contains a Pliocene assemblage more ancient than originally thought (Vrba 1987b), with affinities to the Laetoli beds of East Africa, and the Pinjor Formation of the Siwaliks in India and

Pakistan. Leakey and Harris (1987) using the Potassium-Argon dating method, dated the Lactolil Beds at 3.49 ± 0.12 myr - 4.32 ± 0.06 myr.

The suids *Potamochoeroides shawi* and *Notochoerus capensis*, have apparently been favourably compared with *Metridiochoerus andrewsi* and *Notochoerus capensis* from the Shungura Formation at Omo in East Africa, giving a date of 2.4-2.6myr for the Limeworks Member 3 (White and Harris 1977; Harris and White 1979). Cooke (1978) estimated Member 3 at 1.6-3.3myr using *Potamochoeroides*, and 2.6-3.3myr using *Notochoerus*. Microfaunal analysis (Pocock 1987), especially the presence of *Mystromys darti*, indicated that the Rodent corner area of the Limeworks is close to the Langebaanweg palaeofaunal assemblage in time. This is considered to be late Miocene to Early Pliocene in age (3.5-7myr), but probably around 5myr old (Hendey 1981).

Thus, it appears at present, on the strength of faunal dating, that Member 3 may be regarded as 1.6-4.32myr in age. Furthermore, it is evident that the deposit in general, may be up to 5myr old. In the light of the present study, the approximate date arrived at using *Metridiochoerus andrewsi*, 2.4-2.6myr, is questionable, as indeed is the 1.6-3.3myr estimate using *Potamochoeroides*, since Cooke (1978) regarded the abovementioned genus as belonging to the "*Metridiochoerus* complex". Contemporary research (Pocock 1987; Vrba 1987b) appears biased towards a greater age for elements of the Limeworks fossil fauna, and therefore it is suggested that the 3.49-4.2myr estimate may be closer to the age of the grey breccia.

1.10 GENERAL SUID EVOLUTION

It does not seem possible, at this stage, to determine on which continent the "true suids" (*sensu* Pickford 1986) emerged. During the Oligocene, the probable ancestral group, the Dichobunids, as well as *Propalaeochorus*, the first "true suid", were abundant in Europe (Pickford 1986).

During the Early Miocene (20-17myr), bunolistriodonts and listriodonts were widespread in Europe, Asia and Africa. From the mid-to late Miocene (17-10myr) there is evidence of suid movement between Eurasia and Africa (Pickford 1986). By the late Miocene (10.5-5.5myr), the centre of radiation appears to have moved to Asia, and involved the Tetraconodontinae and the Sanitheriinae. Elements of these two groups seem to have migrated to Europe and North Africa (Cooke and Ewer 1972).

A number of Miocene fossil suid specimens have been found in Namibia and East Africa (Pickford 1986), but generally, Africa remained impoverished of fossil suids until the late Pliocene, possibly early Pleistocene. However, by the early to mid-Pleistocene, they were well represented in Africa. A subsequent adaptive radiation gave rise to a variety of genera, which were probably ancestors to the modern suid genera (White and Harris 1977; Cooke 1978). Currently, African fossil suid specimens have been collected from approximately fifty localities, and were originally assigned to seventy seven species within twenty three genera (White and Harris 1977). Harris and White (1979), recognised seven genera and sixteen species, and their scheme is the most comprehensive with regard to general Plio-Pleistocene suid evolution and biostratigraphic correlation between sites. According to Ewer (1958a), the major trend in evolutionary history of the African Suidae appears to have been the development of phacochoerine types with a highly specialised, hypsodont grinding dentition, from primitive unspecialised *Sus*-like forms with a generalised bunodont, brachydont dentition. It appears that this trend has occurred independently in a number of Plio-Pleistocene lineages, and even within a number of genera. Cooke (1978) recognised three major Plio-Pleistocene suid groups (Fig.4), however White and Harris (1977), Harris and White (1979), recognised four major groups (Fig.5):

1. *Nyanzachoerus* - *Notochoerus*.
2. *Kolpochoerus* - *Hylochoerus*.
3. *Metridiochoerus* - *Phacochoerus*.
4. *Potamochoerus*.

Group one consists of extinct species and is predominately found in Pliocene assemblages. Groups two and three occurred from the early Pleistocene; *Hylochoerus* and *Phacochoerus* are extant members of these groups. Group four has a poor, fragmentary fossil record, but appears for the first time in Africa in the late Pliocene (White and Harris 1977). Within group one, *Notochoerus* sp. specimens are distinct from *Nyanzachoerus* by relative and absolute premolar reduction, increased third molar size, hypsodonty and complexity and differences in cranial anatomy, with the upper canines dorsally flattened in cross-section (Cooke and Wilkinson 1978). *Notochoerus* specimens are common elements in the later Pliocene of East and South Africa (Harris and White 1979).

With reference to group two, the earliest African representatives occur in the Pliocene (Cooke and Wilkinson 1978). *Kolpochoerus limnates*, an early form with a tendency for increased M3 molar size and hypsodonty, gave way to *Kolpochoerus majus* with a primitive molar pattern. *Kolpochoerus* is characterised by its moderately hypsodont, elongated upper and lower M3 molar, upper canines similar to *Hylochoerus*, and by a number of features, especially in early forms, similar to *Potamochoerus* and *Sus* (Cooke and Wilkinson 1978). *Hylochoerus* has a very fragmentary fossil record until the late Pleistocene. It has a number of very specific morphological features which are characteristic of the genus (Cooke and Wilkinson 1978; Harris and White 1979).

From group three, the most primitive members of the genus *Metridiochoerus* occur in southern Ethiopia. The initial appearance of the genus coincided with that of *Kolpochoerus*. *Metridiochoerus* seems to have undergone a substantial radiation during the early Pleistocene. At one stage, four distinct *Metridiochoerus* species co-existed (Harris and White 1979). Cooke (1978), regarded *Metridiochoerus* as part of a group termed the "*Metridiochoerus* complex", with *Metridiochoerus* the core genus. On the basis that they share a reduction in premolars and similar wear patterns in the molars. There is a tendency for the second molar to wear rapidly to produce a crown consisting of large areas of dentine with residual rings of enamel (Cooke and Wilkinson 1978). There is also a trend in this

group to develop some *Phacochoerus* - like anatomical features in the skull and third molar. *Potamochoeroides shawi* is tentatively included within group three by Cooke (1978), and definitely included by White and Harris (1977) and Harris and White (1979). *Potamochoeroides* and *Metridiochoerus* are seen as being derived from a common, *Sus*-like ancestor (Cooke 1978). Morphologically the most primitive specimens of *Phacochoerus africanus* come from the South African sites Kromdraai, Bolts farm and Swartkrans B. There is evidence that the *Metridiochoerus modestus* lineage led to *Phacochoerus antiquus*, both taxa being contemporaneous in Olduvai unit four (White and Harris 1977). *Potamochoerus* is unknown from Europe and there is no evidence for an endemic African derivation, so that an Asian origin is plausible (Harris and White 1979). *Potamochoerus porcus* is considered to be a conservative species, in other words it has changed or evolved little up to the present. Plio-Pleistocene fossils from East Africa are morphologically very similar to the extant species (Harris 1983). *Sus scrofa*, although not a southern African species, is important in later comparative analysis and discussion (Chapters 3 and 5). It is regarded as morphologically primitive (Cooke and Wilkinson 1978), and can be regarded as more primitive than *Potamochoerus* (Cooke and Wilkinson 1978), and close to the ancestral stock of most Plio-Pleistocene suids (Cooke 1978; Cooke and Wilkinson 1978).

1.11 FOSSIL SUIDAE DESCRIBED FROM THE LIMESTONE WORKS

Two fossil suid species from the Limeworks quarry have been described by Dale (1948), *Pronotochoerus shawi* and *Potamochoeroides hypsodon*. *Pronotochoerus shawi*, a previously unrecorded species, was based on a mandible from Member 3, the fossil-rich grey breccia (refer to Fig. 6). Dale (1948) stated that the mandible of *Pronotochoerus shawi* was more massive than that of the extant *Phacochoerus*, but that the general structure of the third molar showed this suid to belong to the phacochoerine group. This specimen is comparable to the species *Pronotochoerus jacksoni* from the Omo River, East Africa, differing in the greater complexity of the talonid (Dale 1948). *Potamochoeroides hypsodon*, also a previously unrecorded genus and species, is based on a maxilla

from the overlying Member 4 (refer to Fig.6). This specimen was reported by Dale (1948) to be fundamentally similar in structure to *Potamochoerus porcus*, but considerably more hypsodont. Cooke and Wilkinson (1978), also stated that *Potamochoeroides* resembled the extant *Potamochoerus*; the differences between them being in particular: the structure of the upper and lower M3 molar, the deep zygoma below the orbits and the short mandibular symphysis.

Ewer (1958a), analysed a further 131 specimens from the Makapansgat Lineworks, which consisted mainly of teeth, with twenty three skull and jaw fragments, and seven upper and lower canine fragments. Of this material, one specimen (mandibular ramus) was doubtfully referred to *Potamochoeroides hypsodon*, and 108 specimens were referred to *Potamochoeroides shawi*. The original description stated " ...further studies increasing our knowledge of *Pronotochoerus*, made it clear that the Makapan mandible cannot belong to that genus. The new maxillary specimens show many resemblances to the type maxilla of *Potamochoeroides hypsodon* it thus seems reasonable to conclude that '*Pronotochoerus shawi*' should be transferred to the genus *Potamochoeroides* Dale." (Ewer 1958a, p330).

Ewer (1958a) retained *Potamochoeroides hypsodon* as a separate species, but Cooke and Wilkinson (1978), considered them conspecific, with the name *P.shawi* having page priority over *P.hypsodon*. The genus *Pronotochoerus* has since been found to be synonymous with *Metridiochoerus andrewsi* Hopwood 1926 (White and Harris 1977). *Pronotochoerus* shows considerable premolar reduction, whereas *Potamochoeroides shawi* has a fully developed premolar series. According to Cooke and Wilkinson (1978) *Potamochoeroides* is generically distinct from *Metridiochoerus*, being separated, not only by the premolars, but also by the possession of *Potamochoerus* or *Sus*-like upper canines, those of *Metridiochoerus* being more phacochoerine. However, Harris and White (1979), regarded *Potamochoeroides shawi* as synonymous with *Metridiochoerus andrewsi* on the basis of third molar characteristics, and on rapid, early wear of the second molar. Harris and White (1979) divided the *Metridiochoerus andrewsi* lineage into three stages, to "reflect the evolutionary development of the third

molar". The Makapansgat specimens are included within stage one, and are thus regarded as primitive within the *Motridtochoerus andrewsi* group.

Ewer (1958a) referred twenty four suid specimens from the Limeworks to *Notochoerus* (*Gerontochoenus*) *cullis*, (a genus and species not previously recorded from this locality), on the basis of its close resemblance to Omo specimens described by Leakey (1943). Since then, the genus *Notochoerus* has become more completely understood. It appears that, on the basis of the antero-posterior length of the lateral aspect on the lingual side of the upper and lower M3, the Limeworks specimens belong to the species *Notochoerus capensis* (Cooke and Wilkinson 1978; Harris and White 1979), regarded as a grazer (Ewer 1958a).

Previous work on the Limeworks suids includes an estimate of the age composition of the *Potamochoeroides* collection (Ewer 1958a), which was used to discuss the taphonomy of the suids. In the first part of the analysis there appears to be an overlap between stages one and two wear categories for the upper and lower P4 and M2. In the second part, using all specimens, the categories selected seem to overlap, and thus cannot be regarded as diagnostic in the determination of age composition.

A discussion on the evolutionary history of both *Potamochoeroides* and *Notochoerus* is presented by Ewer (1958a). This discussion is based on the comparative anatomy of the extant southern African suids *Potamochoerus porcus* and *Phacochoerus aethiopicus* using the structural differences between the upper and lower M3 molars. Past and present research suggests that *Potamochoeroides* was omnivorous in habit, as is typical of the extant *Potamochoerus* and *Sus* (Ewer 1958a; Cooke and Wilkinson 1978). However, *Potamochoeroides* appears not to have had the digging specialisation of the snout which is exclusive to *Potamochoerus* (Ewer 1958b; Smithers 1983).

1.12 EXTANT AFRICAN SUIDAE

"The functional contrasts between the extant brachydont and omnivorous *Potamochoerus porcus* and the extant hypsodont grazer *Phacochoerus aethiopicus* are great and serve as a convenient and enlightening framework in which the fossil suids may be assessed." Harris and White (1979)p8.

The two extant southern African Suidae *Potamochoerus porcus* and *Phacochoerus aethiopicus* were used for comparative purposes, in order to revise and update the taxonomic position of *Potamochoeroides shawi* and *Notochoerus capensis*. Discussion on the palaeoecology of the Lineworks fossil suids is also based on the comparative studies of the extant genera. Previous researchers have made extensive use of the two extant genera in describing the Lineworks fossil suids (Ewer 1958a; Ewer 1958b; White and Harris 1977; Cooke 1978; Cooke and Wilkinson 1979; Harris and White 1979). Reference is made to the wild boar *Sus scrofa*, since past researchers (Ewer 1958a; Cooke and Wilkinson 1978) used this species for comparison with *Potamochoeroides shawi*.

Potamochoerus porcus and *Phacochoerus aethiopicus* are widespread today in South Africa. *Potamochoerus porcus* is associated with forest, thickets, reed beds or tall grass. Dense cover and water appear to be essential requirements. *Phacochoerus aethiopicus*, however, tends to inhabit floodplains and open grassland (Smithers 1983). A number of studies have outlined the ecology of *Potamochoerus* and *Phacochoerus* (Breytenbach and Skinner 1982; Jones 1984). It is well known that *Phacochoerus* is primarily a grazer, whereas *Potamochoerus* has generally been regarded as an omnivore, with a specialised digging and rooting habit. From a study at Lake St Lucia, Breytenbach and Skinner (1982) found that *Potamochoerus* feeds extensively on fruit in summer, and on roots, bulbs, leaves and corms in winter. A study conducted near Tzaneen in the Northern Transvaal on *Potamochoerus* (Skinner, Breytenbach and Maberly 1976), gave details on foraging and diet. It was stated that any dense cover is used for sleeping, and that *Potamochoerus* frequents low lying areas for rooting. *Potamochoerus porcus* is gregarious, moving in sounders of up to twelve, although, at the same

time it appears to be somewhat nomadic. The sounders generally consist of a dominant boar and/or sow, and sows and juveniles (Skinner *et al.* 1976).

Phacochoerus aethiopicus also forms social units. According to Cumming (1975), these also tend to be family units, usually larger during the rainy season (October to February). Maternity groups, that is adult females with offspring and juveniles, are also fairly common. Durable bonds appear to form between females and offspring and they remain together for up to twenty seven months. Adult males form temporary bachelor groups with younger males, and tend to join the females for brief periods, or when the females are in oestrus.

CHAPTER 2. MATERIALS AND METHODS

2.1 EXTINCT AND EXTANT SUID COLLECTIONS

2.1.1 EXTINCT SUIDS

The prepared fossil Suidae collection from the Makapansgat Limeworks is held in the Bernard Price Institute for Palaeontological Research, and comprises some 570 specimens. Previous research (Dale 1948; Ewer 1958a; Harris and White 1979) referred to approximately 170 fossil suid specimens. The present study, after sorting through the prepared collection, and re-examining the previously studied material, found that 210 specimens could be placed within the two fossil suid genera *Potamochoeroides shawi* and *Notochoerus capensis*. One hundred and eighty nine of these specimens belong to *Potamochoeroides shawi* Dale 1948; 106 are skull and maxillary, and eighty three mandibular fragments. The remaining twenty one specimens, of which ten are maxillary and eleven mandibular fragments, are referred to as *Notochoerus capensis* Broom 1925. The list below, gives a more detailed account of the skull remains.

Breakdown of the above mentioned collection indicates that between one third and a half of the specimens either consists of maxillae and lower jaws with teeth, or isolated teeth. This is probably due to the fact that teeth constitute the most resistant portion of any bone assemblage (Brain 1981). As most of the specimens were extracted from the breccia blocks from the limeworkers' rubble dumps to the north and northwest of the main quarry, it is virtually impossible to determine provenance. However, a few specimens were found in situ (Kitching pers. comm.), and include (refer to Fig.3 for their location):

the type specimens of *Potamochoeroides* (Fig.6) from Member 3 (grey breccia) in the main quarry; two *Potamochoeroides* specimens from Member 3, at the Classic Section, associated with blow fly larvae - the Classic section is situated along the western wall of the Main quarry; a *Potamochoeroides* snout

(old individual), adjacent to a pelvis of *Australopithecus africanus* and a specimen of *Makapania broomi* - these specimens were found below the Cone Mouth depository, within a block of Member 3; two *Potamochoeroides* molars within Member 3 at Ledge F, to the east of the Cone Mouth depository; a juvenile *Potamochoeroides* specimen from Member 4, next to "Ledge F".

The assessment of the specimens is as follows:

POTAMOCHOEROIDES SHAWI DALE 1948.

Type specimen - M302, is a right mandibular ramus with P3-M3 (Fig.6). Initially described by Dale (1948) as the type specimen of *Pronotochoerus shawi*, but later reclassified by Ewer (1958a) as *Potamochoeroides shawi*.

Referred Specimens

Skull and maxillary

M2082 - isolated I1.

M371, 373, M382, M1585, M1866, M1991, M1993, M2030, M2037, M2068, M2253, M8403 - isolated canine specimens.

M589 - supracanine flange.

M2048 - isolated P3.

M362, M1875, M2029, M2043, M2047 - P4 specimens.

M356, M358, M1914, M1915, M1949, M1951, M2034, M2039, M2041, M2231 - isolated M2.

M317, M320, M1400, M1572, M1573, M1868, M1924, M1926, M1927, M1929, M2072, M2073, M2074 - isolated M3 specimens.

M2049 - isolated dm3.

M303: originally the type specimen of *Potamochoeroides hypsodon*, M315-319, M321, M326-329, M330-334, M345, M346-348, M353, M383, M385, M1544, M1851, M1853, M1857, M1858, M1868, M1872, M1893, M2000 - 2003, M2006-2008, M2010-2012, M2063-2066, M2080, M2260, M8378, M8399, M8400, M8401 - maxillary fragments.

M1869, M2004 - immature maxillary fragments.

M305, M588, M1391, M2062, M2265, M8270 - skull remains.

Mandibular

M2083 - isolated I1.

M379, M381, M579, M1578, M2057-2059, M8226 - isolated lower canine fragments.

M363, M1959 - P4.

M341, M342, M2060, M2061, M8380 - immature mandibular specimens with dm3 and dm4.

M1586 - isolated dm4.

M312, M2040, M2056, M2072, M8376, M8377 - isolated M3.
 M302, M307-311, M335, M338-340, M344, M1826, M1828, M1838, M1839, M1881, M1882, M1883,
 M1886, M1887, M1888, M1889, M1890, M1892, M2013-2021, M2023, M2024, M2052-2055, M2081,
 M2263, M8217, M8365, M8366, M8367, M8368, M8369, M8370, M8371, M8373, M8381, M8395,
 M8396, M8397, M8398, M8895 - mandibular fragments.

Doubtfully Referred Specimens

M2069 - nasal region of snout.
 M2266 - portion of frontal with left supraorbital foramen.
 M8229 - lower canine.
 M1832, M1845, M1891 - mandibular specimens.

NOTOCHOERUS CAPENSIS BROOM 1925.

Referred Specimens

Maxillary

M2026, M2250, M2426 - canine fragments.
 M368, M369 - isolated M2.
 M325, M8352 - maxillary fragments.
 M324, M2005 - immature specimens.

Mandibular

M357 - isolated M1.
 M2075, M2076 - isolated M2.
 M2025, M2031, M2077, M2079, M8275 - mandibular fragments with M3.
 M336 - immature mandible fragment with M1.

Doubtfully referred

M304 - maxillary/orbital fragment.
 M1561 - lower canine fragment.
 M2022 - immature mandibular fragment.

2.1.2 EXTANT SUIDS

For comparative purposes, skulls of the extant suids *Potamochoerus porcus* and *Phacochoerus aethiopicus* were studied. The former is generally a conservative genus with primitive morphological characters, the latter is advanced with many derived characters (Harris and White 1979). These specimens form part of a collection housed in the B.P.I. Palaeontology, and consist of four complete

Potamochoerus porcus (two male and two female), and eight complete *Phacochoerus aethiopicus* specimens (six male and two female).

An assessment of the specimens studied:

POTAMOCHOERUS PORCUS LINNAEUS 1758.

BPI/C 5 - male, young adult. Port Elizabeth district, Eastern Province.

BPI/C 8 - male, mature. Locality unknown.

BPI/C 4 - female, mature. Kirkwood, Eastern Province.

BPI/C 9 - female, young adult. Locality unknown.

BPI/C 4 is somewhat of an aberrant specimen - the frontal bone is raised above the nasals, so that the profile is not in a straight line. The angle on the mandible is also considerably sharper than in all the other specimens.

PHACOCHOERUS AETHIOPICUS PALLAS 1767.

BPI/C 11 - male, mature. No lower premolars. Locality unknown.

BPI/C PAB2 - male, mature. No lower premolars. Locality unknown.

BPI/C 23 - male, mature. No premolars. Locality unknown.

BPI/C 14 - male, mature. No premolars. Luangwa valley, Zambia.

BPI/C 15 - male, mature. Locality unknown.

BPI/C 12 - male, immature. Klaserie, Eastern Transvaal.

BPI/C 13 - female, immature. Locality unknown.

BPI/C PAB1 - female, mature. No premolars. Locality unknown.

2.2 METHODS

2.2.1 Introduction

Most of the Limeworks fossil suid collection has previously been sorted roughly, according to skull part, into the two species, *Potamochoeroides shawi* and *Notochoerus capensis*. As part of the present

research, this collection was examined, including 30 previously unreported specimens. Three new *Potamochoeroides* specimens (M8399, M8400, M8401), were catalogued and also included.

A table of measurements was used [based on a system employed by Von den Driesch (1976); Harris and White (1979) and Harris (1983)] (Fig.7) to facilitate the description and analysis of fossil specimens and their comparison to the extant suid study collection and fossils from other notable sites.

The fossil suid taxonomy and phylogeny was examined in terms of anatomical features referred to by previous researchers (Dale 1948; Ewer 1958a; White and Harris 1977; Cooke 1978; Cooke and Wilkinson 1978; Harris and White 1979), as well as a number of additional features. These include: the structure of the supracanine flange, of the pterygoid, the fossae for the origin of the internal pterygoid muscle, and the ventro-lingual face of the mandibular ramus.

This study involves comparative analysis with the two extant southern African suid genera *Potamochoerus porcus* and *Phacochoerus aethiopicus*, and, in certain cases, reference to the wild boar *Sus scrofa*. Comparison was also made using relevant literature (Leakey 1958; Harris and White 1979; Harris 1983) with collections from Shungura, Koobi Fora and other relevant East African sites. Where possible, measurements are used to support the anatomical comparisons.

A cladogram was constructed in order to attempt to clarify the phylogenetic position of *Potamochoeroides shani* (Fig.32).

2.2.2 Data Collection Methods

"It is only when truly comparable measurements have been taken that it is possible to say anything objective about the size or form of the animal..." Von den Driesch (1976, p1).

Ten skull and five mandibular measurements, based on measurements devised by Von den Dreisch (1976), Harris and White (1979) and Harris (1983), were applied to the fossil suid collection and the extant suid genera, *Potamochoerus porcus* and *Phacochoerus aethiopicus* (Fig.7). Length and breadth were measured for the upper and lower premolars and molars present. Height was measured on relatively unworn M3 specimens. The antero-posterior and the dorso-ventral breadths were measured on the upper and lower canines. Furthermore, additive and comparative measures, including single tooth parameters and tooth row parameters, were utilised (Fig.7). Most of the measurements were taken on East African Plio-Pleistocene suids by previous researchers, so that comparisons could be drawn [Appendix 1; Harris (1983)].

All the measurements were recorded to the nearest 0.1mm, using hand-held vernier calipers. In order to increase accuracy, each was verified, if the discrepancy was greater than 0.02mm the measurement was repeated until no discrepancy was found.

2.2.4 Age and the Minimum Number of Individuals

Owing to the nature of the *Potamochoeroides* collection, the ages of the individuals at death were estimated using teeth. There are two basic methods for establishing the age of an animal from teeth (Klein and Cruz-Urbe 1984): one counts the annuli (growth increments) in the dentine or cementum; the other, the method used in this study, evaluates age in terms of tooth eruption and wear. This method can be used to determine the absolute age if comparative dentitions of known age are available. In this case they were unavailable with the result that only general age categories could be formed. Upper and lower M3 specimens were used to establish the relative ages of adults and sub-adults which gave an accurate indication of the adult/sub-adult age profile. Juvenile specimens were recorded separately to give the overall age profile.

M2 specimens are the more common but tooth wear and eruption was not as diagnostic as in the M3 group. The M1 group is also large, but M1 tends to wear very rapidly, and is thus not diagnostic in terms of age. P4 is represented by a large number of specimens, but the wear was considered to be too variable for age analysis. The relative age of the adults/sub adults was thus evaluated by separating the upper and lower M3 molars into categories according to eruption and amount of wear. The following categories were used:

- (i) Unerupted, or not fully erupted.
- (ii) Fully erupted.
- (iii) Well-worn.

The numbers of specimens in each group were counted and together with the juvenile specimens, translated to give age profiles. The following categories were used:

- (i) Juvenile.
- (ii) Immature adult.
- (iii) Mature adult.
- (iv) Old adult.

In each case, the specimens were separated into maxillary left and right, and mandibular left and right, to avoid duplication. The minimum number of individuals is the smallest number of individuals necessary to account for all the identified specimens. Maxillary and mandibular specimens containing complete or partial dentitions were found to be the most frequently represented skull parts. The minimum number of individuals (MNI), was investigated by taking these skull parts (Brain 1974), (specifically taking note of the numbers of upper and lower M3) and then following the same procedure outlined in the paragraph above.

CHAPTER 3. THE COMPARATIVE ANATOMY OF THE EXTINCT AND EXTANT SUIDS

3.1 INTRODUCTION

In the following section the anatomy of *Potamochoeroides shawi* and *Notochoerus capensis* is analysed in order to reconsider the taxonomy and phylogeny. For comparative purposes, [in order to be able to discuss taxonomy and phylogeny (Chapter 5)], frequent reference is made to the extant *Potamochoerus porcus* and *Phacochoerus aethiopicus*, and relevant fossil material from East African sites, in particular *Metridiochoerus andrewsi* and *Notochoerus capensis* specimens. Many of the comparisons, specifically with regard to the dentition are based on measurements, where East African specimens are involved the measurements were taken from Harris and White (1979) and Harris (1983). All of the referred extinct and extant specimens are mature unless otherwise indicated.

3.2 POTAMOCHOEROIDES SHAWI

3.2.1 Skull and maxillary

A number of specimens are more complete than the type specimens and are thus referred to individually, before the detailed anatomical descriptions.

M1391

This is the most complete cranial specimen in the collection (Figs. 8 and 9). The premaxillae are missing, as are the canine flanges. The maxillae and the posterior portion of the nasals are intact. The

frontal, although damaged, is preserved. The zygomatic arches are missing. The dorsal outer rim of the left orbit is preserved. The parietals are missing, however, the dorsal rim on the left side, bordering on the frontal and the orbit, is intact. The occiput is missing, but it appears that M588, consisting of the ventral section of an occiput, is in fact part of M1391 (Cooke pers.comm.). The posterior portion of the palate is preserved, although the pterygoid is missing. The P2 alveoli are intact and both P3 and P4 are preserved, as are M2 and M3. The premolars and molars are well worn, indicating that this specimen represents an old animal. Of particular value in this specimen is the good preservation of the fossae for the origins of the levator and depressor rostri muscles on the nasal bones.

This specimen is damaged along the suture between the frontal and the nasals. The damage can be compared to that caused by a man using an elephant scapula on an extant *Potamochoerus domesticus* skull (Kitching pers.comm.), suggesting that the damage may have been caused by *Australopithecus africanus*.

M2062

This cranial specimen (Figs.10 and 11) is well preserved although the portion of the skull, anterior to the nasal frontal suture is missing. The lachrymal and jugal are preserved. The zygomatic arches are missing, although the root is intact on both sides. The orbits are very slightly damaged, however, the frontal and the parietals together with the dorsal section of the occiput, are well preserved. The medial half of the glenoid is present on both sides. The posterior fragment of the palate and the maxillae is preserved with erupting M2 molars. Of particular value is the well preserved structure of the pterygoids.

M321

A well preserved right maxilla fragment with P2-M3 (Fig.19); the posterior portion of P1 is also intact. The premolars are all well worn, as is M2. M1 is extremely well worn. M3 is only partially erupted and there is slight wear on the anterior pillar pair. Part of the palate with the posterior section of the interpalatine groove is intact.

Nasal Region

The nasals in *Potamochoeroides* appear more rounded in comparison with *Potamochoerus*, but similar to *Phacochoerus* in this respect. Although, according to Cooke and Wilkinson (1978), the rounded structure of *Potamochoeroides* is similar to that of *Sus scrofa*. There appears to be a posterior widening in *Potamochoeroides* (Fig.8) which is typically found in *Potamochoerus*. In *Potamochoeroides* specimen M1391 the nasals appear to widen at the canine alveolus. The nasals seem broader than found in *Metridiochoerus andrewsi*. The channels extending forward from the supraorbital foramina, are deeply incised into the *Potamochoeroides* skull roof, which is unlike *Metridiochoerus*.

The fossae for the origins of the levator and depressor rostri muscles can be clearly seen in *Potamochoeroides* specimens M1391 M2060, M2080, M2265, M2266 and M8270. In M1391 (Fig.9) and M8270 the bone around the fossae is not as deeply sculptured as in *Potamochoerus*, possibly due to fossilisation, but the fossae are deeper than in *Phacochoerus*. *Potamochoeroides* thus appears to more closely resemble *Potamochoerus* in terms of the depth of the fossae (Fig.14). However, the high position of the levator rostri fossa and the shallow depressor rostri fossa of *Potamochoeroides* seems to be *Sus*-like (Cooke and Wilkinson 1978). The *Potamochoeroides* fossae are clearly different from the shallow fossae of *Metridiochoerus andrewsi*.

Supracanine Flange

Description of the *Potamochoeroides* supracanine flange is based on specimen M589. It is broadest over the canine alveolus and is separated from the maxilla by a wide, deep groove (Fig.12). The flange tapers posteriorly to suture with the maxilla and anteriorly to suture with the premaxilla. Anterior to and above the canine alveolus, although slightly damaged, it appears to recurve over the alveolus towards the premaxilla (Fig.13). The position of the canine alveolus indicates that the upper canines pointed forward, differing from the lateral curve of the *Phacochoerus* upper canine, but similar to *Potamochoerus* in this respect (Fig.14). A small flange is present in the extant female *Potamochoerus*, and a short narrow groove extends between it and the maxilla, whereas in the male the flange is elevated (Fig.14) and the groove is broad. In *Phacochoerus* on the other hand, no clear distinction exists between this bone in males and females; a broad shallow groove extends the length of the flange. The *Potamochoeroides* supracanine flange appears to be similar to that of the female *Potamochoerus*, although, according to Cooke and Wilkinson (1978), it is *Sus*-like. It appears generally similar to the flange in *Metridiochoerus andrewsi*, but also seems similar to *Kobolpochoerus limnetes*.

Orbits

The upper half of the orbit is preserved in *Potamochoeroides* specimens M1391, M2062 (Fig.11) and M8270. Cooke and Wilkinson (1978), considered the orbits of *Potamochoeroides* to be more elevated than in *Potamochoerus*. They appear slightly less elevated than in *Metridiochoerus andrewsi*. It seems that the *Potamochoeroides* maximum inner orbit length is considerably greater than in the two extant species, although the mean is based on only three measurements.

Means of the maximum inner orbit lengths:

	<i>Potamochoeroides</i>	<i>Potamochoerus</i>	<i>Phacochoerus</i>
number of			
specimens	3	5	8
max.orb.len.	40.9mm	37.3mm	37.4mm

Lachrymal

In *Potamochoeroides* specimens M2062 and M8270 the lachrymal is short and compares favourably with that of *Potamochoerus*, but appears considerably shorter than in *Metridiochoerus andrewsi*.

Zygoma

A complete zygoma is not preserved in any of the *Potamochoeroides* specimens. However, it appears to be broad below the orbits and thus is possibly closer in structure to the broad *Metridiochoerus andrewsi* and *Phacochoerus* zygoma. According to Cooke and Wilkinson (1978), the maxillary root of the zygoma of *Potamochoeroides* is similar to that of *Sus*.

(Figures 15 and 16 indicate that the zygoma differs between male and female in both *Potamochoerus* and *Phacochoerus*. The male, in both genera, exhibits a more pronounced "flaring" of the zygoma.

Glenoid

In *Potamochoeroides* specimens M2062 and M8270 the medial half of the glenoid is preserved. The articular surface is broad, and resembles *Potamochoerus*, but differs from the narrow articular surface in *Metridiochoerus andrewsi*. The height of the glenoid above the occlusal plane in *Potamochoeroides*

(Fig.11) also appears similar to *Potamochoerus*. This is in contrast to the elevated position above the occlusal plane in *Metridiochoerus andrewsi* and *Phacochoerus*.

Skull Roof

The cranium in *Potamochoeroides* expands posteriorly from the nasal and frontal suture to the orbits. Posterior to the orbits, it tapers gradually back to the lambdoidal crest (Fig.10). The back of the braincase or occipital region, as in *Potamochoerus*, does not appear elevated (Fig.11), in contrast to the antero-posteriorly compressed *Metridiochoerus andrewsi* braincase.

Occipital and Parietals

From the *Potamochoeroides* specimens M305 and M2062 (Fig.10), it can be seen that the narrow parietal constriction is similar to that in *Potamochoerus* and *Phacochoerus*, and in contrast to the broad parietal constriction found in *Metridiochoerus andrewsi*. Although the comparative measurements below indicate that the *Potamochoeroides* parietal is possibly wider than in the two extant species.

Means of the minimum parietal breadth:

	<i>Potamochoeroides</i>	<i>Potamochoerus</i>	<i>Phacochoerus</i>
number of specimens	3	5	8
min.par.br.	39.3mm	34.1mm	35.74mm

The occipital region in *Potamochoeroides* specimens M305 and M2062, also appears similar in shape and size to that in *Potamochoerus* and *Phacochoerus*, however, preservation is not good enough to be able to establish closer affinities. In *Potamochoerus* the occiput is fairly narrow and there is a central

ridge from half way down. The *Phacochoerus* occiput is similar, but flatter and slightly broader with no central ridge.

Palatal region



M1391 is the only *Potamochoeroides* specimen with a fairly complete palate (the anterior section of the nasals and the premaxillae are missing). M2002 and M2007 are fragments in which the structure of the palate immediately behind the canine alveolus is preserved. Palantine grooves are prominent in all three specimens. The taper of the grooves is lateral towards the canine alveoli, where the palate is at its widest. The palate tapers lingually and posteriorly from the position of M2. In *Potamochoerus* the palate appears broader than that of *Phacochoerus* (68.1mm compared with 62.4mm). In *Potamochoeroides* M1391, the measurement is 74.7mm, thus indicating a possible similarity in terms of size, with *Potamochoerus*. The palate appears different from that in *Metridiochoerus andrewsi*, in which it tends to be strongly flared at the canine alveolus, in contrast to the roughly parallel sided *Potamochoeroides* palate.

Pterygoid

In *Potamochoeroides* specimen, M2062, it can be seen that the surface of the pterygoid protrudes ventrally (Fig.17). In this respect it is closer in structure to *Potamochoerus* (Fig.20) than *Phacochoerus* or *Metridiochoerus andrewsi*, in which the ventral surface of the pterygoid does not protrude. In *Phacochoerus* the fossa for the attachment of the internal pterygoid muscle, ventral and posterior to the pterygoid, is larger than in *Potamochoerus* (Ewer 1958b). The ventral surface of the pterygoid serves as the origin of the internal pterygoid muscle in both *Potamochoerus* and *Phacochoerus*. It may be therefore that in *Potamochoeroides*, as in *Potamochoerus*, the internal pterygoid muscle is smaller than that of *Phacochoerus*.

Lateral profile

The lateral profile of *Potamochoeroides* can be clearly seen only in M1391 (Fig.9). It is somewhat steeper than in the average extant *Potamochoerus* specimen, in which the lateral profile is generally straight, with a slight change of angle at the nasal and frontal suture, but generally not as steep as in *Phacochoerus* or *Metridiochoerus andrewsi*. However the notable change of angle at the nasal and frontal suture does indicate a possible affinity with the latter two genera.

Comparison of the cranial measurements (Table 1; Harris 1983), although based on few specimens indicates that the maxilla is narrower in *Potamochoeroides* than in *Metridiochoerus andrewsi*. It seems to be wider or broader in the above mentioned two genera compared with the two extant genera under study.

3.2.1.1 Upper Dentition

Incisors

M2082 is the only I-1 specimen of *Potamochoeroides*. This specimen is similar to that in the extant *Potamochoerus* in shape, but it is smaller. M2069 is a *Potamochoeroides* specimen with six incisor alveoli. It appears that the alveoli are all similar in size, in contrast to *Potamochoerus*, in which the I-1 alveolus is the largest, with I-2 and I-3 progressively smaller.

Canines

The upper canine of *Potamochoeroides* closely resembles that of the extant *Potamochoerus* (Fig.18). It is triangular in cross-section, with a broad, longitudinal ribbed enamel band along the ventral surface, and narrow, single enamel ridges on the posterior and dorsal surfaces. The wear facet in

Potamochoeroides, is more laterally sloping than in the extant *Potamochoerus*, so that the upper canine in *Potamochoeroides* tends to be longer, with the point not so abruptly truncated. The *Potamochoerus* canine is small and curves laterally. There is a broad, longitudinal ribbed ventral enamel band, and single antero-dorsal and postero-dorsal enamel ridges. In *Phacochoerus* and *Metridiochoerus andrewsi* the canines are large and curve laterally and upwards.

Table of the means of the antero-posterior (a-p) and the dorso-ventral (d-v) canine breadths:

	<i>Potamochoeroides</i>	<i>Potamochoerus</i>	<i>Phacochoerus</i>
number of specimens	7	8	10
a-p br.	21.3mm	19.5mm	28.6mm
d-v br.	18.5mm	15.74	23.3mm
d-v/a-p index	0.86	0.81	0.81

The *Potamochoeroides* upper canine appears to be generally larger than the *Potamochoerus* upper canine, although not as large as in *Phacochoerus*. The upper canine in all three species appears similar in terms of the d-v/a-p index, although in *Potamochoeroides* it appears broader. There is considerable variation in size for all three of the above genera.

Premolars

No complete upper P1 specimens of *Potamochoeroides* are preserved. Specimen M321 has fragments of P1 preserved and specimens M1391 and M1544 have roofed alveoli preserved. In the extant *Potamochoerus*, P1 is shed early or does not erupt, and in *Phacochoerus* and *Metridiochoerus andrewsi*, it does not erupt at all. The presence of a P1 fragment in *Potamochoeroides* specimen M321 (Fig.19)

thus seems to indicate a similarity to the situation in *Potamochoerus* or *Sus* (Cooke and Wilkinson 1978) in which the upper P1 is present.

The *Potamochoeroides* specimens M321 (Fig.19), M353 and M1544 have an upper P2 which is double rooted and similar in structure to *Potamochoerus* (Fig.20). The posterior cusp forms a ridge-like extension of the main anterior cusp. Anterior and posterior to the main cusp is a style of variable size. A cingulum is present on the lingual side, although it is extremely variable in size and extent.

P2 in *Potamochoeroides* appears smaller than in *Potamochoerus* (Table 2). P2 generally appears not to erupt in *Metridiochoerus andrewsi* (Harris and White 1979).

In *Potamochoeroides* specimens M321, M326 and M353 it can be seen that the upper P3 is basically triangular in cross-section (Fig.19) and triple rooted, with the main-cusp anteriorly situated. There is an adjacent posterior cusp, with a well developed cingulum on the lingual face, and two styles included within the cingulum. The structure of P3 in *Potamochoerus* is similar, except that there are four roots, and what appears as one of the lingual styles in *Potamochoeroides*, is a cusp in *Potamochoerus* adjacent to the posterior buccal cusp (Fig.20). According to Ewer(1958a), the *Potamochoeroides* P3 is similar in structure to *Sus*. The measurements (Table 3; Appendix 1) indicate that *Potamochoeroides* and *Metridiochoerus andrewsi* are generally similar, although the mean breadth of the former is greater. The *Potamochoerus* upper P3 is generally larger.

The *Potamochoeroides* specimens M303, M326, M329, M1851, M2043 and M2065 indicate that the upper P4 is almost square in plan view (Fig.19) and has four roots. The main cusp on the buccal side, is somewhat laterally compressed. There are two subsidiary cusps on the lingual side and surrounding these is a well developed lingual cingulum. P4 is worn into a flat grinding surface in the same way as in *Potamochoerus*. In the latter, there are two main cusps on the buccal side, and a lingual cusp surrounded by a cingulum (Fig.20). P4 is thus smaller in *Potamochoeroides*, although similar in structure. It appears that the *Potamochoeroides* P4 is closer to *Potamochoerus* than it is to *Sus*, which

is more blade-like. Dimensions indicate that *Potamochoeroides* is generally broader and more square in plan view than is *Metridiochoerus andrewsi*, although they are generally similar in area (Table 4; Appendix 1).

The mean of the sum of the P3 and P4 areas (Fig. 7), is slightly greater in *Potamochoeroides*, in relation to *Metridiochoerus andrewsi* (Table 5; Appendix 1). In *Potamochoerus* it is considerably greater. *Metridiochoerus andrewsi* and *Potamochoeroides* are generally similar in terms of P3 and P4 combined length.

Molars

The enamel on all the upper *Potamochoeroides* molars, particularly M3, is thick and a cement covering is present. Deciduous upper molars, dm3 and dm4 are preserved in specimens M1869, M1876, M2004 and M2049. dm3, which has one anterior cusp and a posterior lateral column pair of cusps, is very similar to that of *Potamochoerus* (Ewer 1958a). dm4 is usually badly worn in all specimens and contains two lateral column pairs of cusps.

The *Potamochoeroides* upper M1 structure could be determined from specimens M326, M329, M1851 and M2012. Two pairs of lateral pillars are present. An anterior and a posterior pair, with a space on the buccal side between the two, a small medial buccal cusp is also present. The pillars are four lobed and stellate shaped in cross-section. On the extreme posterior end of the tooth is a small median cusp with 2-3 adjacent styles, a similar smaller anterior complex is also present. The structure in *Potamochoerus* is almost identical, except that the posterior median cusp is more closely associated with the posterior pillar pair, and is smaller than in *Potamochoeroides*. The *Metridiochoerus andrewsi* upper M1 is generally larger than in *Potamochoeroides* (Table 6; Appendix 1), there is also a considerable difference in cross-sectional shape. *Potamochoeroides* is broader than it is long, almost square, whereas *Metridiochoerus andrewsi* is longer than it is broad.

The structure of the upper M2 in *Potamochoeroides* can be seen in specimens M321 (Fig. 19), M326, M329, M1851, M1915 and M2012. Two pairs of lateral pillars are present which are separated by a small median cusp, with a gap between the pillar pairs on the buccal side, and a median lingual style often associated with the lingual posterior pillar. A small anterior median cusp surrounded by 2-4 styles, and a similar posterior median cusp surrounded by 2-4 styles, are evident. The *Potamochoerus* M2 structure is very similar, except that the anterior and posterior median complexes, but particularly the posterior one, are smaller (Fig. 23). The *Metridiochoerus andrewsi* upper M2 is generally somewhat larger than in *Potamochoeroides*, in the latter it is slightly broader than it is long, basically square, whereas in *Metridiochoerus andrewsi* it is longer than it is broad (Table 7; Appendix 1). The *Potamochoerus* M2, although larger than in *Potamochoeroides*, is on average almost square in cross-section and thus very similar to the latter (Table 7).

In *Potamochoeroides* the upper M3 basically consists of an anterior pillar and a talon complex. The roots are considerably longer in *Potamochoeroides* than in *Potamochoerus* (20.5mm in *Potamochoeroides*, 8mm in *Potamochoerus*), although similar in structure.

The anterior pillar complex is made up of two lateral pillar pairs, an anterior pair and a posterior pair, with a gap between the buccal anterior and posterior pillars. There is a small anterior median cusp surrounded by 2-4 styles, closely associated with the buccal anterior pillar. A small second median cusp, and in a few cases a third, is closely associated with the lingual anterior pillar and situated between the two pillar pairs. A single style is present between the anterior and posterior buccal pillars, and 1-2 median styles between the lingual anterior and posterior pillars. The cusps are also four lobed and stellate shaped in cross-section (Figs. 21, 22, 23). M3 is generally smaller and broader than is found in *Metridiochoerus andrewsi* (Tables 8a and 8b; Appendix 1). The means of the Lt/Br ratios indicate that *Potamochoeroides* is almost exactly half way between *Metridiochoerus andrewsi* and *Potamochoerus*. Clearly the average height of the upper M3 in *Potamochoeroides* is closer to

Potamochoerus, and markedly smaller than in *Metridiochoerus*. The average Ht/Lt ratio shows the *Potamochoeroides* upper M3 to be closer to *Potamochoerus* than to *Metridiochoerus*.

In *Potamochoeroides* specimens M316, M321, M346, M385 and M2063 the buccal posterior pillar has two close associated styles. The structure of the anterior complex is similar for all *Potamochoeroides* specimens. Differences occur in the talon complex, and it was found that the upper M3 specimens could be separated into three groups.

Group 1 - has one median cusp and 3-4 surrounding styles comprising the talon (Fig.21).

Potamochoeroides specimens M347, M1926, M2067 and M2073 are contained within this group.

Group 2 - the talon consists of two median cusps, and 3-5 styles (Fig.22). *Potamochoeroides* specimens M303, M385, M1573, M1574, M1927, M1929, M1932, M2063, M2067 and M2074 all fall within this group.

Group 3 - has three median cusps and 4-8 styles comprising the talon (Fig.23). *Potamochoeroides* specimens M316, M318, M319, M321, M330, M346, M1400, M1572 and M1924 are contained within this group.

There is some variation in tooth wear within all three groups, with the lingual pillars generally higher and therefore less worn, than the buccal pillars. The groupings did not appear to be affected by the relative age of the specimens.

In *Potamochoerus* (Fig.20) two lateral pillar pairs are also present, with a gap between the anterior and posterior buccal pillars. In cross-section, the pillars are not as clearly four lobed as they are in *Potamochoeroides*. There is sometimes an anterior median cusp, with 2-4 surrounding styles, closely associated with the anterior buccal pillar. A single central median cusp with an adjacent lingual style is also present. Within the talon complex there is a small median cone and 2-4 styles. *Potamochoerus*

specimen BPI/C 4 is unusual in having a number of additional styles on the buccal and lingual faces. The *Phacochoerus* upper M3 is different in having 5-7 lateral column pairs and 7-9 central median cusps. The cusps are oblong shaped in cross-section. There thus appear to be similarities between the *Potamochoeroides* upper M3 and that of *Potamochoerus*, although the *Potamochoeroides* tooth is considerably more hypsodont and has a more extensive talon complex and longer roots.

Reference can now be made to the upper tooth row parameters in Table 5 and Appendix 1:

The sum of the molar row lengths compared with Harris and White's (1979) parameters shows that in *Potamochoeroides* it is generally somewhat shorter than found in *Metridiochoerus andrewsi*, basically in between *Metridiochoerus andrewsi* and *Potamochoerus* but possibly closer to *Potamochoerus*.

Comparison of the premolar/molar lengths is of questionable significance, since there is only a single measurement in *Metridiochoerus andrewsi* and *Potamochoeroides*, the former is 0.274 and the latter 0.268, in *Potamochoerus* the mean ratio is 0.353. For both Area P3 + P4/M3 and Area P4/M3 *Potamochoeroides* is between *Potamochoerus* and *Metridiochoerus*.

3.2.2 Mandible

There are several good mandibular specimens that warrant individual mention. Anatomical detail is considered under specific headings.

M2081

This (Fig.24) together with M384, is one of the more complete lower jaw specimens. All six incisor alveoli are intact. Both canines are broken off approximately one third of the way up from the bases. The symphysis is well preserved. The left corpus is partially intact as far as the anterior pillars of M3. The right corpus is intact only as far as M1. Both P1 alveoli are well preserved, however, the P2 and P3

alveoli are damaged. P4 is well worn and intact on the left and right sides. M1 is extremely well worn on both sides. M2 is well preserved on the left side and well worn. M3 is only intact on the left side and is still in the process of erupting. It is slightly worn only on the anterior and posterior pillar pairs.

M384

Five of the six incisor alveoli are preserved, as are both canine roots. The diameter of the canines indicates that this was a young adult. The symphysis is basically complete. The right corpus is complete as far as the commencement of the upward curve of the ascending ramus, which is missing. The left corpus is complete as far as M1, but it is badly preserved. The P1 and P2 alveoli are preserved on both sides, they are very slightly worn. M1 on the right side is damaged anteriorly, but well preserved on the left side. It is well worn. M2 is complete and fairly well worn on the right side, only the anterior pillars are preserved on the left side. M3 on the right side is just beginning to erupt. Of particular interest in this specimen is the deeply scooped lingual face of the right corpus at the insertion of the digastric muscle.

M8217

Right mandibular fragment with P4 - M3 (Fig. 25).

The corpus is preserved posterior to P2. The basal section of the ascending ramus is also intact. Of particular importance is the origin of the insertion of the digastric muscle on the lingual face. The alveolus and part of the root of P3 is preserved. P4 is badly damaged. M1 is damaged and extremely well worn. M2 is also damaged and is well worn. M3 is moderately worn, although the talonid is unworn. It is apparently not fully erupted.

M8365

This is a somewhat poorly preserved specimen in that the bone appears "swollen" so that the original shape is altered. The anterior surface of the symphysis is partially preserved, the incisor alveoli are absent. The root of the right canine is intact. The right and left corpus are broken off behind M2. On both sides the P1 and P2 alveoli are intact, on the left side the posterior section of P3 is preserved. P4 is also preserved and M1 and M2 are intact. On the right side P4 is slightly damaged, M1 and M2 are intact. All of the teeth are extremely well worn, indicating an old animal.

The swollen bone does not appear to be the result of water action, as the bone structure can be clearly seen on the posterior surface of the symphysis and is free of calcite crystallisation. It is thus possible that the swollen bone is the result of a form of osteoporosis.

Ramus and corpus

Among the specimens studied, no complete *Potamochoeroides* ramus is preserved. In M8217, the most complete specimen, the mandible extends back only as far as the upward curve of the ramus (Fig.25). However, the angular process appears to ascend steeply, and closely resembles the situation in *Potamochoerus*. The ventral, or outer edge, on the horizontal ramus of *Potamochoeroides* specimens M302, M308, M339, M1890, M8217 and M8367, has an "inward curve" (Fig.25), comparing favourably with that of *Potamochoerus*. Immature *Potamochoeroides* specimens M341 and M2017 also manifest a curving ventral surface, although in the immature specimen M384, the curvature is not obvious. In all of the above mentioned *Potamochoeroides* specimens, the mandible is thickened in the region of M2 and M3 similar to that of *Potamochoerus*. The lingual face of the mandible in *Potamochoeroides*, at the insertion of the digastric muscle, from behind the symphysis to below the posterior M3 alveolus, is dorsally deeply scooped (Fig.25). This is similar to the situation in *Potamochoerus*, where the digastric muscle is larger than that of *Phacochoerus* (Ewer 1958b). Although the mandibular ramus appears heavy in a number of specimens, variation in measurements and observation indicate that much of the

heaviness and thickness of the corpus is due to matrix infill. It appears that the *Potamochoeroides* mandible is dorso-ventrally narrower in comparison with *Potamochoerus*, but broader than *Phacochoerus*. It appears to taper more sharply from in front of the lower M1, to the anterior edge of the P2 alveolus than in *Potamochoerus* and *Phacochoerus*.

Symphyseal region

There are three *Potamochoeroides* specimens (M384, M2081 and M8365) in which the symphysis is complete, with M8365 being the only mature specimen. M2081 is a fragment of the ventral side of the symphysis. The *Potamochoeroides* symphysis has a broad, fairly flat, rounded inferior profile, but appears to be not as broad as in *Metridiochoerus andrewsi*. There is a fluted platform for the incisor alveoli, and a gradual slope of the ventral surface towards the incisors. The fluted platform is similar to that of *Metridiochoerus andrewsi* and *Phacochoerus*, although the shape of the anterior part of the mandible, described above, appears to resemble *Sus* (Ewer 1958a). There is no evidence of the small shelf at the back of the symphysis which is typical of the extant *Potamochoerus*, further indication of a similarity with *Sus* (Cooke and Wilkinson 1978). Leakey (1943) described a mandible from Olduvai belonging to *Potamochoerus majus* - Harris and White (1979) indicated that this has close affinity to *Kolpochoerus*. The mandible of *Potamochoeroides shawi* seems to resemble this specimen. In both species the mandible lacks the elongation and lateral compression characteristic of the extant *Potamochoerus* (Figs 24 and 26). In *Phacochoerus*, the symphyseal region is considerably longitudinally extended in comparison with *Potamochoerus*, and there is a greater outflaring anterior to the post canine constriction (Fig. 27).

In terms of lower jaw parameters [Table 9; Harris (1983)], comparison with *Metridiochoerus andrewsi* revealed that the mean of the maximum width of the corpus at M3, is smaller in *Potamochoeroides*, which in turn is greater than in *Potamochoerus*. Comparison of the maximum width at the canine alveolus, revealed *Metridiochoerus andrewsi* to be far greater than in *Potamochoeroides*, while

Phacochoerus falls between these, with *Potamochoerus* closer to *Potamochoeroides*. Comparison of the symphyseal lengths revealed that *Metridiochoerus andrewsi* was generally the longest, followed by *Potamochoerus*, then *Potamochoeroides* and *Phacochoerus*. In terms of the width at the postcanine constriction, *Potamochoeroides* and *Potamochoerus* are close, *Metridiochoerus andrewsi* is considerably larger.

3.2.2.1 Lower Dentition

Incisors

Six evenly spaced incisor alveoli are present in *Potamochoeroides* specimens M384 and M2081, in M8366 there are three evenly spaced alveoli on the left side, similar to that in *Potamochoerus*. In *Metridiochoerus andrewsi* I-1 and I-2 are close together with I-3 intermediate between I-2 and the canine. The *Potamochoeroides* I-1 is long and broad, I-2 is similar in shape but slightly recurved. I-1 appears similar to *Potamochoerus* in structure, but is somewhat smaller in size. In *Potamochoeroides*, I-2 appears short and peg-like. I-3 and other isolated incisors also appear peg-like, however some of the specimens are fairly long and not as curved as those of *Potamochoerus*. In *Phacochoerus* all three incisor pairs are short and peg-like, with the second pair slightly inwardly curved. Thus although the *Potamochoeroides* I-1 appears to be similar to *Potamochoerus*, I-2 and I-3 appear closer in structure to *Phacochoerus*. In *Metridiochoerus andrewsi* there are apparently six incisors, all extremely small, almost like milk teeth (Cooke and Wilkinson 1978).

Canines

The *Potamochoeroides* lower canine is triangular in cross-section, with the antero-dorsal face being the longest, in this respect *Potamochoeroides* resembles *Potamochoerus*. The *Potamochoeroides* and *Potamochoerus* lower canine curves round and upwards, almost perpendicular to the palatine (Figs. 24

and 26). (This is in contrast to the *Metridiochoerus andrewsi* and *Phacochoerus* canine which is dorso-ventrally flattened and curves laterally and then posteriorly). In *Potamochoeroides* specimen M2057, the shallow groove on the antero-ventral surface is close to the outer edge, similar to the situation in *Phacochoerus*.

Table of mean lower canine measurements (a-p is antero-posterior breadth; d-v is dorso-ventral breadth):

	<i>Potamochoeroides</i>	<i>Potamochoerus</i>	<i>Phacochoerus</i>
number of specimens	7	6	6
a-p br.	16.12mm	13.46mm	14.85mm
d-v br.	13.55mm	13.31mm	10.81mm
d-v/a-p index	0.84	0.98	0.72

The lower canine in *Potamochoeroides* appears to be larger than in *Potamochoerus*, and falls inbetween the two extant genera in terms of the d-v/a-p index.

Premolars.

The lower P1 is not preserved in any specimens of *Potamochoeroides*. In M339, M384, M1832, M2023 and M2025, the P1 alveolus is situated approximately two thirds of the distance from P2 towards the lower canine. In M2081 the alveolus is situated about half way between the lower canine and P2 (Fig.24). P1 had not erupted in any of the *Phacochoerus* specimens studied, and only exists in one of the *Potamochoerus* specimens (BPI/C 4) in which the alveolus is situated two thirds of the way between the lower canine and P2. It appears that P1 does not erupt in *Metridiochoerus andrewsi*.

According to Cooke and Wilkinson (1978), *Sus* is the only extant African suid in which the lower P1 exists. In this respect *Potamochoeroides* is similar to *Sus*.

No completely preserved lower P2 is known in *Potamochoeroides*, but eleven specimens exist in which the root structure is preserved. P2 has two roots, an anterior and posterior root. In M2015 and M2081, the posterior root appears to be divided into two (Fig.24). In all of the specimens, the posterior root is the largest. The root and alveolar structure appears to be very similar to that in *Potamochoerus*. The lower P2 does not generally erupt in *Metridiochoerus andrewsi* (Cooke and Wilkinson 1978).

In *Potamochoeroides* specimens M302, M384 and M2015 the lower P3 is present. The anterior cusp is the largest, linked by a ridge-like extension to a small posterior cusp (Fig.6). There is a small medial anterior and a small medial posterior stylid. There are four roots, similar in size, with the posterior roots possibly slightly smaller. The lower P3 is considerably smaller than the upper P3 and has no lingual cingulum which is prominent in the upper P3. The lower P3 is rectangular in shape whereas the upper P3 is triangular. The *Potamochoeroides* P3 closely resembles *Potamochoerus* in structure (Figs.6 and 26). *Metridiochoerus andrewsi* and *Potamochoeroides* are fairly close in dimensions (Table 10; Appendix 1), although *Potamochoeroides* is generally somewhat larger in area. It is also generally broader. *Potamochoerus* is on average considerably larger but more blade-like.

In *Potamochoeroides* the lower P4 is preserved in specimens M302, M310, M384, M2015, M2054R, and M8369R. The morphology of the lower P4 is very similar to the lower P3, but P4 is considerably larger and the cusps are more elongated (Fig.6). There are 1-2 anterior medial stylids and 2-3 stylids adjacent to the posterior cusp. The lower P4 is considerably smaller than the upper P4, and without the lingual cusps and lingual cingulum. The upper P4 tends to be square in shape (Fig.19), whereas the lower P4 is rectangular (Fig.24). The *Potamochoerus* lower P4 structure is very similar to that of *Potamochoeroides* with 1-3 anterior stylids and 2-3 posterior stylids. As with the lower P3,

Potamochoeroides and *Metridiochoerus andrewsi* are close in terms of dimensions (Table 11; Appendix 1), except that the former is generally somewhat greater in area, and broader. *Potamochoerus* is on average considerably larger and more blade-like.

In terms of the lower tooth row parameters (Table 12; Appendix 1):

L1P3 + L1 P4, - *Potamochoeroides* and *Metridiochoerus andrewsi* are similar, *Potamochoerus* is generally considerably larger.

Area P3 + Area P4, - *Potamochoeroides* is generally in between *Metridiochoerus andrewsi* and *Potamochoerus*, possibly closer to the former.

Molars

Potamochoeroides specimen M341 is a juvenile with deciduous molars dm3 and dm4. dm3 has a single central laterally compressed cusp with a small anterior stylid and two posterior medial stylids. dm4 has three lateral pillar pairs with two central median cusps between the pillar pairs. A posterior median cusp is present and is surrounded by 1-2 stylids. The milk teeth appear to be very similar to those of *Potamochoerus* (Ewer 1958a).

M1 in *Potamochoeroides* is generally heavily worn (Fig. 24), but in specimens M384, M2017, M2053, M2054 the structure can be seen. The lower M1 is similar to that of the upper M1, but is generally smaller and more rectangular in cross-section in contrast to the upper M1 which is square in cross-section. The gap between the anterior and posterior pillar pairs in the lower M1 is on the lingual face, with a small buccal cusp between the pillar pairs. The posterior median cusp has 1-2 adjacent stylids on the buccal and lingual face. In *Potamochoerus*, the lower M1 structure is almost identical, except that the posterior median cusp is more closely associated with the posterior pillar pair, and appears slightly smaller. *Metridiochoerus andrewsi* in comparison with *Potamochoeroides* is generally greater in

area, the latter is broader in cross-section and appears to be on average closer in area and overall size to *Potamochoerus*, which in turn is smaller than the former two species (Table 13; Appendix 1).

In *Potamochoeroides* specimens M384, M1839, M1882, M2017, M2053 and M2054 it can be seen that the lower M2 is similar in structure to the upper M2. There is sometimes a second median cusp between the anterior and posterior pillar pairs, the gap between the anterior and posterior pillars is on the lingual face. The anterior median cusp is variable in size and has 1-2 stylids on the lingual and buccal faces. The posterior median cusp also has 1-2 stylids on the lingual and buccal faces. The *Potamochoeroides* lower M2 is similar in structure to *Potamochoerus* (Figs. 26 and 29). *Metridiochoerus andrewsi* appears generally greater in size, but particularly in area, compared to *Potamochoeroides*, although the lower M2 is generally broader in the latter. *Potamochoerus* is similar in size to *Metridiochoerus andrewsi*, in particular it is on average similarly broad (Table 14; Appendix 1).

The basic *Potamochoeroides* lower M3 morphology is similar to that of the upper M3 although the latter tends to be broader and more triangular in cross-section. In the lower M3, the stylid between the anterior and posterior pillars is on the buccal face and the gap between the pillar pairs on the lingual face (Figs. 28, 29, 30). A second median cusp is present and in some specimens a third is closely associated with the anterior lingual column. As in the upper M3, the main differences between specimens is in the arrangement of the talon/talonid complex. In the lower M3 as in the upper M3, it was found that the specimens could be divided into three groups:

Group 1 - one median cusp is present in the talonid complex, and 2-3 stylids on the lingual and buccal faces (Fig. 28). Three specimens are referred to this group, M1892, M2263 and M8895.

Group 2 - two median cusps in the talonid complex and 2-5 stylids on the lingual and buccal faces (Fig. 29). Specimens M311, M1290, M2013, M2020, M2081, M8366, M8367 and M8377 are placed in this group.

Group 3 - has three median cusps in the talonid complex and 2-4 stylids on the lingual and buccal faces (Fig.30). Eight specimens are placed in this group, M302, M308, M1887, M1889, M2024, M8217, M8370 and M8376.

As was the case with the upper M3 groupings, it appears that the lower M3 groupings are not affected by the relative age of the specimens according to tooth wear.

The lower M3 structure of *Potamochoeroides* is similar to *Potamochoerus*, except that in *Potamochoerus* the anterior median complex is smaller and the talonid consists of a single median cusp, with 2-4 stylids on the buccal and lingual faces (Fig.26). The structure is thus similar to the *Potamochoeroides* Group one specimens, although the Group one specimens are greater in length. *Metridiochoerus andrewsi* is considerably greater in area compared to *Potamochoeroides* (Tables 15a and 15b; Appendix 1), however as with the other molars the latter is on average broader. The means of the Lt/Br ratios differ, thus indicating that the cross-sectional shape differs between the two genera. As with the upper M3, the average height in *Potamochoeroides* is much smaller than in *Metridiochoerus*. Ht/Lt shows *Potamochoeroides* and *Potamochoerus* to be close. *Potamochoerus* is considerably smaller in area in comparison with *Potamochoeroides* but tends to have a similar broad cross-sectional shape.

In terms of the lower tooth row parameters (Table 12; Appendix 1):

Lt M1 + Lt M2 + Lt M3 - *Metridiochoerus andrewsi* and *Potamochoeroides* are similar. *Potamochoerus* is considerably smaller.

Lt P3 + P4/M1 + M2 + M3 - once again *Metridiochoerus andrewsi* and *Potamochoeroides* are similar. *Potamochoerus* is considerably larger.

Area P3 + P4/M3 - there is no value given for *Metridiochoerus andrewsi*, *Potamochoeroides* is considerably smaller than found in *Potamochoerus*.

Area P4/M3 - *Potamochoeroides* is inbetween *Metridiochoerus andrewsi* and *Potamochoerus*, but closer to the former.

3.2 NOTOCHOERUS CAPENSIS

Notochoerus capensis is not very well represented in the Limeworks fossil suid collection, with only twenty one specimens and a minimum number of individuals (MNI) of five. The material is very fragmentary so that few relevant measurements could be made. Most of the specimens were too fragmentary to compare with material from other sites. The only skull material consists of one doubtfully referred orbital and one palatal specimen.

3.1.1 Skull and maxillary

Orbit

In specimen M304 which is doubtfully referred to *Notochoerus* (Ewer 1958a), the orbit measures 39.55mm across the greatest inner length, compared to 36.25mm and 34.45mm in two individuals of *Potamochoeroides*. The orbit which appears thickened about the rim, is rounded and dorsally in line with the frontal bone.

Zygoma

In M304 only the anterior portion of the zygoma root is preserved. The zygoma appears to be broader and thicker than that of the extant *Phacochoerus* and *Potamochoerus*. According to Cooke and Wilkinson (1978) the zygoma is robust with lateral projections in the male.

Area P3 + P4/M3 - there is no value given for *Metridiochoerus andrewsi*, *Potamochoeroides* is considerably smaller than found in *Potamochoerus*.

Area P4/M3 - *Potamochoeroides* is in between *Metridiochoerus andrewsi* and *Potamochoerus*, but closer to the former.

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Orbit

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Zygoma

In M304 only the anterior portion of the zygoma root is preserved. The zygoma appears to be broader and thicker than that of the extant *Phacochoerus* and *Potamochoerus*. According to Cooke and Wilkinson (1978) the zygoma is robust with lateral projections in the male.

Palatal Region

A single immature *Notochoerus* specimen (M2005), has the left dm2, dm3, dm4, M1 and a right dm3 and dm4 preserved on the maxillae. A broad anterior/posterior interpalatine ridge is present. Two shallow palatine grooves are situated on either side of the interpalatine ridge, diverging towards the canines. *Notochoerus* specimen M324 is a palatal fragment with a very shallow palatal groove. These characteristics are typical to both the extant and extinct suids studied, and so are not diagnostic in this case.

3.3.1.1 Upper Dentition

Canines

The structure of the upper canine is well preserved in *Notochoerus* specimens M2026, M2250 and M2426. These specimens compare favourably with *Notochoerus capensis* specimens from East African sites. A broad, longitudinally ribbed ventral enamel band, and single, narrow antero-dorsal and postero-dorsal enamel ridges, are present. The upper canine resembles the *Potamochoeroides* and *Potamochoerus* canine in structure, except that in *Notochoerus* it is usually considerably bigger, and more dorso-ventrally flattened. The dorsal surface is almost flat and a groove extends down its entire length, which is especially evident in the larger canines. The small canines appear to taper more sharply towards the points. The angle of the canine within the canine alveolus indicates that the canine pointed slightly forward.

Molars

Immature *Notochoerus* specimens M324 and M2005 have the dm2, dm3 and dm4 deciduous molars preserved. dm2 consists of a single central, laterally compressed cusp, a small anterior style and a posterior lingual cusp with 2-3 adjacent medial styles. dm3 is preserved only in M2005 where it is heavily worn so that the structure could not be easily determined. It is triangular in cross-section, with a posterior lateral pillar pair and a single anterior cusp. Two pairs of lateral pillar pairs are present in dm4 and are separated by a central median cusp.

In *Notochoerus* specimens M324 and M2005, the upper M1 is moderately worn. Two pairs of lateral pillars are present, with adjacent, well developed anterior and posterior median cusps with 1-3 styles on the buccal and lingual faces. The specimens are characterised by the pronounced anterior and posterior bulge of the respective median pillar complexes. A single median cusp exists between the lateral pillars, with a style on the buccal side between the pillar pairs. The lateral pillars tend to be laterally elongated so as to appear dumb-bell shaped in cross-section, especially the second pillar pair. Only one specimen could be measured (length 23.5mm, breadth 18.8mm) (Table 16). This is comparable to that found in *Notochoerus capensis* from East Africa (Appendix 1). Thus the upper M1 of *Notochoerus* appears to be considerably larger than *Potamochoeroides* or the two extant genera.

From unworn *Notochoerus* specimens M368 and M369, it can be seen that the upper M2 is similar in structure to the upper M1, but almost double the size. As in M1, M2 is also characterised by the pronounced bulge of the anterior and posterior median complexes. The lateral pillar pairs tend to be more characteristically dumb-bell shaped than in the M1 specimens. M2 appears to be high crowned and thickly covered with cement (Ewer 1958a). The upper M2 of *Notochoerus* appears closer to *Phacochoerus* in cross-sectional plan view, but is generally considerably larger than in the other three genera. (Tables 7 and 16). The average measurements appear similar to those for East African *Notochoerus capensis* specimens (Appendix 1).

No complete upper M3 *Notochoerus* specimens exist. Specimen M8352 is a fragment with the posterior mid-section preserved, and appears to be somewhat broader than the lower M3.

3.2.2 Mandible

Corpus and Ramus

From *Notochoerus* specimen M2025, it appears that the corpus is broad and thickened on the buccal side in the region of M3, but seems considerably heavier than in *Potamochoeroides* and *Potamochoerus*. The ramus is preserved only in *Notochoerus* specimen M336, which is a juvenile. There are indications of an inward curve on the outer edge of the horizontal ramus. In this respect the ramus appears somewhat similar to *Potamochoeroides* and *Potamochoerus*.

3.3.2.1 Lower Dentition

Canines

Specimen M1581 consists of a fragment of a lower left canine which has been doubtfully referred to *Notochoerus*, mainly because it appears considerably larger than those found in *Potamochoeroides*. Part of the wear facet and anterior aspect are preserved. A broad shallow groove exists on the anterior surface, close to the ventral apex.

Premolars

M2022 is an immature specimen, doubtfully referred to *Notochoerus* (Ewer 1958a). It consists of an erupting premolar, presumably P2 (Ewer 1958a). No structure could be determined other than that a medial main cusp, with anterior and posterior ridge-like extensions, exists.

Molars

In *Notochoerus* specimen M2022 the deciduous lower molars dm3 and dm4 are preserved. dm3 is small with a single central cusp, an anterior stylid and three median posterior stylids. dm4 consists of three lateral pillar pairs, with two median cusps between the pillar pairs, a small anterior median complex and a large talonid. In M357, the lower M1 is moderately worn. It is very similar in structure to the upper M1, but narrower. The dimensions appear similar to East African *Notochoerus capensis* specimens (Table 16; Appendix 1).

In *Notochoerus* specimens M2075 and M2076, the lower M2 is also structurally similar to the upper M2 except narrower. There are however, no stylids adjacent to the central median between the two lateral pillar pairs.

Three lower M3 specimens, M2025, M2077 and M8275 are preserved, with M2077 being the only complete specimen. M3 is extremely large and hypsodont (Fig.31). The enamel is covered by a thick layer of cement. It has four main pillar pairs and a well developed talonid complex, consisting of a small pair of lateral pillars and a median cusp separating it from five stylids. The lateral pillars vary from being clearly dumb-bell shaped in cross-section at the first pillar pair, to star-shaped at the fourth pair. There are four median cusps between each column pair and no stylids on the buccal or lingual sides. The median cusps gradually vary from star-shaped at the anterior first median, to circular at the fourth. All three *Notochoerus* lower M3 specimens are distinctly symmetrical about the median cusps.

Table of mean lower M3 length and breadth measurements (mm) (*Noto* = *Notochoerus*, *Potoides* = *Potamochoeroides*, *Pota* = *Potamochoerus*, *Phaco* = *Phacochoerus*):

	<i>Noto.</i>	<i>Potoides.</i>	<i>Pota.</i>	<i>Phaco.</i>
number of specimens	1	17	4	16
len.	100.4	45.5	31.57	47.05
br.	22.7	21.1	17.31	12.00
br/len	0.23	0.46	0.54	0.26

Clearly the lower M3 of *Notochoerus* is similar to *Phacochoerus* in cross-sectional shape, although considerably larger. It appears to be similar in dimension to the East African *Notochoerus capensis* (Table 16; Appendix 1).

CHAPTER 4. RESULTS

4.1 AGE AND THE MINIMUM NUMBER OF INDIVIDUALS (MNI)

Study of the prepared fossil snail specimens made it possible to calculate the minimum number of individuals preserved in the collection, and to estimate the age profile of the two genera. From Table 17 the following observations with regard to the distribution of the relative ages of *Potamochoeroides* specimens could be determined:

Maxillary		Mandible	
Left	Right	Left	Right
immature 5	6	7	3
mature 6		17	11
old 4	1	4	2

In addition there are three juvenile maxillary and five juvenile mandibular specimens.

From the table above an overall age distribution of *Potamochoeroides* specimens appears to be:

Old animals - 4 individuals.

Mature adults - 17 individuals.

Immature adults - 7 individuals.

Juveniles - 5 individuals.

In the study of the minimum number of individuals, the 189 *Potamochoeroides* specimens were firstly divided into upper and lower jaw specimens containing complete or partial dentitions. These two categories of specimens were then divided into left and right:

Upper jaw left - 25 specimens.

Upper jaw right - 31 specimens.

Lower jaw left - 25 specimens.

Lower jaw right - 31 specimens.

Thus the MNI is thirty one for *Potamochoeroides*. The same procedure was carried out for the twenty one *Notochoerus* specimens:

Upper jaw left - 5 specimens.

Upper jaw right - 3 specimens.

Lower jaw left - 3 specimens.

Lower jaw right - 3 specimens.

The MNI for *Notochoerus* is thus five.

4.2 SUMMARY

An age profile utilizing the *Potamochoeroides* M3 specimens was constructed, to be discussed in the taphonomic section of the following chapter. The minimum number of individuals is estimated for both *Potamochoeroides* and *Notochoerus*.

CHAPTER 5 DISCUSSION

5.1 TAXONOMY AND PHYLOGENETIC AFFINITIES

"Problems previously encountered in the use of suid remains to obtain valid correlations have stemmed partly from difficulties in establishing phylogenetic relationships within the genera *Notochoerus* and *Metridiochoerus*..." White and Harris (1977 p6).

In order to address the taxonomic and phylogenetic position of the Limeworks suids, the cranial morphology of *Potamochoeroides shawi*/*Metridiochoerus andrewsi* and *Notochoerus capensis* is examined and discussed in relation to other African Plio-Pleistocene suids, and the four extant African suids. Where possible the functional anatomy is compared and relationships commented upon.

5.1.1 *Potamochoeroides shawi*

To establish the phylogenetic relationship of *Potamochoeroides*, the taxonomic position of this genus needs to be clarified. Harris and White (1979) considered *Potamochoeroides shawi* synonymous with *Metridiochoerus andrewsi*. Cooke (1978), although finding *Potamochoeroides shawi* generically distinct from *Metridiochoerus andrewsi*, stated that *Potamochoeroides shawi* could be part of a "*Metridiochoerus*-complex". This is defined as a group including all the species of *Metridiochoerus*.

The anatomical characters which formed the basis for previous taxonomic and phylogenetic classification are listed below. These are the characters which according to Cooke (1978), separate *Potamochoeroides shawi* from *Metridiochoerus andrewsi*:

*Potamochoeroides**Metridiochoerus*

- | | |
|--|---|
| 1. Upper canine <i>Potamochoerus</i> -like | 1. Upper canine <i>Phacochoerus</i> -like |
| 2. At least 3 premolars in adult | 2. At most 2 premolars |
| 3. Premolars <i>Sus</i> -like | 3. Premolars reduced |
| 4. Lower canine deeply rooted | 4. Tendency for rapid wear of M2 |
| 5. Short snout | |
| 6. Narrow parietal | |

Before any conclusions can be made it is necessary to consider the comparative study made in Chapter 3, with respect to *Potamochoeroides* and *Metridiochoerus andrewsi*.

The nasal region appears to differ between the two genera, in *Potamochoeroides* the nasals widen posteriorly (Fig. 8.) whereas in *Metridiochoerus andrewsi* they generally seem to be parallel sided, in addition, they appear to be broader in the former. The fossae for the origins of the levator and depressor rostri muscles are clearly very different, *Metridiochoerus andrewsi* seems more similar to *Phacochoerus* in this regard. The supracanine flange, although similarly comparable in both genera, also appears similar to at least one other genus (*Kolpochoerus limnetes*), thus cannot be regarded as diagnostic. In terms of elevation of the orbits, *Potamochoeroides* (Fig. 11) seems slightly less elevated than *Metridiochoerus andrewsi*, the lachrymal in the former is considerably shorter than in the latter. The zygoma appears generally similar, but in *Potamochoeroides* apparently closer to *Sus*. The glenoid and skull roof differ in structure between the genera, with *Potamochoeroides* seemingly closer to *Potamochoerus*. The occipitals and parietals (Fig. 12) markedly, the palatal region also appears to be different in structure as does the pterygoid. The lateral profile appears similar in both genera, however, on the basis that there is only one *Potamochoeroides* specimen in which this feature could be examined (fig. 9), its validity is questionable. In terms of the upper dentition, the upper canines are obviously very different; this is referred to by Cooke and Wilkinson (1978). The presence of upper P1

alveoli and the upper P2 in *Potamochoeroides*, whereas they generally do not erupt in *Metridiochoerus andrewsi*, is clearly diagnostic.

The upper P3 and P4 appear generally different in terms of the Lt/Br ratio or cross-sectional shape, the fact that they are comparable in length and breadth therefore does not appear to be of taxonomic significance (Tables 3 and 4; Appendix 1). The upper M1 and M2 seem markedly different in cross-sectional shape between the two genera (Tables 6 and 7; Appendix 1). The upper M3 Lt/Br ratio on average differs, indicating that the cross-sectional shape is different. In terms of the Ht/Lt ratio, the difference between *Potamochoeroides* and *Metridiochoerus* is considerable (Tables 8a and 8b; Appendix 1).

Comparison of lower jaw measurements indicated considerable differences between the two genera [Table 9; Harris (1983)]. In addition, the *Potamochoeroides* symphysis appears to be generally narrower than found in *Metridiochoerus andrewsi*. In terms of the lower dentition, the lower incisors are different, as are the lower canines. As is the case with the maxilla, lower P1 alveoli and the lower P2 are preserved in *Potamochoeroides* specimens, and not found in *Metridiochoerus andrewsi*. Similarly, the lower P3 and P4, M1, M2 and M3 appear to differ in cross-sectional shape. As is the case with the upper M3, the Lt/Br and Ht/Lt ratios indicate considerable differences between the two genera (Tables 10, 11, 13, 14, 15a, 15b; Appendix 1).

In general the *Potamochoeroides* premolars and molars are broader than found in *Metridiochoerus andrewsi*.

Detailed anatomical comparison between the two genera in question thus reveals considerable differences.

The table below compares the size and structure of anatomical features found in *Potamochoeroides*, with the size and structure of similar features found in the other Plio-Pleistocene African Suidae (the table below is based on work done in the present study, plus Cooke and Wilkinson 1978; Harris and

White 1979). Although size was considered, structure was regarded as more important in deciding to what extent genera were comparable (Cooke pers.comm.; Harris and White 1979). Thus with regard to *Metridiochoerus andrewsi*, although the dentition is comparable in size in a number of instances, there are differences in cross-sectional shape. A+ indicates that at least one species within the genus is very similar to *Potamochoeroides* with regard to the particular feature, +/- indicates general similarity and - no similarity.

(Nyan = *Nyanzachoerus*, Noto = *Notochoerus*, Kolp = *Kolpochoerus*, Metr = *Metridiochoerus*, Pota = *Potamochoerus*, Phaco = *Phacochoerus*, Hylo = *Hylochoerus*)

	Nyan	Noto	Kolp	Metr	Pota	Phaco	Sus	Hylo
1. Nasals	-	-	-	-	+/-	-	+/-	-
2. l/d rostri o	?	-	?	-	-	-	+	-
3. suprac. flange	+/-	+/-	+/-	+/-	-	-	-	+/-
4. orbit	-	-	-	+/-	+	-	+/-	-
5. zygoma	-	-	-	+/-	+/-	-	+/-	-
6. skull roof	-	-	-	-	+/-	-	+/-	-
7. Par/Occ	-	-	-	-	+/-	-	+/-	-
8. Palatal	?	-	?	-	+/-	-	+/-	?
9. Etekygoid	?	?	?	-	+	-	+	-
10. Lat/ profile	-	+/-	+/-	+/-	+/-	+/-	+/-	+/-
11. uIncisors	+/-	-	+/-	?	+	-	+	-
12. uCanines	-	-	-	-	+	-	+	-
13. uP1	-	-	?	-	+	-	+	-
14. uP2	+/-	-	+/-	-	+	-	+/-	-
15. uP3	+/-	-	+/-	+/-	+	-	+	-
16. uP4	+/-	-	+/-	+/-	+	-	+/-	-
17. uM1	-	-	+/-	+/-	+	-	+	-
18. uM2	+/-?	?	+/-	+/-	+	-	+	-
19. uM3	-	-	-	+/-	-	-	-	+/-
20. overall size	+	-	+	+	+	+/-	+	+/-
21. Ramus, corpus	+/-	-	+/-	-	+/-	+/-	+/-	-
22. Symphysis	-	?	+/-	-	+/-	+/-	+/-	+/-
23. lIncisors	-	-	-	-	+/-	-	+/-	-
24. lCanine	-	-	-	-	+/-	-	+/-	-
25. lP1	+/-?	-	-	-	+	-	+	-
26. lP2	+/-	-	+/-	-	+	-	+	-
27. lP3	+/-	-	+/-	+/-	+	-	+/-	-
28. lP4	+/-	-	+/-	+/-	+	-	+/-	-
29. lM1	+/-	-	+/-	+/-	+	-	+	?
30. lM2	+/-	-	+/-	+/-	+	-	+?	-
31. lM3	-	-	-	+/-	-	-	-	-
	7.5	1	8.5	8	22	2	20.3	2.5

In order to estimate *Potamochoeroides*' affinities with the abovementioned suids, the + and +\ were totaled. One point was given for a +, and a half a point for a +\-. The above table, although not to be regarded as taxonomically definitive, does indicate that *Potamochoeroides* has many similarities with the extant *Potamochoerus* and *Sus*, and that it has few similarities with *Metridiochoerus* and *Phacochoerus*, regarded by Harris and White (1979) as the relevant modern analogue.

Thus it appears that the work of Cooke (1978) is confirmed. That is to say that *Potamochoeroides shawi* seems generically distinct from *Metridiochoerus andrewsi*. It is suggested that the genus name *Potamochoeroides* be retained on the basis that it was erected for its similarity to the extant *Potamochoerus* (Dale 1948; Cooke and Wilkinson 1978), and the species name *P. shawi* be retained, since *P. shawi* has page priority over the original species name *P. hypsodon*, which was synonymised with the former (Cooke and Wilkinson 1978).

Reduction of premolars, one of the two features characteristic of the "*Metridiochoerus* complex" (Cooke and Wilkinson 1978), does not occur in *Potamochoeroides*. On this basis, and because of a lack of similarity between *Metridiochoerus* and *Potamochoeroides*, it is questionable whether *Potamochoeroides* can be included within the "*Metridiochoerus* complex". If *Potamochoeroides* does not belong to the abovementioned complex, then what is its position relative to the other Plio-Pleistocene African suids?

Past (Dale 1948; Ewer 1958a; Cooke 1978; Cooke and Wilkinson 1978) and present study has shown that there are a large number of anatomical characteristics which *Potamochoeroides* has in common with *Potamochoerus* and *Sus*. The following similarities between the genera in question are not convergent with respect to the other Plio-Pleistocene African Suidae, and hence are indicative of the phylogenetic relationship between them. *Potamochoeroides* and *Sus* are similar with regard to the following characteristics:

fossae for the origins of the levator and depressor rostri muscles; root of the zygoma; presence of an upper P1 and the alveolus for the lower P1; structure of the upper P3; shape of the anterior part of the mandible.

Potamochoeroides and *Potamochoerus* are similar with regard to the following characteristics:

posterior widening of the nasals, structure of the lachrymal, the glenoid, the pterygoid; the upper and lower premolars and molars are structurally very similar; the lower M3 in *Potamochoerus* is similar in structure to the *Potamochoeroides* lower M3 group one specimen.

Both *Potamochoerus* and *Sus* have similar upper and lower canines, very similar to *Potamochoeroides*.

It thus appears that *Potamochoeroides* is closely related to *Sus* and *Potamochoerus*. Both the latter two genera are regarded as anatomically primitive and conservative (Cooke and Wilkinson 1978). In order to examine the phylogenetic position of *Potamochoeroides*, its phylogenetic affinities were investigated relative to *Potamochoerus*, *Kolpochoerus*, *Hylochoerus*, *Metridiochoerus* and *Phacochoerus*. The abovementioned six genera can be regarded as having a common ancestor (Cooke 1978). A *Sus*-like form is generally regarded as ancestral to the six suid genera (Cooke and Wilkinson 1978; Harris and White 1979), thus their phylogenetic history is examined as a group. A cladogram was constructed (Fig.32), based on features considered derived relative to primitive ancestral features (Mayr 1974; Disney 1983). The following character suites were determined, using shared derived anatomical features in comparison with those primitive characters of *Sus* (Cooke and Wilkinson 1978). The polarity, or direction of evolutionary change is in general agreement with relevant research articles (Cooke and Wilkinson 1978; Harris and White 1979). The derived anatomical features were partly determined from the present research and partly from Cooke and Wilkinson (1978) and Harris and White (1979). This cladogram is directed on a generic level, thus, as far as possible, anatomical features applicable to the entire genus were selected.

Suite 1: (Synapomorphies separating *Potamochoeroides*, *Potamochoerus*, *Kalpochoerus*, *Hylochoerus*, *Metridiochoerus* and *Phacochoerus* from *Sus scrofa*)

1. Nasals widen at the canine alveolus
2. Zygoma laterally expanded in the male

Suite 2: (Synapomorphies of *Potamochoeroides* and *Potamochoerus*)

1. Complete dentition, upper and lower P1 often shed
2. P4 similar to *Sus* but more square in cross-section
3. M1 and M2 similar in structure to *Sus*, but more hypsodont
4. Posterior widening of the nasals
5. Inflated corpus of the mandible

Suite 3: (Autapomorphies of *Potamochoeroides*)

1. P2, P3 and P4 slightly reduced in size relative to *Potamochoerus*
2. M3 structure similar to *Potamochoerus* but the talon/talonid more developed
3. Short snout
4. Fossa for origin of levator rostri muscles, high, deeply scooped and *Sus*-like.
5. Fossa for origin of depressor rostri muscles, shallow and *Sus*-like
6. Frontal broad between the orbits

Suite 4: (Autapomorphies of *Potamochoerus*)

1. M3 similar to *Sus* but lateral pillars more columnar in shape
2. Tall narrow supracanine flange in the male, rugose on dorsal surface
3. Fossa for origin of levator rostri muscles shallow
4. Fossa for the origin of the depressor rostri deeply scooped
5. Distinct small shelf at the back of the symphysis

Suite 5: (Synapomorphies of *Kolpochoerus*, *Hylochoerus*, *Metridiochoerus* and *Phacochoerus*)

1. Large upper canines
2. Upper canine projects outwards
3. Reduction in number of premolars
4. Lower canines verrucose or oval in cross-section
5. Dorsally concave frontal, slight development of supraorbital ridges
6. Jugals laterally expanded
7. Broad occiput
8. Dorso-ventrally flattened outward flaring lower canines

Suite 6: (Synapomorphies of *Kolpochoerus* and *Hylochoerus*)

1. Characteristic male upper canine structure, robust and outflaring
2. Bulging, inflated area of hollow bone on the zygoma
3. Supraorbital ridges
4. Very broad occiput
5. Very inflated corpus, followed by a narrowing level with the middle of M3

Suite 7: (Autapomorphies of *Kolpochoerus*)

1. M3 moderately hypsodont, talon/talonid developed
2. U-shaped lower canine
3. Long low broad supracanine flange in the male, rugose on dorsal surface, somewhat similar to *Potamochoeroides*

Suite 8: (Autapomorphies of *Hylchoerus*)

1. M3 brachydont, talon/talonid expanded
2. Long low supracanine flange
3. Broad occiput
4. Sagittal crest on occiput
5. Temporal condyles lower than the foramen magnum
6. Flat profile of symphysis
7. Wide mandibular angle
8. large overall body size

Suite 9: (Synapomorphies of *Metridiochoerus* and *Phacochoerus*)

1. Small peglike incisors
2. Root of zygoma raised and maxilla heightened
3. Braincase antero-posteriorly shortened
4. Symphysis somewhat flattened, square anterior border
5. High ascending ramus of mandible

Suite 7: (Autapomorphies of *Kolpochoerus*)

1. M3 moderately hypsodont, talon/talonid developed
2. U-shaped lower canine
3. Long low broad supracanine flange in the male, rugose on dorsal surface, somewhat similar to *Potamochoeroides*

Suite 8: (Autapomorphies of *Hylochoerus*)

1. M3 brachydont, talon/talonid expanded
2. Long low supracanine flange
3. Broad occiput
4. Sagittal crest on occiput
5. Temporal condyles lower than the foramen magnum
6. Flat profile of symphysis
7. Wide mandibular angle
8. large overall body size

Suite 9: (Synapomorphies of *Metridiochoerus* and *Phacochoerus*)

1. Small peglike incisors
2. Root of zygoma recessed and maxilla heightened
3. Braincase antero-posteriorly shortened
4. Symphysis somewhat flattened, square anterior border
5. High ascending ramus of mandible

Suite 10: (Antapomorphies of *Metridiochoerus*)

1. Characteristic early wear of M2
2. M3 in early forms similar to *Potamochoeroides*
3. Long low broad supracanine flange in male rugose on dorsal surface.

Suite 11: (Antapomorphies of *Phacochoerus*)

1. Anterior molars shed
2. M2 and M3 highly specialised
3. Front of snout droops markedly below the occlusal plane
4. Frontal very broad between orbits
5. Orbits greatly elevated
6. Temporal condyles higher than the top of the foramen magnum

The cladogram (Fig.32), although similar to the one constructed by Harris and White (1979), differs in a number of aspects:

firstly, their cladogram is not strictly correct, since *Nyanzachoerus* and *Notochoerus* apparently do not have an ancestor in common with the other Plio-Pleistocene African suids (Cooke 1978; Cooke and Wilkinson 1978) and thus cannot be included in the same cladogram. Although essentially the same in terms of taxonomic rank, Figure 32 differs in that *Potamochoeroides* and *Potamochoerus* are regarded as sister groups, whereas Harris and White (1979) regard *Potamochoeroides* as part of the "*Metridiochoerus* complex". In Figure 32 *Potamochoerus* is shown to be more advanced than *Potamochoeroides*, on the strength of fewer *Sus*-like features. Similarly, *Kolpochoerus* and *Hylochoerus*, and *Metridiochoerus* and *Phacochoerus*, are regarded as more advanced on the basis of fewer *Sus*-like characters. On this basis, it seems that the *Potamochoeroides* is more primitive than previously considered. This could mean that the Limeworks Member 3 may be older than considered

in previous biostratigraphic analyses. Vrba (1987b) for one, postulated that Member 3 contains a Pliocene assemblage with particular affinities to the Laetoli Beds in East Africa. Leakey and Harris (1987) gave a Potassium-Argon date of $3.49 \pm 0.12 \text{ myr}$ - $4.32 \pm 0.06 \text{ myr}$ for the Laetoli beds.

5.1.2 *Notochoerus capensis*

Notochoerus from the Limeworks had previously been classified as *Notochoerus capensis* by a number of researchers (Cooke and Wilkinson 1978; Harris and White 1979). The classification was based on the twenty one specimens studied in the B.P.I. collections. Due to its fragmentary nature, it is not possible to revise the taxonomic position of the *Notochoerus* collection, the few comparisons made with East African specimens indicated a similarity with *Notochoerus capensis*. On the basis of the antero-posterior length of the lateral wall of the lingual face in M3, it appears that *Notochoerus capensis* is distinct from *Notochoerus eulius* and *Notochoerus scottii* (Cooke and Wilkinson 1978).

Cooke and Wilkinson (1978) and Harris and White (1979) constructed very similar phylogenies for *Notochoerus*, in which it is derived from *Nyanzachoerus*. *Notochoerus eulius* is considered generally more primitive and ancestral to *Notochoerus capensis*, which in turn is regarded as ancestral to *Notochoerus scottii*.

5.2 PALAEOECOLOGY

Indications from the *Potamochoeroides* skull anatomy are that *Potamochoeroides*' feeding habits were, in many ways similar to those of the extant *Potamochoerus* (Ewer 1958b). The present study shows that this is generally true, on the basis of a number of additional anatomical characteristics.

The *Potamochoeroides* pterygoid bone (Fig.17), as in *Potamochoerus* (Fig.20), protrudes further ventrally than in the extant *Phacochoerus*, this suggests that the internal pterygoid muscle was small and reduced as in *Potamochoerus* (Ewer 1958b). This in turn implies that the temporalis muscle was adapted for a quick snapping or chopping jaw action, typical of the omnivore *Potamochoerus* (Ewer 1958b), as opposed to the grinding jaw action in the herbivorous *Phacochoerus* (Ewer 1958b). The structure of the lingual face of the mandibular ramus in *Potamochoeroides* (Fig.25) is similar to that in *Potamochoerus* in that a large deeply scooped ventral face is present, which served for the insertion of an enlarged digastric muscle and is associated with a chopping or snapping type of jaw action, as in *Potamochoerus* (Ewer 1958b).

The paragraph above indicates that *Potamochoeroides* had similar masticatory habits to the extant omnivorous *Potamochoerus*. However, the hypsodont elongated M3 in contrast to the brachydont M3 found in *Potamochoerus*, indicates a response to rapid wear of M3. It appears that it is a grazing habit which requires repeated periods of mastication and thus causes teeth to wear down rapidly (Brink 1987). Dental wear seems to reflect contact and friction between opposing teeth, rather than the abrasiveness of food (Fortelius 1985). This supports the conclusion of Ewer (1958b), that the *Potamochoeroides* diet, in contrast to that of *Potamochoerus*, did include a large proportion of grass.

The high position of the levator rostri fossa and the shallow depressor rostri fossa in *Potamochoeroides* (Fig.9) are in contrast to the condition in the extant *Potamochoerus* (Fig.14). According to Cooke and Wilkinson (1978), these characteristics are typical of *Sus scrofa*. This implies that in *Potamochoeroides* (as in *Sus*) the snout was possibly not used as a specialised digging and rooting organ as it is in *Potamochoerus* (Ewer 1958b).

The hypsodont nature of the *Notochoerus capensis* M3 and the reduction in the number and relative size of the premolars indicate that, as in the extant *Phacochoerus*, *Notochoerus* was almost exclusively a grazer (Ewer 1958b). Its large size and the presence of a number of other large grazing animals (Vrba 1987b) indicates a high production of low quality grass, possibly coarse grass (Brink 1987).

The masticatory habit of *Potamochoerus* *shawi* indicates the presence of varied vegetation types. The apparent dietary habits of *Potamochoerus* *shawi* and *Notobatus* *capensis* suggest the presence of a more extensive grassland than at present. The valley floor at the time of deposition of the Limeworks breccia was much higher, therefore a more extensive grassland can be inferred (Kitching pers. comm.). The slopes of the dolomitic hills in the Makapan valley are normally covered in coarse grasses, and it is evident that what is vast crop land today was grassland (Kitching pers. comm.).

5.3 TAPHONOMY

"The mode of accumulation of the extremely bone-rich Makapansgat Limeworks Grey Breccia has been a controversial issue ever since Dart described the deposit as a midden of the carnivorous, predacious, bone-collecting and tool-making hominid *Australopithecus prometheus* (now known as *A. africanus*)...." (Maguire et al. 1980 p1).

Discussion in this section is confined to the grey breccia (Member 3), since it has yielded most of the suid specimens. Study of a number of unprepared Member 3 breccia blocks containing suid specimens, and, according to Kitching (pers. comm.), it would appear that individual suid specimens are generally closely associated with individual specimens belonging to other mammalian forms such as hominids, hyaenas and bovids. It therefore seems that, in considering the taphonomy of the Limeworks fossil suid collection, the taphonomy of the entire fauna should be included.

Little information is available on the provenance of individual faunal specimens. It was therefore necessary to examine individual suid specimens for bone damaging patterns which could be diagnostic as to the bone accumulating agents (Maguire et al. 1980; Brain 1981). In this way an attempt was made

to investigate the taphonomy of the suid collection, and its bearing on the taphonomy of the prepared fossil faunal collections.

Two broad categories of damage or modification to individual suid specimens can be defined: modification due to biological taphonomic agents and modification due to non-biological agencies (Brink 1987):

Category of modification	Description of modification
Biological	1. punctate depressions 2. ragged edge gnawing 3. skull roof with punctate-type hole 4. Fragmentary canines
Non-biological	1. calcite crystals in marrow cavity 2. "swollen" bone

The biological modifying agents, 1, 2 and 3 could be attributed to *hyaena* action (Maguire *et al.* 1980). However, the punctate depressions and the ragged edged gnawing could also be attributed to hominid activity (Maguire *et al.* 1980). These two features together with the hole in the skull roof, were thus not considered as evidence of *hyaena* activity on the Limeworks fossil collection.

Although study of the suid collection thus does not indicate that *hyaenas* were definite bone accumulating agents, previous taphonomic studies (Brain 1981; Maguire *et al.* 1980) show that *hyaenas* and other carnivores probably were major bone accumulators of the fossil fauna. Since three species of fossil porcupines are present, it is to be expected that gnawed fossil bone would be found, however, less

than 2% of a sample of Member 3 breccia showed evidence of porcupine damage, indicating that porcupines had little to do with accumulating Member 3 (Maguire et al. 1980).

A number of specimens in the collection appear to reflect hominid activity. Within the suid collection are eleven upper and lower canine fragments, longitudinally split in half and similar to the splintered bovid long bone tool fragments described by Dart (1957) (Fig 33). There appear to be scrape marks along the sharp antero-ventral edge which is typical of hominid activity. Dart (1957) attributed this type of canine flake modification to the activity of *Australopithecus africanus*. It is thus suggested that these canine fragments were used as tools by *Australopithecus africanus*. Damage to a *Phocoeroides* specimen M1391 seems to indicate possible human-like activity (Kitching pers.comm.) (see description in Chapter 3 of M1391).

The non-biological agencies can also be valuable indicators of taphonomy. The presence of well formed calcite crystals in numerous suid specimens and other faunal remains, indicates the presence of supersaturated waters (Wells 1971). This, and the presence of a number of specimens "swollen" due to submersion in water (Schrenk 1984), supports the hypothesis of Maguire et al. (1980) that water was a possible bone concentrating mechanism for the Limeworks faunal assemblage. This hypothesis is based on a study of bone orientation, using stereographic projections. The results of the projections indicate that a combination of water current action and gravity, were responsible for the present configuration of the bones.

An additional aid in elucidating the taphonomy is age profile. Age profiles can be used to determine the possible carnivore or hunter responsible for the particular bone accumulation. Brink (1987) considered that the age profile of a prey population can be indicative of the hunting strategy. Hunting strategies in turn, may be specific to the hunter. Thus by examining the age profile of the Limeworks suid collection, its hunter or accumulating agent can possibly be identified. The assumption that the suids were preyed or hunted upon is based on above mentioned points relating to bone damage. The age profiles for both fossil genera reflect that of a normal living population (Klein and Cruz-Urbe

1984). In this particular case it is evident that the largest group of fossils consists of mature adults, probably at the optimum reproductive age. The groups of old adults, immature adults and juvenile individuals are smaller. Such a normal age profile has been interpreted as a catastrophic age profile (Klein and Cruz-Uribe 1984). These authors also stated that the catastrophic age profile could be fixed by hominid hunters, if, for example, the hunting was carried out on a communal drive basis and the animals were driven into a trap. Individuals of various ages, in accordance with the age proportions of the living population would thus be killed. With regard to carnivores, it appears that felids tend to pick out or select their prey. Mature, prime adults are likely to be the largest group, with the groups of old adults, immature adults and juvenile individuals smaller. The age profile of a felid bone accumulation would thus tend to be normal (Brink 1987).

Thus the scenario sketched by Maguire *et al.* (1980), in which hyaenas and other carnivores are seen as important bone accumulating agents (hominid action is not discounted), and a combination of water current action and gravity important bone concentrating agents, can easily be envisaged in terms of the present study. Maguire *et al.* (1980) stressed that a variety of animals were probably involved, including hyaenas, porcupines, sabre-toothed cats as well as hominids. The age profiles of the Lineworks suids indicate that felids may have been at least partly responsible for bone accumulation in Member 3. Additional evidence for carnivore activity can be found in the general distribution of the fossil suid skeletal parts. This collection is exclusively made up of cranial material, with the dentition the largest section. This could be due to sampling biases, but it could also be the result of the general vulnerability of the postcranial elements to the bone breaking activities of scavengers (Pienaar 1969).

5.4 SUMMARY

Study of the complete, prepared *Potamochoeroides shawi* collection compared to relevant fossil and extant suids indicates that the former is generically distinct from *Metridiochoerus andrewsi*. A cladogram, constructed to establish the relationship of *Potamochoeroides* to the other African Suidae, shows that *Potamochoeroides* and the extant *Potamochoerus* are sister groups. This suggests that *Potamochoeroides* was more primitive and may indicate that *Potamochoeroides* is older than previously considered. On this basis it is possible that Member 3, and *Australopithecus africanus* are older than previously envisaged. Possibly of a similar age to the Laetoli Beds in East Africa ($3.49 \pm 0.12 \text{ myr}$ - $4.32 \pm 0.06 \text{ myr}$).

The similarity of *Potamochoeroides* to *Potamochoerus* with regard to a number of anatomical features indicates that the former was omnivorous. However, the functional implications of the M3 molar structure shows that the diet of *Potamochoeroides* probably included a large proportion of grass. *Notochoerus capensis* appears to have been a specialised grazer, similar in this regard to *Phacochoerus aethiopicus*.

The palaeoenvironmental implications from the two fossil suid species are that during the deposition of Member 3, the Makapan valley environment was similar to the present, but with more extensive grassland.

The taphonomy of the fossil suid bone accumulation indicates that the suids probably were hunted by carnivores including hyaenas and felids, and the hominid *Australopithecus africanus*, and that the suid bone accumulation may have later been concentrated, together with the entire faunal assemblage, by a combination of water current action and gravity.

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ABBREVIATIONS

- a-p br - antero-posterior breadth
- BR - breadth
- d - fossa, insertion of digastric muscle
- d-v br - dorso-ventral breadth
- dr - fossa, origin of depressor rostri muscle
- HT - height
- ip - fossa, attachment internal pterygoid muscle
- l - lower
- lat/prof - lateral profile
- l/d rostri o. - origins, levator, depressor rostri muscles
- len - length
- lt - fossa, origin of levator rostri muscle
- LT - length
- max. orb. len. - maximum orbital length
- min. par. br. - minimum parietal breadth
- myr - million years
- par/occ - parietal/occipital
- suprac. flange - supracanine flange
- u - upper

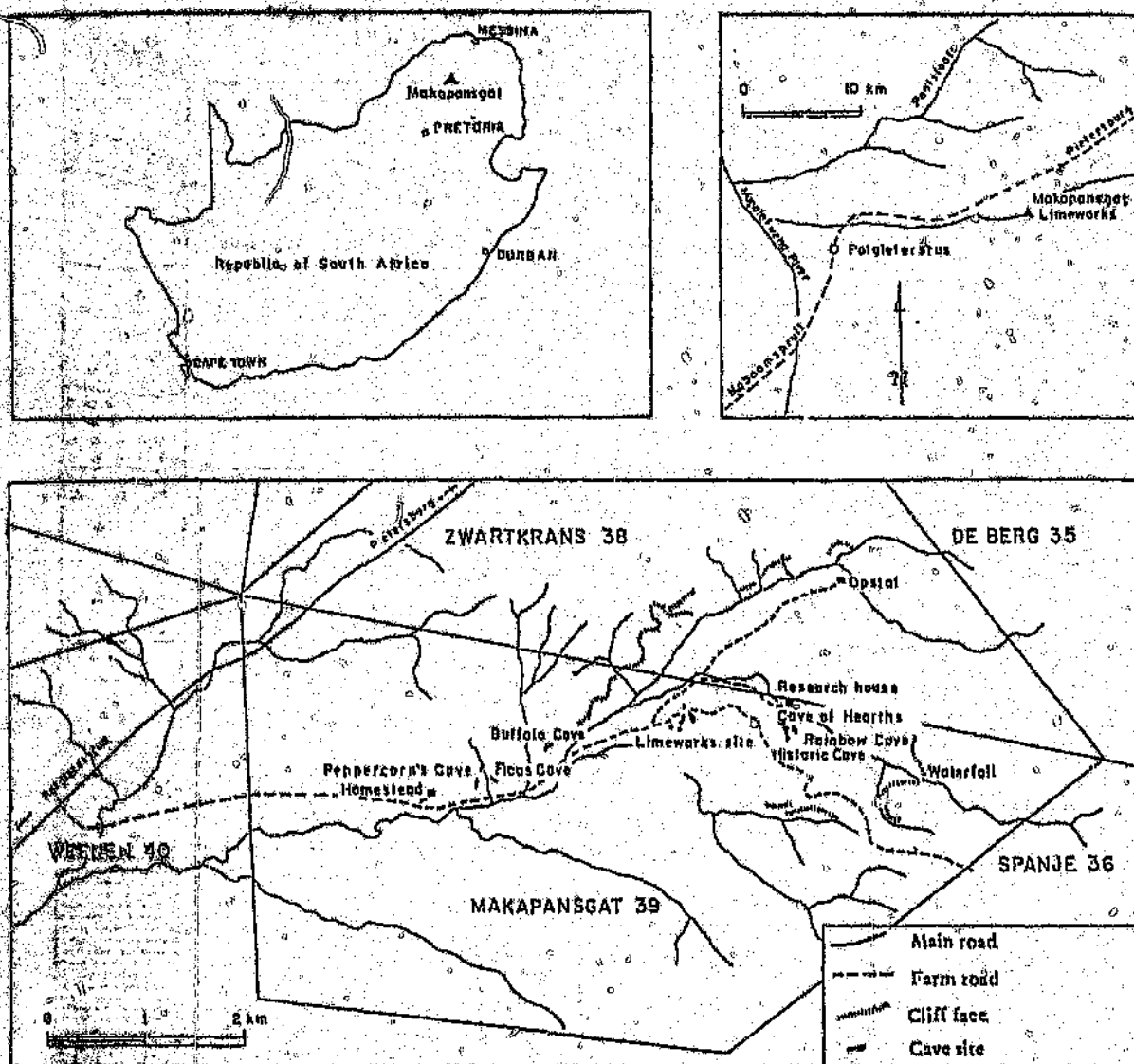


Figure 1. Locality maps of the Makapansgat valley showing the Limeworks (after Maguire *et al.* 1985).

	Wells and Cooke (1956)	Brain (1958)	Partridge (1979)
	Coarser brownish red sandy breccia	Sandy breccia with gravel bands	MEMBER 5
			BED E
			D
			C
			B
	Coarse pink breccia	UPPER-PHASE I Highly calcified breccia with weathered dolomite blocks	MEMBER 4
			BED B
			BED A ('RODENT BRECCIA')
			MEMBER 3
	Grey fossil-rich cemented marl	LOWER-PHASE I Red calcified mud, often bone rich, and contaminated travertine	
	Stratified pink or red breccia		MEMBER 2
	Manganous layer of mixed travertine and fine pink sand		
	Floor travertine		MEMBER 1
	Dolomite		Dolomite floor

Figure 2. Stages in the development of the lithostratigraphy of the Makapansgat Limeworks (after Maguire et al, 1985).

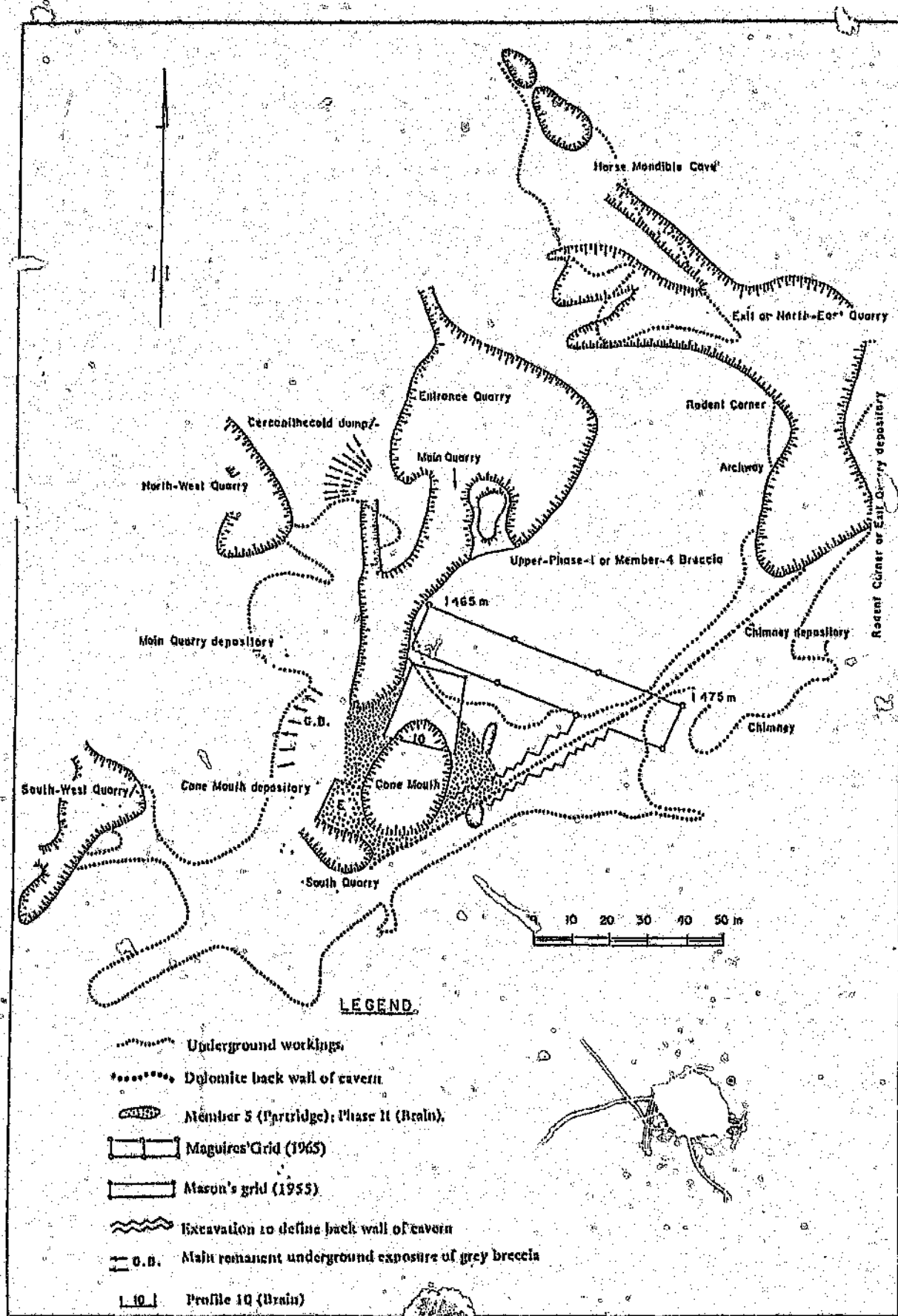


Figure 3. Map of the Makapansgat Limeworks site showing the important features (after Maguire *et al.* 1985).

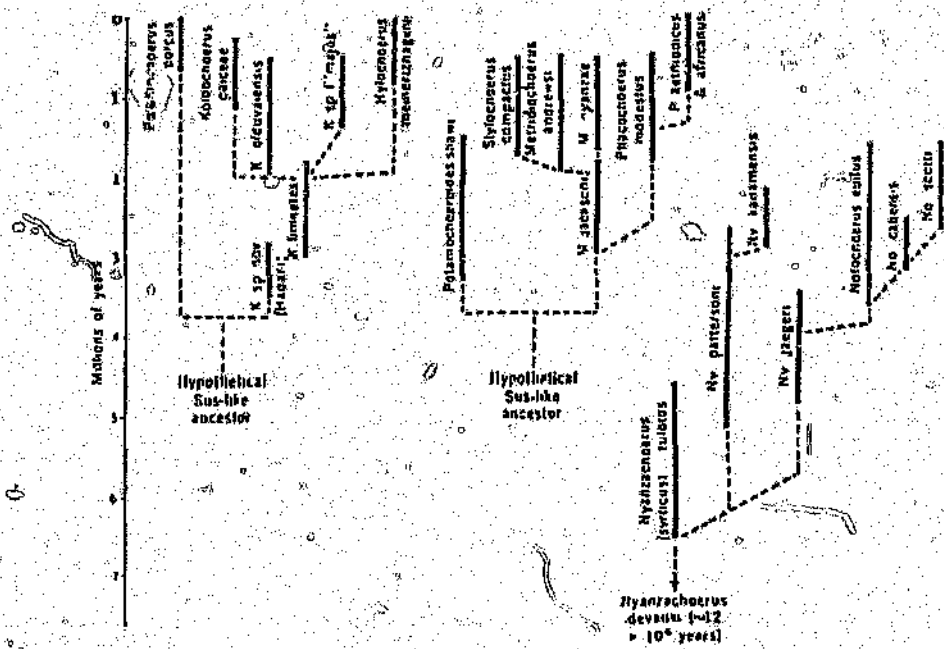


Figure 4. Phylogenetic relationships of the Plio-Pleistocene African Suidae (after Cooke 1978).

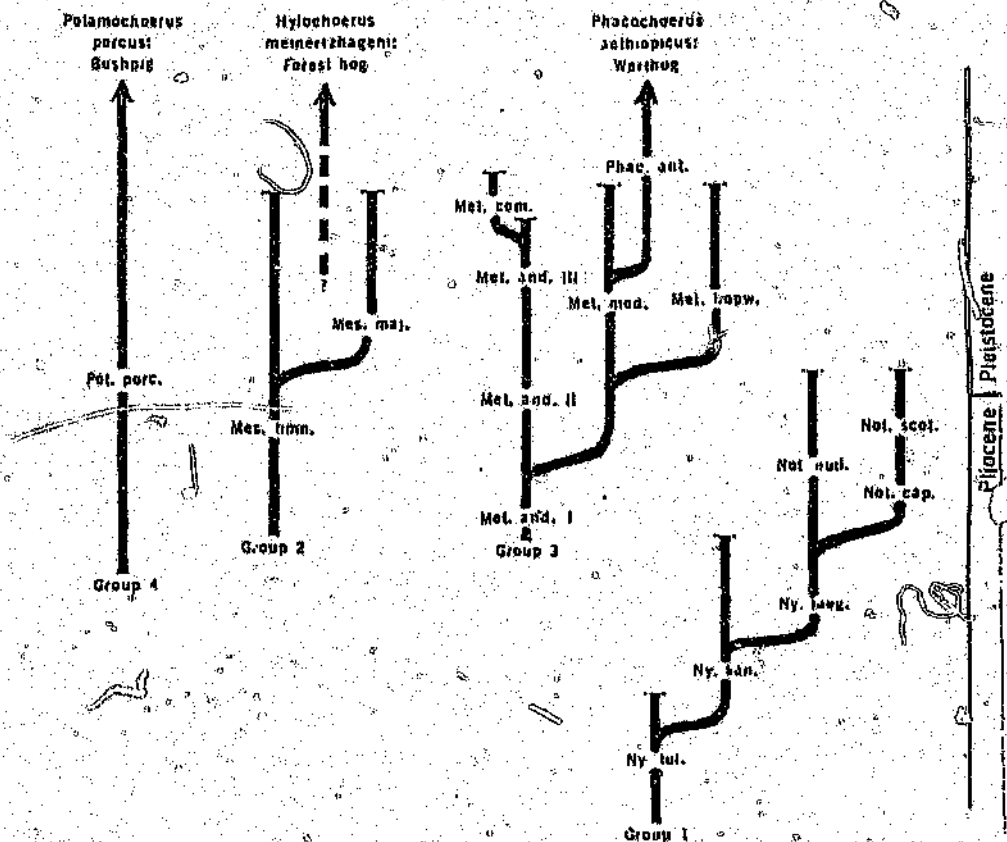


Figure 5. Phylogenetic relationships of the Plio-Pleistocene African Suidae (after White and Harris 1977; Harris and White 1979).



Figure 1. The type specimens of the genus *Potamochoeroides* [specimens M302 (mandibular), and M303 (maxillary)].

Figure 7. Table of maxillary and mandibular measurements. (based on Von den Dreisch 1976; White and Harris 1979; Harris 1983).

SKULL AND MAXILLARY.

1. Greatest inner length of the orbit.
2. Maximum width of the maxilla at P3.
3. Maximum width of the maxilla at M3.
4. Minimum breadth of the parietal.
5. Dentition.

Canine measurements: a. maximum anterior - posterior diameter, b. maximum dorsal - ventral diameter.

- a. Premolar length (Lt) - maximum length at the enamel/root junction.
- b. Premolar breadth (Br) - maximum breadth perpendicular to the occlusal plane. Taken on the enamel crown shoulders at the point of greatest breadth.
- c. Molar length (Lt) - as for premolars, a maximum length at the cervical/enamel line.
- d. Molar breadth (Br) - as for the premolars, a maximum crown breadth perpendicular to the mesio-distal crown axis.
- e. Crown height (Ht) - taken only on third molars. It is a direct length from the cervical enamel line at the centre of the base of the first major unworn pillar of the talon(id), to the pillar apex. May be oblique to the occlusal or basal plane, but this measure must be parallel to the pillar axis. It may be taken on the buccal or lingual side (lingual preferred). For measurement, the pillar must be unworn or very slightly worn.

6. Additive and comparative measures.

a. Single tooth parameters.

Premolar area ($\text{Area} = \text{Lt} \cdot \text{Br}$)

Molar area.

Lt/Br of M3.

Ht/Lt of M3.

b. Tooth row parameters.

Lt P3 + Lt P4

Area P3 + Area P4

Lt M1 + Lt M2 + Lt M3

Lt P3 + Lt P4 / Lt M1 + Lt M2 + Lt M3

Area P3 + Area P4 / Area M3

Area P4 / Area M3

MANDIBLE.

1. Maximum width at the canine alveolus.
2. Maximum width at the postcanine constriction.
3. Maximum symphysis length.
4. Maximum corpus width at M3.
5. Dentition.

As for the skull and maxillary.



Figure 8. Dorsal view of *Potamochoeroides*, M1391, showing the posterior widening of the nasals.



Figure 9. Lateral view of *Potamochoeroides* nasals showing the fossae for the origins of the levator and depressor rostri muscles (specimen M1391).



Figure 10. Dorsal view of the *Potamochoeroides* braincase, showing the parietals (specimen M2062).



Figure 11. Lateral view of *Potamochoeroides* M2062, indicating that the braincase is not elevated as it is in the extant *Phocaenoides*.



Figure 12. Dorsal view of *Potamochoeroides* supracanine flange showing the broad groove between the premaxilla/maxilla and the supracanine flange (specimen M589).

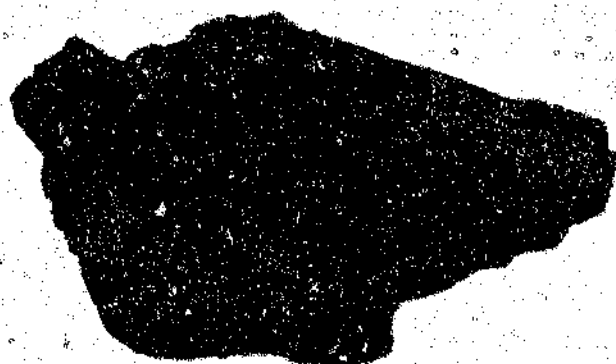


Figure 13. Dorso-lateral view of *Potamochoeroides* supracanine flange (specimen M589).

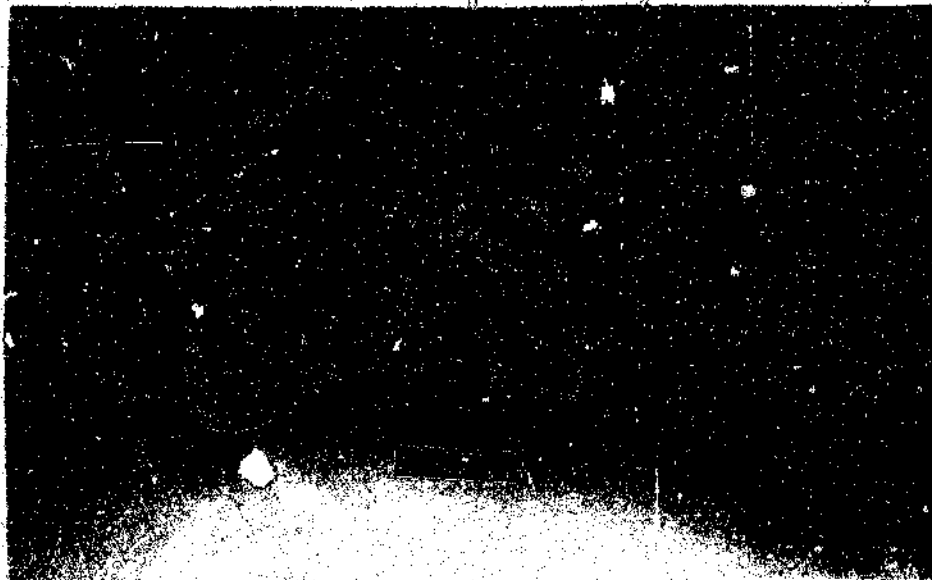


Figure 14. Lateral view of extant *Potamochoerus* male specimen BPI/C 8, showing the supracanine flange.



Figure 15. Dorsal view of extant *Phacochoerus* male BPI/C 11 and female BPI/C 13, showing the difference between male and female in terms of the lateral outward flaring of the zygoma.

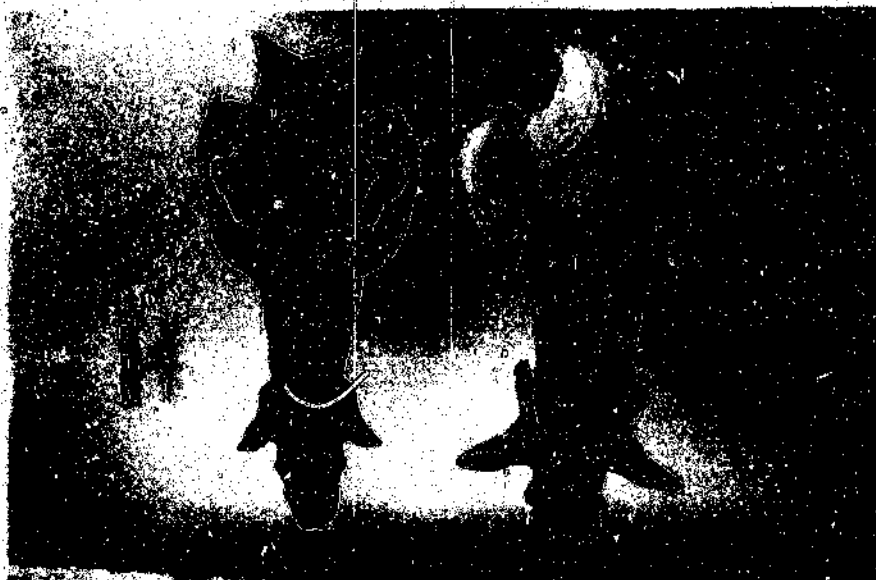


Figure 16. Dorsal view of the extant *Potamochoerus* male BPI/C 8 and the female BPI/C 9, showing the difference between male and female in terms of the lateral outward flaring of the zygoma.



Figure 17. Ventral view of *Potamochoeroides* M 062, showing the structure of the pterygoid.

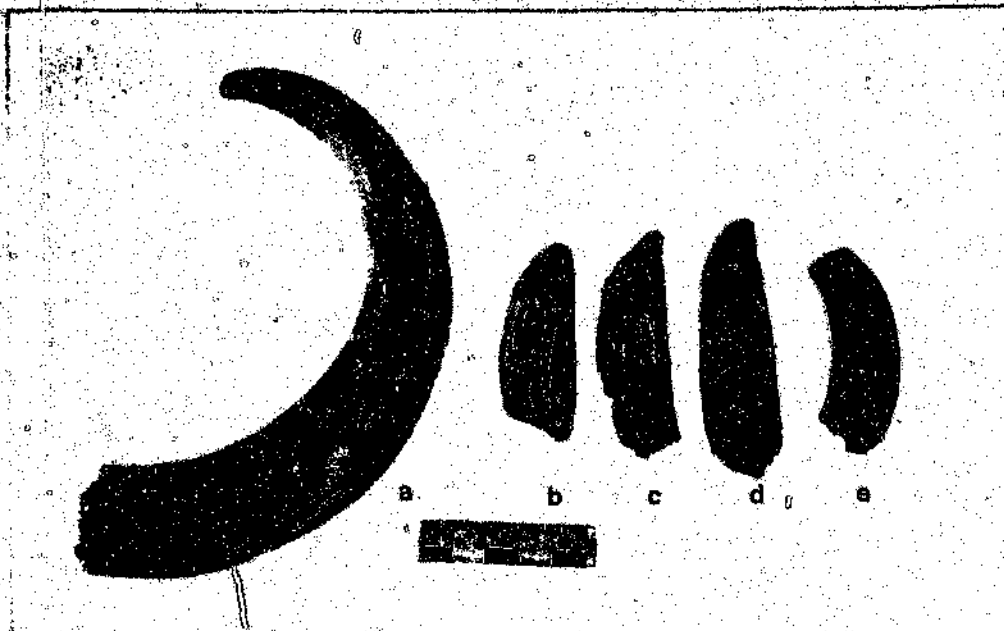


Figure 18. Lateral view of the upper canine of the extant *Phacochoerus* (a), and ventral views of the upper canine of the extant *Potamochoerus* (b,c,d), and the extinct *Potamochoeroides* (e).



Figure 19. Ventral view of *Potamochoeroides* maxillary specimen M321, showing the structure of the P2, P3 and P4 premolars.



Figure 20. Ventral view of extant *Potamochoerus* skull, BPI/C 8, in which premolar and molar structure can be seen.

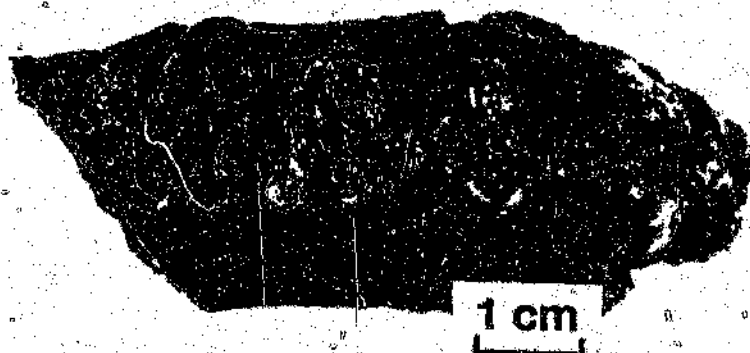


Figure 21. Ventral view of *Potamochoeroides* upper M3, M347, illustrating that this specimen belongs to M3 talon category Group 1.



Figure 22. Ventral view of *Potamochoeroides* upper M3, M1573, illustrating that this specimen belongs to M3 talon category Group 2.



Figure 23. Ventral view of *Potamochoeroides* upper M3, M346, illustrating that this specimen belongs to M3 talon category Group 3.

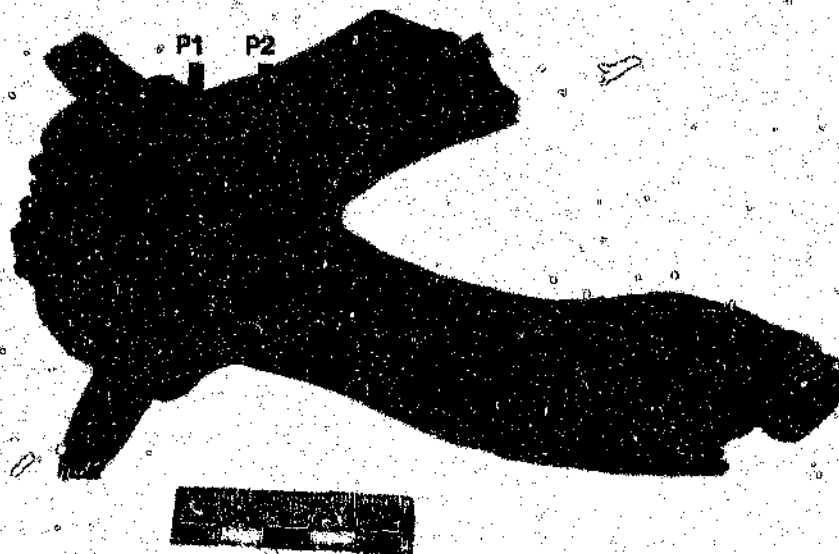


Figure 24. Dorsal view of *Potamochoeroides* mandibular, M2081, showing the short symphysis with the lack of lateral compression.



Figure 25. Lingual view of *Potamochoeroides* mandibular, M8217, showing the depressed dorso-lingual aspect.



Figure 26. Dorsal view of extant *Potamochoerus* mandible, BPI/C 8.

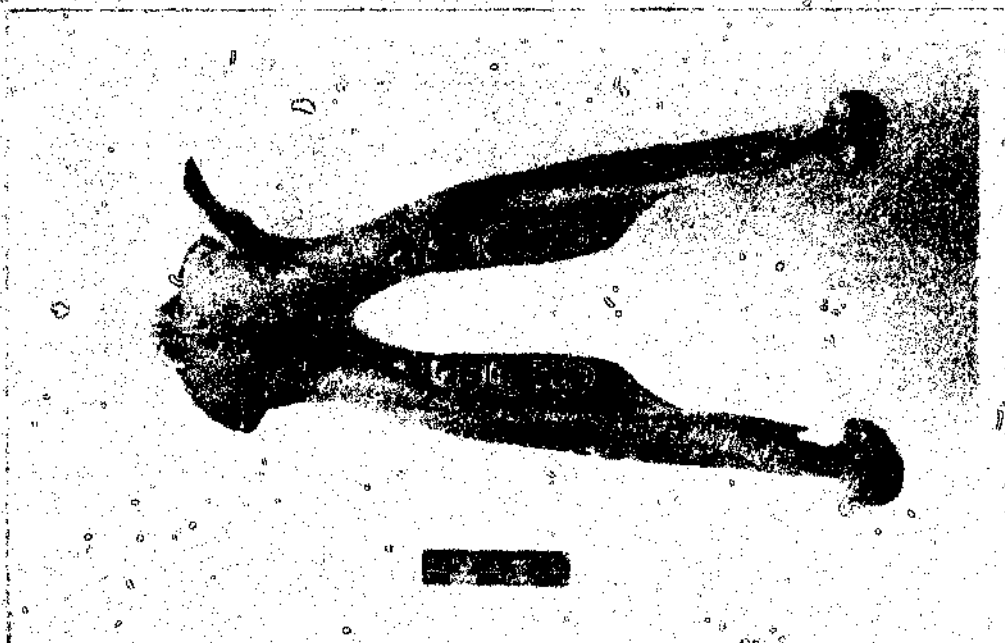


Figure 27. Dorsal view of extant *Phacochoerus* mandible, BPI/C 13.



Figure 28. Dorsal view of *Potamochoeroides* lower M3, M8895 and M2263, indicating that these specimens belong to M3 talonid category Group 1.

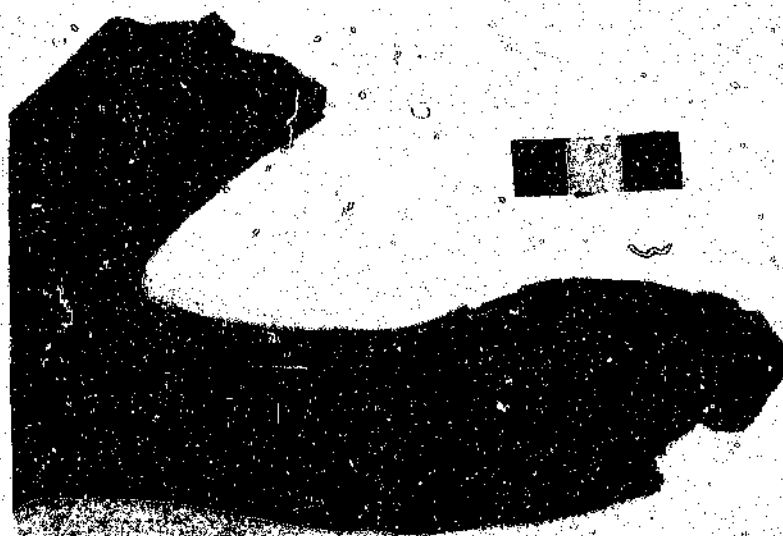


Figure 29. Dorsal view of *Potamochoeroides* M2081, indicating that the lower M3 belongs to M3 talonid category Group 2.



Figure 30. Dorsal view of *Potamochoeroides* M8217, indicating that the lower M3 belongs to M3-talonid category Group 3.

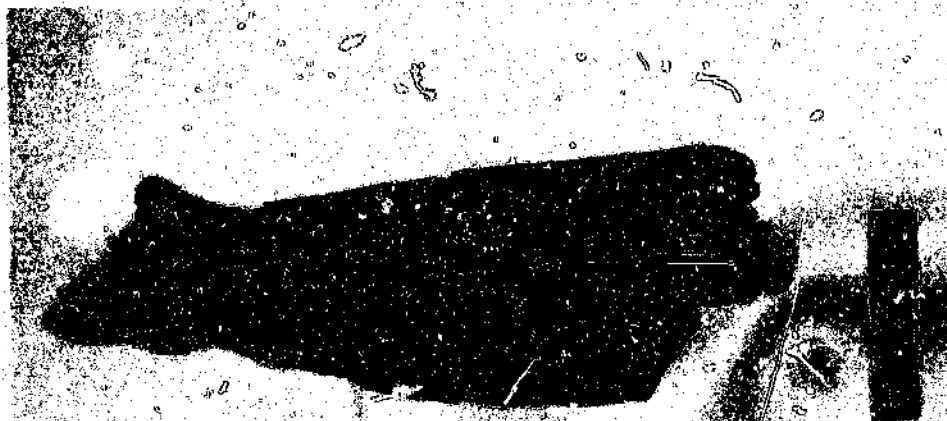


Figure 31. Dorsal view of *Neorhoenys* specimen M2025, illustrating the structure of the lower M3.

Hypothetical SUS-LIFE ancestor

POTAMOCHOERCIDES

POTAMOCHOERUS

KOLPOCHOERUS

HYLOCHOERUS

METRIDIOCHOERUS

PHACOCHOERUS

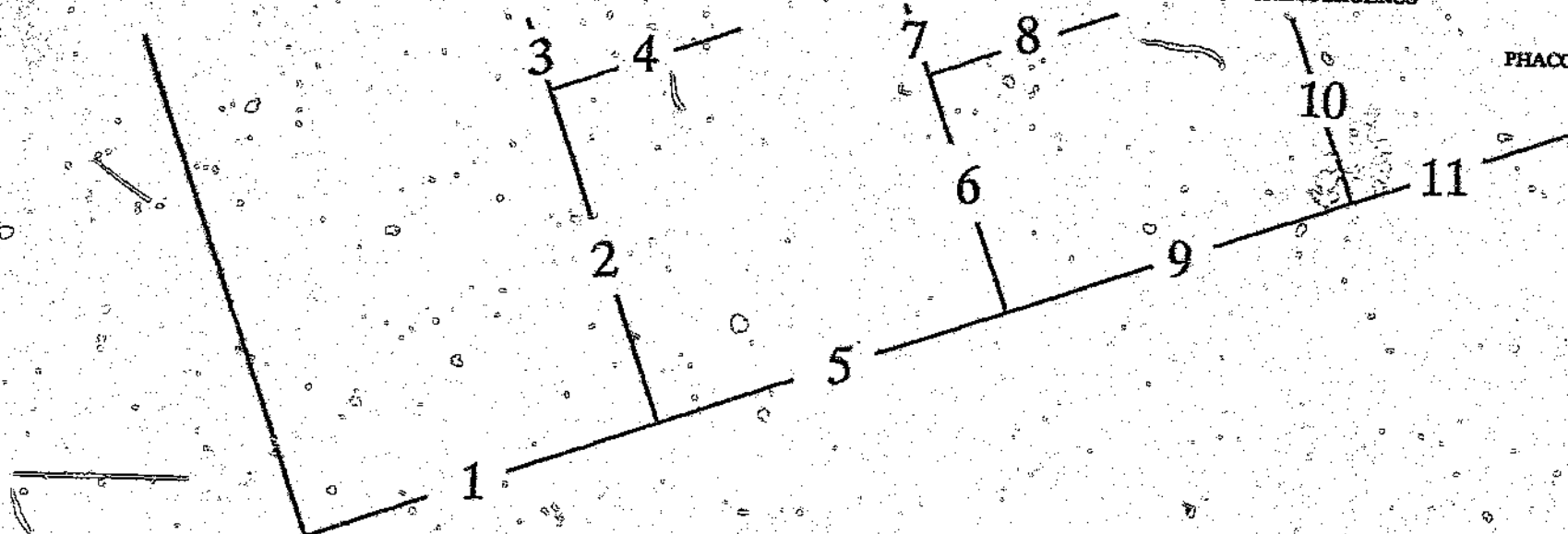


Figure 32. Cladogram showing the phylogenetic relationship of *Potamochoeroides* to other Pliocene African Suidae.

Hypothetical SUS-LIKE ancestor

POTAMOCHOEROIDES

POTAMOCHOERUS

KOLPOCHOERUS

HYLOCHOERUS

METRIDIOCHOERUS

PHACOCHOERUS

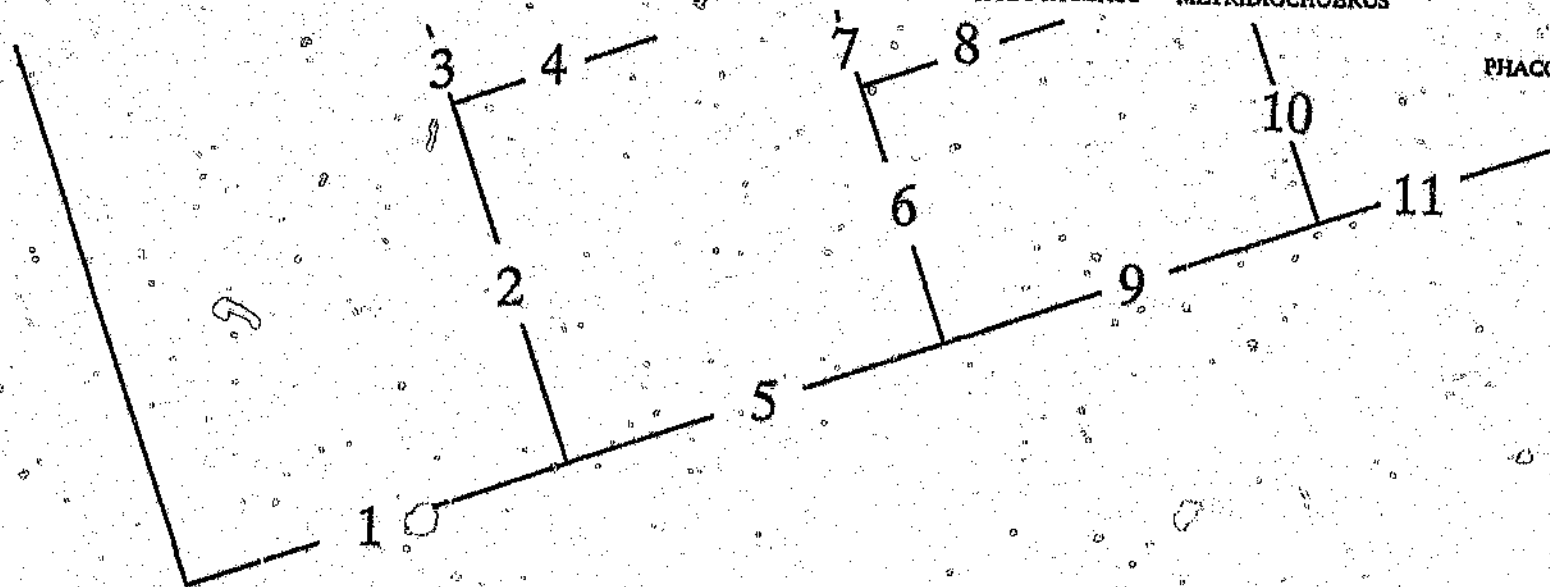


Figure 32. Cladogram showing the phylogenetic relationship of *Potamochoeroides* to other Plio-Pleistocene African Suidae.

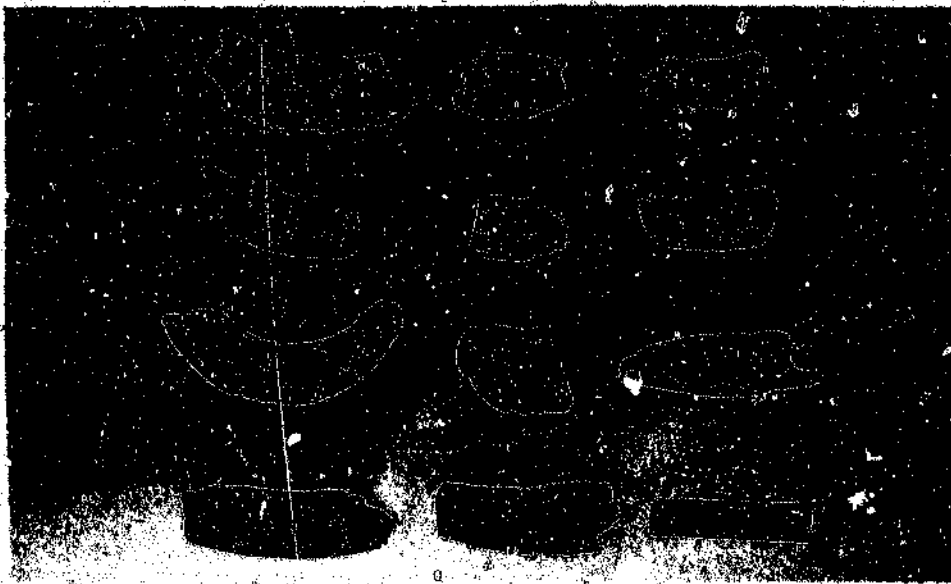


Figure 33. *Potamochoeroides* upper and lower canine specimens. It is suggested that these fragments were used as tools by *Australopithecus africanus*.

Potamochosroides cranial measurements (mm)

number	P3	M3
M1391	67.4	81.5

P3 = maximum width of the maxilla at P3
M3 = maximum width of the maxilla at M3

Potamochoerus cranial measurements (mm)

number	P3	M3
9	51.9	
5	46.9	67.4
4	65	70.8
8	53.6	62.3
Max	53.6	70.8
Min	46.9	62.3
Mean	54.35	66.83333
Std.dev.	6.623631	3.493157

P3 = maximum width of the maxilla at P3
M3 = maximum width of the maxilla at M3

Phacochoerus cranial measurements (mm)

number	M3
PAB2	67.6
PAB1	53.9
15	33.6
13	58
14	70.2
23	62.2
11	76.4
Max	76.4
Min	33.6
Mean	60.35714
Std.dev.	12.82406

M3 = maximum width of the maxilla at M3

Table 1. Potamochosroides, Potamochoerus and Phacochoerus cranial measurements.

Potamochoeroides Upper P2 (mm)

number	length	breadth	area
M353	9.2	6.2	57.04
M321	8.1	5.5	44.55

Potamochoerus Upper P2 (mm)

number	length	breadth	area
8	10.2	7.1	72.42
8	10.2	7.2	73.44
9	10.4	6	62.4
9	11.2	7.1	79.52
5	9.4	6.5	61.1
5	10.1	7.05	71.2
4	11.3	8.4	94.92
4	10.6	7.2	76.32
Max	11.3	8.4	94.92
Min	9.4	6	61.1
Mean	10.425	7.06875	73.915
Std. dev.	0.576085	0.639793	9.906193

Table 2. Potamochoeroides and Potamochoerus upper P2 measurements.

Potamochoeroides Upper P3 (mm)

number	length	breadth	area
M1391	12.6	10.8	136.08
M326	10.65	10.9	116.08
M358	11.6	10.2	118.32
M2000	12.5	10.4	130
M2002	11.6	11.5	133.4
M1872	11.9	12.5	148.75
M2007	10.2	9.9	100.98
M321	10.4	9.9	102.96
M2048	10.5	11	115.5
M331	11.5	9.6	110.4
M2010	10.8	10.3	111.24
Max	12.6	12.5	148.75
Min	10.2	9.6	100.98
Mean	11.29545	10.63636	120.3372
Std.dev.	0.800129	0.795753	14.21553

Potamochoerus Upper P3 (mm)

number	length	breadth	area
8	11.9	10.5	124.95
8	11.7	10.3	120.51
9	14.5	11.35	164.57
9	12.8	11.5	147.2
5	13.45	13.0	177.54
5	12.7	11.25	142.87
4	11.5	9.5	109.25
4	11.35	9.9	112.36
Max	14.5	13.2	164.57
Min	11.35	9.5	109.25
Mean	12.4875	10.9375	137.4062
Std.dev.	1.021870	1.086493	23.27844

Phacochoerus Upper P3 (mm)

nu.	length	breadth	area
15	5.05	6.1	30.8
12	7.15	6	42.9
12	7.2	6.2	44.64
13	5.15	5	25.75
12	7.9	5.95	47
11	7.3	5.9	43.07
Max	7.9	6.2	47
Min	5.05	5	25.75
Mean	6.625	5.858333	39.02666
Std.dev.	1.106326	0.396249	7.856873

Table 3. Potamochoeroides, Potamochoerus and Phacochoerus upper P3 measurements.

Potamochoeroides Upper P4 (mm)

number	length	breadth	area
M1391	10.6	13.6	144.16
M1391	11.6	13.9	161.24
M1851	10.8	12.4	133.92
M2002	10.65	14.4	153.36
M2000	10.7	13	139.1
M303	10.6	12.2	129.32
M326	10.5	13.9	145.95
M353	11.45	14.1	161.45
M1872	11.4	13.8	157.32
M1875	11.1	13.3	147.63
M2012	11.8	13.8	162.84
M329	10.2	13.2	134.64
M2007	10.3	12.3	126.69
M2007	10.6	12.4	131.44
M321	10.9	12	130.8
M1858	10.2	12.9	131.58
M362	11.1	14.5	160.95
M2043	11.4	14.1	160.75
M331	12	14.4	172.8
M2011	10.6	12.8	135.68
M2066	11.2	13.4	150.08
M333	10.8	13.6	146.88
M2065	11.8	14.6	172.28
Max	12	14.6	172.8
Min	10.2	12	126.69
Mean	10.96956	13.41739	147.4286
Std. dev	0.512674	0.778880	13.97898

Potamochoerus Upper P4 (mm)

number	length	breadth	area
8	12	13.7	164.4
8	12	13.4	160.8
9	14.8	16	236.8
9	12.3	16.05	197.41
5	13.3	14.5	192.85
5	12.7	14.75	187.32
4	11.95	12.1	144.59
4	11.6	12.35	143.26
Max	14.8	16.05	236.8
Min	11.6	12.1	143.26
Mean	12.58125	14.10625	178.4287
Std. dev	0.972733	1.401213	29.46183

Phacochoerus Upper P4 (mm)

number	length	breadth	area
15	9	9.1	81.9
12	9.3	9.5	88.35
12	8.8	8.95	78.76
13	7.4	8.2	60.68
13	8.35	8.1	67.63
Max	9.3	9.5	88.35
Min	7.4	8.1	60.68
Mean	8.57	8.77	75.464

Table 4. Potamochoeroides, Potamochoerus and Phacochoerus upper P4 measurements.

Potamochoeroides Upper tooth row parameters (mm)

number	Lt P	Area P	Lt M	Lt P/M	Area P/M	Area P4/M
M1872	23.3	306.07				
M1391	23.2	297.32			0.279	0.151
M326	21.15	262.03				
M353	23.05	279.77				
M2000	23.2	269.1				
M2002	22.25	286.76				
M2007	20.5	227.67				
M321	21.3	233.76	79.2	0.268	0.246	0.138
M331	23.5	283.2				
M303			69.2			0.166
Max	23.5	306.07				
Min	20.5	227.67				
Mean	22.38333	271.7422				
Std dev	1.060660	25.25469				

$$\text{Lt P} = \text{LtP3} + \text{LtP4}$$

$$\text{Area P} = \text{Area P3} + \text{Area P4}$$

$$\text{Lt M} = \text{LtM1} + \text{LtM2} + \text{LtM3}$$

$$\text{Lt P/M} = \text{Lt P3+P4/M1+M2+M3}$$

$$\text{Area P/M} = \text{Area P3+P4/M3}$$

$$\text{Area P4/M} = \text{Area P4/M3}$$

Potamochoerus Upper tooth row parameters (mm)

number	Lt P	Area P	Lt M	Lt P/M	Area P/M	Area P4/M
8	23.9	289.35	66.5	0.359	0.451	0.256
8	23.7	281.31	66	0.359	0.439	0.251
9	29.3	401.37				
9	25.1	344.61				
5	26.75	370.39				
5	25.4	330.19				
4	23.45	253.84	67.04	0.349	0.361	0.206
4	22.95	255.62	66.15	0.346	0.367	0.205
Max	29.3	401.37	67.04	0.359	0.451	0.256
Min	22.95	253.84	66	0.346	0.361	0.205
Mean	25.06875	315.835	66.4225	0.35325	0.4045	0.2295
Std. dev.	1.974515	50.83421	0.400023	0.005847	0.040776	0.024067

Phacochoerus Upper tooth row parameters (mm)

number	Lt P	Area P	Area P/M	Area P4/M
15	14.05	112.7	0.107	0.077
12	16.45	131.25		
12	16	123.4		
13	13.5	86.43		
Max	16.45	131.25		
Min	13.5	86.43		
Mean	15	113.445		
Std. dev.	1.250499	16.92989		

Table 3. Potamochoeroides, Potamochoerus and Phacochoerus upper tooth row parameters.

Potamochoeroides Upper M1 (mm)

number	length	breadth	area
M1851	15	14.9	223.5
M8378	14.75	15.7	231.57
M2002	14.45	15.85	229.03
M303	13.9	14	194.6
M326	15.1	16.4	247.64
M328	14.2	14.25	202.35
M2260	15	15	225
M2080	13.6	14.8	201.28
M2012	15.4	15.2	234.08
M329	14.9	14.9	222.01
M2007	13.1	13.9	182.09
M2006	12.4	12.4	153.76
M321	14.6	15	219
M1858	14.4	15.8	227.52
M2065	15	15.7	235.5
Max	15.4	16.4	247.64
Min	12.4	12.4	153.76
Mean	14.38666	14.92	215.262
Std.dev.	0.800097	0.960520	23.54004

Potamochoerus Upper M1 (mm)

number	length	breadth	area
8	14.5	15.8	229.1
8	14.1	15.8	222.78
9	17.3	16.6	287.18
9	19.05	16.8	320.14
5	14.9	16.4	244.36
3	14.7	17.7	260.19
4	14.05	16.1	226.2
4	13.95	15.4	214.83
Max	19.05	17.7	320.14
Min	13.95	15.4	214.83
Mean	15.31875	16.325	250.5975
Std.dev.	1.733662	0.675925	34.30719

Phacochoerus Upper M1 (mm)

number	length	breadth	area
12	11.85	12.8	151.68
12	11.7	13.55	158.53
13	11.5	10.4	119.6
13	10	9.6	96
11	14.6	13.65	199.29
Max	14.6	13.65	199.29
Min	10	9.6	96
Mean	11.93	12	145.02
Std.dev.	1.489832	1.678392	35.27391

Table 6. Potamochoeroides, Potamochoerus and Phacochoerus upper M1 measurements.

Potamochoeroides Upper M2 (mm)

number	length	breadth	area
M1391	20	20.05	401
M1391	20.25	21.2	429.3
M2008	22.65	21.95	497.17
M1851	21.4	19.65	420.51
M347	21.2	20.95	444.14
M2002	20.25	19.25	389.81
M303	19.1	18.1	345.71
M326	20.1	20.5	412.05
M2063	21.8	20.7	451.26
M385	21.6	20.85	450.36
M328	19.6	19.3	378.28
M1914	19.5	21.9	427.05
M1893	21.6	21.6	466.56
M332	18.9	21	396.9
M2003	22.7	20.2	458.54
M2012	19.3	20.4	393.72
M356	19.3	19.8	382.14
M330	21.9	22.2	486.14
M345	18.8	22.1	415.48
M2006	15.4	15.3	238.7
M321	19.6	19.85	389.06
M2231	22.2	22.4	497.28
M1915	21.2	22.3	472.76
M1915	21.9	21.95	480.7
M2041	18.2	21.4	389.48
M1949	21	21.6	453.6
M2001	22.9	22	503.8
M2039	21.2	20.8	440.96
M2064	20.6	20.3	418.18
Max	22.9	22.4	503.8
Min	15.4	15.3	238.7
Mean	20.48793	20.68275	425.1944
Std.dev.	1.59117	1.437327	53.46108

Potamochoerus Upper M2 (mm)

number	length	breadth	area
8	19.8	20.1	397.98
8	19.9	20.1	399.99
9	23.5	22.65	532.27
9	24.8	22	545.6
5	22	23.6	519.2
5	22.95	23.7	543.91
4	18.6	18.5	344.1
4	18	18.8	338.4
Max	24.8	23.7	545.6
Min	18	18.5	338.4
Mean	21.19375	21.18125	452.6812
Std.dev.	2.307655	1.943569	85.39202

Phacochoerus Upper M2 (mm)

number	length	breadth	area
PAB2	17.2	17	292.4
PAB2	17	16.35	277.95
15	14	11.8	165.2
12	20	13.45	269
12	20.7	13.85	286.69
13	17.53	14.5	254.47
13	16.8	14.5	243.6
14	18.25	17.3	315.72
14	17.3	16.8	290.64
23	16.7	14.8	247.16
23	16.53	14.8	244.94
Max	20.7	17.3	315.72
Min	14	11.8	165.2
Mean	17.45909	15.01363	262.5245
Std.dev.	1.697367	1.620758	37.91975

Table 7. Potamochoeroides, Potamochoerus and Phacochoerus upper M2 measurements.

Potamochoeroides Upper M3 (mm)

number	length	breadth	area	Lt/Br	Ht	Ht/Lt
M1391	43.6	24.45	1066.02	1.78		
M1391	44.45	25.4	1129.03	1.75		
M1400	46.2	22.65	1046.43	2.04	18.2	0.393
M1572	46.2				25.5	0.551
M2072	49.1	22.95	1126.84	2.14	26.15	0.532
M347		22.5				
M320	43.05	23.8	1024.59	1.81	21.1	0.49
M319	38.65					
M1926	43.2	26.8	1157.76	1.61	20.9	0.413
M1927	44.1	24.1	1062.81	1.83	23.75	0.538
M318	44.35	25.25	1119.84	1.76		
M1929	44.35	24.5	1086.57	1.81	17.85	0.402
M346	42.2	23	970.6	1.83	19.3	0.457
M303	36.2	21.5	778.3	1.68		
M2063	48.6	25	1215	1.94	21.6	0.444
M385	50.4	24.7	1244.88	2.04	19.05	0.377
M2073	40	24	960	1.66	26.1	0.65
M8400	43.2	21.1	911.52	2.04		
M1573	42.7	23.8	1016.26	1.79	23	0.538
M1924	43.3	24.2	1047.86	1.78	18.9	0.436
M317	49.3	21.6	1064.88	2.29		
M330	48.4	26.8	1297.12	1.8	19.1	0.394
M2074	45.3	24.1	1091.73	1.89	21.1	0.465
M316	42.25	22.9	967.52	1.84	23.65	0.559
M321	45	21.1	949.5	2.13	25.1	0.557
M8399	45.2	25	1130	1.8		
M1868	45.9	23.2	1064.88	1.98		
Max	50.4	26.8	1297.12	2.29	26.15	0.65
Min	36.2	21.1	778.3	1.61	17.85	0.377
Mean	44.43076	23.776	1063.747	1.875833	21.78529	0.486235
Std.dev.	3.192059	1.521651	109.3207	0.163067	2.771268	0.073016

Table 8a. Potamochoeroides upper M3 measurements.

Potamochoerus Upper M3 (mm)

number	length	breadth	area	Lt/Br	Ht	Ht/Lt
8	32.2	19.9	640.78	1.62	13.15	0.408
8	32	20	640	1.6	13.8	0.432
4	34.4	20.4	701.76	1.58	10.7	0.311
4	34.2	20.35	695.97	1.68	11.2	0.327
Max	34.4	20.4	701.76	1.68	13.8	0.431
Min	32	19.9	640	1.6	10.7	0.311
Mean	33.2	20.1625	669.6275	1.645	12.2125	0.36925
Std. dev.	1.104536	0.216145	29.31037	0.035707	1.295364	0.051217

Phacochoerus Upper M3 (mm)

number	length	breadth	area	Lt/Br
PAB2	50.4	16.7	841.68	3.01
PAB2	48.8	15.4	751.2	3.16
15	64.5	16.3	1051.35	3.96
15	63.6	16.4	1043.04	3.88
PAB1	46.9	14.4	675.36	3.32
PAB1	47.4	14	663.6	3.38
14	51.7	16.7	863.39	3.09
14	52.2	17.05	890.01	3.06
23	44	15	660	2.93
23	44.55	15.2	677.16	2.93
11	63.5	16.4	1041.4	3.87
11	62.85	16.15	1015.02	3.89
Max	64.5	17.05	1051.35	3.96
Min	44	14	660	2.93
Mean	53.36666	15.80833	847.795	3.37333
Std. dev.	7.626552	0.941371	153.9432	0.394384

Table 8b. Potamochoerus and Phacochoerus upper M3 measurements

Potamochoeroides Lower Jaw measurements (mm)

number	M3	C	S	PG
M1890	45.5			
M8217	32.8			
M8367	39.05			
M1882	38.95			
M8370	45.05			
M1887	35.9			
M1889	44.9			
M8366	41.5			
M302	46.4			
M339	34.9			
M2017	31.3			
M384	35.9		65	67.65 40.3
M8365			104.1	48.2
M2081		69.7	61.2	37.6
Max	46.4		91	104.1 48.2
Min	31.3		65	61.2 37.6
Mean	39.34583	75.23333	77.65	42.03333
Std.dev.	5.058015	11.31262	18.88742	4.497653

M3 = Maximum corpus width at M3

C = Maximum width at canine alveolus

S = Symphysis length

PG = Maximum width at postcanine constriction

Potamochoerus Lower Jaw measurements (mm)

number	M3	C	S	PG
9			53.1	65.35 32.4
5	29.5		63.4	82.1 35.8
4	33.9		69.8	85.9 54.4
8	30.2		66.7	87.6 34
Max	33.9		69.8	87.6 54.4
Min	29.5		53.1	65.35 32.4
Mean	31.2		63.25	80.2375 39.15
Std.dev.	1.80457	6.281918	8.822937	8.886365

Phacochoerus Lower Jaw measurements (mm)

number	M3	C	S	PG
PAB2	34.6		97.4	72.4 39.4
PAB1	32.3		81.4	54.45 39.4
15	33.6		86.1	65.9 38.9
12			91.1	70.55 33.2
13	27.3		79.5	61.6 34.5
14	40.5		111.4	81.6 37.5
23	30		90	71.1 37.5
11	32.3		83.9	57.7 42.7
Max	40.5		111.4	81.6 42.7
Min	27.3		79.5	54.45 33.2
Mean	32.94285		90.1	66.9125 37.8875
Std.dev.	3.810043	9.685556	8.281611	2.795280

Table 9. Potamochoeroides, Potamochoerus and Phacochoerus lower jaw measurements.

Potamochoeroides Lower P3 (mm)

number	length	breadth	area
M302	10.7	8.4	89.88
M2015	8.3	5.9	48.97
M384	10.7	8.2	87.74
M384	11.1	7.8	86.58
Max	11.1	8.4	89.88
Min	8.3	5.9	48.97
Mean	10.2	7.575	78.2925
Std.dev.	1.109053	0.990896	16.97068

Potamochoerus Lower P3 (mm)

number	length	breadth	area
8	11.5	7.15	82.22
8	11.4	6.95	79.23
9	12.9	8.45	109
9	12.45	8.3	103.33
5	12.7	8.25	104.77
5	12.1	9.2	111.32
4	11.7	7.3	85.41
4	10.05	7.5	75.37
Max	12.9	9.2	111.32
Min	10.05	6.95	75.37
Mean	11.85	7.8875	93.83125
Std.dev.	0.854034	0.729618	13.71852

Table 10. Potamochoeroides and Potamochoerus lower P3 measurements.

Potamochoeroides Lower P4 (mm)

number	length	breadth	area
M302	11.6	10.8	125.28
M363	11.7	10.9	127.53
M1959	12.9	10.6	136.74
M339	12.7	10.7	135.89
M8367	12.2	11.1	135.42
M2015	12	10.9	130.8
M2018	12	10.8	129.6
M2018	11.3	10.7	120.91
M310	12.9	11.1	143.19
M1828	13.6	10.9	148.24
M8402	12.4	11.8	146.32
M384	12.4	11.2	138.88
M384	13.1	10.8	141.48
M338	11.7	10.7	125.19
M8369	12.2	10.7	130.54
M8365	12.2	10.1	123.22
M8365	12.4	10	124
Max	13.6	11.8	148.24
Min	11.3	10	120.91
Mean	12.31176	10.81176	133.1311
Std.Dev.	0.576890	0.389392	8.202180

Potamochoerus Lower P4 (mm)

number	length	breadth	area
8	13.3	10.8	143.64
8	12.6	10.9	137.34
9	16.2	12.1	196.02
9	16.4	12.2	200.08
5	15.2	12.65	192.28
5	14.6	12	175.2
4	12.6	10	126
4	12.55	10.35	129.9
Max	16.4	12.65	200.08
Min	12.6	10	126
Mean	14.18125	11.375	162.5575
Std.dev.	1.526830	0.916515	29.51206

Phacochoerus Lower P4 (mm)

number	length	breadth	area
15	10.2	8.5	86.7
15	9.8	8	78.4
12	9.7	7.6	73.72
12	9.9	7.4	73.26
13	9.7	6.6	64.02
13	9.2	6.5	59.8
Max	10.2	8.5	86.7
Min	9.2	6.5	59.8
Mean	9.75	7.433333	72.65
Std.dev.	0.298607	0.713364	8.865489

Table 11. Potamochoeroides, Potamochoerus, and Phacochoerus lower P4 measurements.

Potamochoeroides Lower tooth row parameters (mm)

number	Lt P	Area P	Lt M	Lt P/M	Area P/M	Area P4/M
M302	22.3	215.16	80.8	0.275	0.234	0.136
M2015	20.3	179.77				
M384	24.2	226.62				
M384	23.1	228.06				
M8367			80.1			0.155
M2081			88.3			0.121
M339						0.135
Max	24.2	228.06	88.3			0.155
Min	20.3	179.77	80.5			0.121
Mean	22.475	212.4025	83.2			0.13675
Std. dev.	1.425438	19.49216	3.608323			0.012090

$$Lt\ P = Lt\ P3 + Lt\ P4$$

$$Area\ P = Area\ P3 + Area\ P4$$

$$Lt\ M = Lt\ M1 + Lt\ M2 + Lt\ M3$$

$$Lt\ P/M = Lt\ P3 + P4/M1 + M2 + M3$$

$$Area\ P/M = Area\ P3 + P4/M3$$

$$Area\ P4/M = Area\ P4/M3$$

Potamochoerus Lower tooth row parameters (mm)

number	Lt P	Area P	Lt M	Lt P/M	Area P/M	Area P4/M
8	24.8	225.86	61.65	0.402	0.454	0.289
8	24	216.57	61.95	0.387	0.444	0.281
9	29.1	305.02				
9	28.85	303.41				
5	27.9	297.05				
5	26.7	286.52				
4	24.3	211.41	63.95	0.379	0.316	0.188
4	22.6	205.25	64.9	0.348	0.32	0.202
Max	29.1	305.02	64.9	0.402	0.454	0.289
Min	22.6	205.25	61.65	0.348	0.316	0.188
Mean	26.03125	256.3862	62.075	0.379	0.3835	0.24
Std. dev.	2.283492	42.26852	29.77220	0.019710	0.065610	0.045359

Phacochoerus Lower tooth row parameters (mm)

number Area P4/M

15 0.105
15 0.097

Table 12. Potamochoeroides, Potamochoerus and Phacochoerus lower tooth row parameters.

Potamochoeroides Lower M1 (mm)

number	length	breadth	area
M302	14.8	12.6	186.48
M8367	15.2	13.6	205.36
M2015	14.3	12.2	174.46
M2017	15.3	12.8	195.84
M2081	15.6	12.9	201.24
M2081	14.7	12.8	188.16
M310	14.5	13.8	200.1
M1828	15.5	13.1	203.05
M2054	14.9	13.9	207.11
M384	15.4	12.2	187.88
M340	14.8	12.8	189.44
M338	15.7	13.2	207.24
M8369	16.2	12.9	208.98
M2053	14.8	13.7	202.76
M2061	15.6	11	171.6
M8381	15.3	14.4	220.32
M8396	15.2	13.8	209.76
M2060	15	14.2	213
Max	16.2	14.4	220.32
Min	14.3	11	171.6
Mean	15.15	13.10555	198.4877
Std.dev.	0.462180	0.808614	12.74612

Potamochoerus Lower M1 (mm)

number	length	breadth	area
8	14.05	12.15	170.7
8	14.4	11.5	165.6
9	17.85	13.55	241.87
9	17.8	13.9	247.42
5	15.95	13.35	212.93
4	13.55	11.6	157.18
4	13.7	12.06	172.62
Max	17.85	13.9	247.42
Min	13.55	11.5	157.18
Mean	15.32857	12.66428	195.4742
Std.dev.	2.738812	0.889508	35.15400

Phacochoerus Lower M1 (mm)

number	length	breadth	area
12	12.7	10.5	133.35
12	12.5	10.7	133.75

Table 13. Potamochoeroides, Potamochoerus and Phacochoerus lower M1 measurements.

Potamochoeroides Lower M2 (mm)

number	length	breadth	area
M302	20.3	17.2	349.16
M8371	21.1	17.1	360.81
M1839	19.8	16.4	324.72
M1889	20.9	17.7	369.93
M1886	21.2	12	254.4
M8366	21.7	18.3	397.11
M339	21.5	18.4	395.6
M8367	22.1	17.7	391.17
M2017	20.1	17.1	343.71
M2081	20.9	17	355.3
M310	21.4	18.2	389.48
M1828	21.5	19.3	414.95
M8373	20.5	16.7	342.35
M2054	22.6	18.5	418.1
M307	20.6	19.2	395.52
M1882	18.8	17.6	330.88
M384	22.1	17	375.7
M338	20.3	17	345
M8369	20.9	16.9	353.21
M8365	19.2	16.6	318.72
M8365	19	16.5	310.5
Max	22.6	19.3	418.1
Min	18.8	12	254.4
Mean	20.78571	17.25714	359.0152
Std.dev.	0.999183	1.436785	38.15083

Potamochoerus Lower M2 (mm)

number	length	breadth	area
8	17.85	16.9	301.66
8	18.95	16.9	320.25
9	24.4	19.1	466.04
9	22.7	19.5	442.65
5	20.8	18.65	384.19
4	15.4	14.7	226.38
4	17.1	15.1	258.21
Max	24.4	19.5	466.04
Min	15.4	14.7	226.38
Mean	19.37142	17.26428	342.7683
Std.dev.	2.952463	1.765283	84.33041

Phacochoerus Lower M2 (mm)

number	length	breadth	area
12	19.2	11.5	220.8
12	18.9	11.4	213.46
13	18.8	13.1	246.28
13	18.7	12.95	242.16
14	18.4	13.45	247.48
14	17.5	14.8	259
23	17.45	12	209.4
23	16.55	12.1	200.25
Max	19.2	14.8	259
Min	16.55	11.4	200.25
Mean	18.1875	12.6625	230.1037
Std.dev.	0.859778	1.070263	19.88982

Table 14. Potamochoeroides, Potamochoerus and Phacochoerus lower M2 measurements.

Potamochoeroides Lower M3 (mm)

number	length	breadth	area	Lt/Br	Ht	Ht/Lt
M302	45.7	20.1	918.57	2.27	12.95	0.283
M8217	45.4	18.1	821.74	2.5		
M8377	51.7	19.9	1028.83	2.6		
M8895	42.8	19.3	826.04	2.2		
M1892	42.2	20.3	856.66	2.07	19.85	0.47
M311	49.8	22.7	1130.46	2.19		
M1889	40	19.9	796	2.01		
M1886	47	20.5	963.5	2.29		
M8366	44.1	19.8	873.18	2.23		
M2024	51.8	22.8	1181.04	2.27	16.25	0.313
M1890	38.9	19.7	766.33	1.97		
M339	47.3	21.2	1002.76	2.23		
M8367	43.3	20.1	870.33	2.15		
M2013	42.4	20.2	856.48	2.1		
M2056	45.3	19.4	896.94	2.33	17.8	0.392
M8376	39.2	20.4	799.68	1.92	21.65	0.552
M2081	51.8	20.6	1067.8	2.5	14.85	0.286
M309	47.8	23.4	1118.52	2.04		
M1882	47.2	19.9	939.28	2.37		
Max	51.8	23.4	1181.04	2.6	21.65	0.552
Min	38.9	18.1	766.33	1.92	12.95	0.283
Mean	43.45789	20.43684	932.3231	2.223157	17.225	0.382666
Std.dev.	3.961168	1.257487	120.7330	0.180322	2.934528	0.100431

Table 15a. Potamochoeroides lower M3 measurements.

Potamochoerus Lower M3 (mm)

number	length	breadth	area	Lt/Br	Ht	Ht/Lt
8	29.75	16.7	496.82	1.78	9.5	0.319
8	28.6	17.05	487.63	1.68	11.25	0.393
4	35.2	19	668.8	1.85	11.2	0.318
4	34.1	18.8	641.08	1.81	13.1	0.385
Max	35.2	19	668.8	1.85	13.1	0.393
Min	28.6	16.7	487.63	1.68	9.5	0.318
Mean	31.9125	17.8875	573.5825	1.78	11.2625	0.35375
Std. dev	2.794721	1.022481	82.01005	0.062849	1.273467	0.035365

Phacochoerus Lower M3 (mm)

number	length	breadth	area	Lt/Br
PAB2	49.9	13.65	681.13	3.65
PAB2	49.05	14	686.7	3.5
PAB1	45.55	12.1	551.15	3.76
PAB1	47.4	12.1	573.54	3.91
15	60.1	13.7	823.37	4.39
15	59.1	13.65	806.71	4.33
14	50.9	16.1	819.49	3.16
14	50.75	15.9	806.92	3.16
23	45.6	11.85	540.36	3.19
23	44.2	12.4	548.08	3.56
11	58.05	14.25	827.21	4.07
11	60.1	13.65	820.36	4.4
Max	60.1	16.1	827.21	4.4
Min	44.2	11.85	540.36	3.16
Mean	51.725	13.6125	707.085	3.756666
Std. dev.	5.757404	1.327297	118.8940	0.448559

Table 15b. *Potamochoerus* and *Phacochoerus* lower M3 measurements.

Notochoerus Upper and Lower Jaw measurements (mm)

Maxillary

M1

number	length	breadth
M324	23.5	18.8

M2

number	length	breadth
M368	27.1	25.2
M369	28.7	24.6

Lower Jaw

M1

number	length	breadth
M357	26.1	14.05

M3

M2077	100	22.7
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Table 16. *Notochoerus capensis* dentition measurements.

MAXILLARY

<u>Left</u>	<u>Right</u>
M316 e	M303 u
M317 w	M318 w
M346 e	M319 e
M347 e	M320 e
M352 e	M321 u
M1391 w	M322 u
M1400 e	M330 e
M1573 u	M385 e
M1857 w	M1572 e
M1924 u	M1926 u
M1925 e	M1927 u
M2063 e	M1929 e
M2072 u	M1932 e
M2073 u	M2034 u
M8399 w	M2067 e
	M8400 e

MANDIBLE

<u>Left</u>	<u>Right</u>
M302 e	M309 w
M305 w	M311 e
M307 e	M1881 u
M310 e	M1886 w
M312 u	M1889 e
M339 e	M1892 e
M344 u	M2018 e
M384 u	M2024 e
M1838 u	M2056 u
M1882 u	M2263 e
M1883 w	M8217 e
M1887 e	M8367 e
M1890 e	M8368 e
M2013 e	M8370 e
M2020 e	M8371 u
M2040 e	M8377 e
M2052 w	
M2081 u	
M8366 e	
M8376 u	
M8397 e	
M8398 w	
M8895 e	

u - unerupted, e - fully erupted, w - well worn.

Table 17. Wear categories of *Potamochoerus* maxillary and mandibular M3 specimens.

APPENDIX 1

Dental metrics for all specimens of African suid species measured by Harris and White (1979).

[illegible]

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Author: Bender Patrick Alan.

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