



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

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**NEW SKULLS OF *KOLPOCHOERUS PHACOCHOEROIDES* (SUIDAE,  
MAMMALIA) FROM THE LATE PLIOCENE OF AHL AL OUGHLAM,  
MOROCCO**

by

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

**Key-words:** Africa, Pliocene, Pleistocene, Suidae, Mammalia, *Kolpochoerus*, cladistics

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## INTRODUCTION

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

In 1993, I published a description of the material of *K. phacochoeroides* available at that time. The amount of fossils recovered from this site has greatly increased since then, and

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

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

## SYSTEMATIC PALEONTOLOGY

Genus *Kolpochoerus* van Hoepen & van Hoepen, 1932

*Mesochorus* Shaw & Cooke, 1941

*Omochoerus* Arambourg, 1943

*Promesochorus* Leakey, 1967

*Ectopotamochoerus* Leakey, 1967

*Type-species* : *K. sinuosus* van Hoepen & van Hoepen, 1932

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

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

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

### Currently recognised species

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

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

### Sexual dimorphism in *Potamochoerus*

Among the above-mentioned species, the best-known form is *K. heseloni*, followed by *K. afarensis*, *K. paiceae* and *K. majus*, while the remaining 3 species are known only by teeth. However, almost all known *K. heseloni* skulls are of male individuals, while *K. paiceae* is known only by female skulls. In order to limit the effects of this drawback on the comparisons, I have tried to evaluate the sexual dimorphism in *Potamochoerus*, the only close relative of the fossil genus which could be illustrated by enough specimens (16 females and 18 males, all fully adult, from the MNHNP).

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

***Table 1 about here***

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

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

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

**The *Kolpochoerus* from Ahl al Oughlam**

*Kolpochoerus phacochoeroides* (THOMAS, 1884)

*Sus phacochoeroides* Thomas, 1884: 10

*Holotype*: mandible fragment from the limestones of Aïn el Bey, Algeria (Thomas, 1884, pl.10, fig. 1-2). MNHNP, N° AFN-1. Besides Ahl al Oughlam, it is not known from any other locality.

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

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

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

### ***Figure 1 about here***

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

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

The maxilla forms a long canine sheath along the tooth but this sheath is antero-posteriorly short, being little expanded behind the alveolus. Along its dorsal part, the crest

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

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

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

As a consequence of the shortness snout, the infra-orbital foramen is located above M2, whereas it is above M1 in *K. majus* (Asbole), *K. paiceae* (Hendey & Cooke 1985, Fig.2), late *K. heseloni* (Peninj), and in the living forms.

In the males from Ahl al Oughlam, although the morphology is that of their sex, the degree of inflation of the zygomatic arches is smaller than in the evolved form of *K. heseloni*, and even than on the female Peninj skull, being more similar to *Hylochoerus*. The maximum thickness of the zygomatic inflation is 86 mm on KNM-ER-788, but only 42 mm on AaO-



4565, 41 mm on AaO-3655, and 46 mm on AaO-3656. As in the modern forms, the anterior borders of the zygomatic arches, when seen from above, are transversal, whereas they slant clearly posteriorly in the female, as in all females of *Kolpochoerus*. Lateral inflation is poor in all females, except in the Peninj skull, the only well-preserved female skull of *K. heseloni*.

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

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

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

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

### ***Table 2 about here***

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

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

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

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

**Table 3 about here**

**Figure 2 about here**

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

shorter, while that between I3 and C is longer. Skull L6-10 of *K. majus* from Bodo, and *K. paiceae*, have no I3s. I2 and I3 are normally absent in *Hylochoerus*, and I1 is often missing as well.

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

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

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

#### **Table 4 about here**

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

premolars, and *Hylochoerus-Phacochoerus*, with premolars so reduced that they become spared by wear.

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

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

**Figure 3 about here**

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

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

**Table 5-6 about here**

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

The morphology of M3 is homogeneous, the smallest and largest teeth differing mostly in the number of talon pillars. They are rather hypsodont, more so than those of *K. heseloni* from Omo member G, and more like those of the KBS member of Koobi Fora. The enamel is never as thick as in some Omo-G specimens, and is certainly thinner on the average. The main and secondary pillars have the same general pattern as in *K. heseloni* (Harris & White 1979: 39-40), but are better isolated in their apical portion. This combination of thin enamel and isolated pillars prevents the formation of flat areas of the occlusal surface consisting only of enamel, as found in slightly worn teeth of *K. heseloni*. An accessory pillar usually blocks the lingual valley between the first and second pairs of pillars, but the corresponding labial valley is wide. There is a marked tendency for the accessory pillars of the talon to subdivide above the base, so that they are hard to count objectively. The shortest and most simple tooth (AaO-906) has but about 6 pillars distal to the second pair, but this number may reach almost 20 in the longest M3 (AaO-3521) which can be compared, in size and morphology, to advanced members of the *K. heseloni* lineage (e.g. KNM-ER-788: Harris & White 1979, fig.65-66).

As described by Harris & White (1979: 40-41), the M3s of *K. majus* have a main lingual talon pillar. In the simplest teeth of this species (female skulls ASB-198-2 from Asbole; L6-10 from Bodo), only 2 or 3 more labial pillars are added labially to build up the talon, but more complex examples, such as ASB-169 and ASB-200 from Asbole, have many more secondary pillars, some of them circling lingually the main talon pillar. In every case, the furrows on the main trigon pillars are shallow, so that these pillars have a more rounded outline than in *K. phacochoeroides* and *K. heseloni*, where they are usually more X- or H-shaped. Still, distinction of isolated teeth is certainly not straightforward.

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

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

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

#### ***Tables 7-9 about here***

The lower premolars are very characteristic, being rounded rather than rectangular, and with a strong size gradient. The p2 is a minute tooth, definitely shed in some old specimens. The p3 has a thick ovoid outline and no central constriction (in contrast to all other species of *Kolpochoerus*). It is clearly smaller, relative to the width of m2 used as a proxy for overall size, than in *K. heseloni* (Fig. 4). There may be a weak anterior accessory cusp. The p4 has the same thick rounded ovoid outline as p3, with a maximum width at talonid level. The talonid is short, and its components, even in early wear, are transversally set, mainly because of a strong lingual buttress, which often becomes an isolated pillar. Distally, a strong labial buttress also supports the central talonid pillar. The main cusp is conical, but may also be buttressed on either the labial or lingual sides. Mesially, it quickly narrows, usually without any anterior accessory cusp. In any case, as in *K. afarensis*, this mesial part is never expanded transversally, in sharp contrast to *K. heseloni* and especially *K. majus*, where this tooth is much more rectangular.

#### ***Figures 4-5 about here***

On m3, the double median pillars between the second main pair and the "talonid", which is a characteristic feature of other species of *Kolpochoerus*, is seldom seen here, and is usually replaced by a single flattened median pillar. It is normally followed by a 3<sup>rd</sup> pair,

where symmetry is preserved, then by one or two median pillars, and by a complex of pillars where symmetry is lost. Comparative measurements are shown in Fig. 5.

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

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

**Table 10 here**

### **Phylogeny of *Kolpochoerus***

Although several recent papers deal with Plio-Pleistocene African suids, the question of the inter-relationships of the various fossil (*Nyanzachoerus*, *Notochoerus*, *Kolpochoerus*, *Metridiochoerus*) and living (*Potamochoerus*, *Hylochoerus*, *Phacochoerus*) genera has seldom been addressed in detail. It is generally agreed that *Nyanzachoerus* gave rise to *Notochoerus*, *Metridiochoerus* to *Phacochoerus*, and that *Potamochoerus*, *Hylochoerus* and *Kolpochoerus* are closely related, but the consensus ends up here. Leaving aside the former two genera, which belong to the Tetraconodontinae, a group of African Suidae remains. *Metridiochoerus*, which should include *Phacochoerus* to form a natural group (but with the latter name having priority), appears in the fossil record soon after the earliest definite member of the *Kolpochoerus* group, *K. afarensis* (Harris & White, 1979; Harris, 1983). It is therefore likely that it belongs to a different clade (Pickford, 1993, fig.13) and *Metridiochoerus* will not be considered here, as a detailed phylogeny of all African suids is beyond the scope of this paper. I shall only briefly discuss further down the cladogram of Bender (1992). Recent molecular analyses (Gongora et al., 2004), unfortunately, did not

consider *Hylochoerus*, and therefore shed no new light on the interrelationships of the African forms.

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

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

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

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

This cladogram incorporates more features and more taxa than a previous version (Geraads 1993). Some of the characters used in 1993 have not been retained in the present analysis, mainly because a better evaluation of intra-specific variability prevented clear



distinction of character states. The main difference in the resulting cladogram is that *K. afarensis*, which appeared as close to *Potamochoerus* (as also accepted by Cooke, 1997), now returns to *Kolpochoerus*. The main reason for the former placement was the ventrally directed upper canine; I have not retained this character because it is known on a single female specimen.

**Tables 11-12 about here**

**Figure 6 about here**

These African taxa are defined by a broader forehead and a more anterior canine relative to the cheek-teeth. These characters, of course, are unknown in *K. deheinzeli*. I take *Potamochoerus* as the sister taxon of a large group including all other species of *Kolpochoerus* and *Hylochoerus*. This large group can be called *Kolpochoerus*; no synapomorphy supports the inclusion of *K. deheinzeli* in it (and none was put forward by Brunet & White 2001). *Kolpochoerus*, as here understood, is defined by a concave cranial profile, a deep zygomatic shelf, a more extensive pneumatization (as in *Propotamochoerus*), a mesio-lingual cusp on P3, and two pillars between the second and third lobes of m3. *Kolpochoerus afarensis* arises at the base of this group, but these features bar it from the ancestry of the bush pig. More derived *Kolpochoerus* have a convex parietal profile, a more oblique auditory duct, the occipital condyles higher above the tooth-row, a longer ante-canine part, reduced snout muscle scars, a verrucose lower canine, a larger upper canine with a trifoliate section, and longer third molars. In agreement with the chronology of the fossil record, the early version of *K. heseloni* branches next, but is followed by *K. majus*, the earliest record of which is only at Konso-Gardula (Asfaw & al. 1992). The reduction of the supra-canine flange marks a further step in the loss of fossorial habits. The late version of *K. heseloni*, *K. paiceae*, and *K. phacochoeroides* + *Hylochoerus* form an unresolved trichotomy; they all have reduced anterior premolars, longer M3/m3s, and more complex tubercles. The latter grouping is somewhat unexpected, but is defined by a reduced supra-canine flange, an occipital condyle not so high above the tooth-row, reduced upper central incisors, short premolars, and only one pillar between the second and third lobes of m3. *Hylochoerus* is mostly defined by a large number of reversals.

This cladogram can be compared with that of Bender (1992), who made a valuable attempt to propose a cladogram of African non-tetraconodont suids. He suggested that *Metridiochoerus-Phacochoerus* are the sister-group of *Hylochoerus-Kolpochoerus*, this clade

of 4 taxa being the sister-group of *Potamochoerus-Potamochoeroides*. However, as this cladogram was not calculated by parsimonious analysis, the features defining each node may not be true synapomorphies. Those defining the *Hylochoerus-Kolpochoerus* clade are roughly the same as I have accepted here. On the other hand, those defining the *Potamochoerus-Potamochoeroides* clade are either primitive (Bender's character 1), or shared by many other African suids (2-5). Of the characters said to define its sister-group of 4 taxa, I recognize only the size of the upper canine as valid. I do not see any major difference in the direction of the upper canine or shape of the lower one, and the others are valid only for the most derived members of this group. Still, his cladogram has the merit of incorporating all non-tetraconodont genera, including those of the *Metridiochoerus* group that I have not considered here

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

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

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### **Captions to Figures**

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

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

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

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

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

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

|  | mean ♀<br>N = 16 | mean ♂<br>N = 18 | ♀ in % ♂                  |
|--|------------------|------------------|---------------------------|
| condylo-basal length                   | 298.9            | 314.8            | 94.9 **                   |
| length from back of condyle to M3      | 95.2             | 97.0             | 98.1                      |
| length from back of M3 to front of I1  | 198.8            | 205.5            | 96.7                      |
| length from orbit to front of canine   | 153.8            | 167.3            | 91.9 **                   |
| length from front of P2 to front of I1 | 92.7             | 102.3            | 90.6 **                   |
| bizygomatic width                      | 158.9            | 171.2            | 92.8 **maximum bi-orbital |
| width                                  | 101.0            | 108.7            | 93.0 *                    |
| minimum bi-orbital width               | 71.6             | 76.8             | 93.2 **                   |
| minimum width between temporal lines   | 36.4             | 39.1             | 93.1                      |
| width over occipital crest             | 78.4             | 85.4             | 91.8                      |
| minimum occipital width                | 63.0             | 67.0             | 94.0                      |
| width over external auditory meatus    | 118.5            | 129.9            | 91.2 **                   |
| occipital height                       | 82.1             | 89.5             | 91.8 *                    |

\* = significant difference ; \*\* = highly significant difference

TABLE 1 – MEASUREMENTS OF MODERN *POTAMOCHOERUS* SKULLS



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

TABLE 2. COMPARATIVE MEASUREMENTS OF *KOLPOCHOERUS* SKULLS. IN PART FROM HARRIS (1983) AND HENDEY & COOKE (1985).



|                           | width over<br>canine alveoli | minimum<br>width | sagittal<br>length |
|---------------------------|------------------------------|------------------|--------------------|
| <i>K. phacochoeroides</i> |                              |                  |                    |
| AaO-5                     | 116                          | 85               | 123                |
| AaO-37                    | 111                          | 84               |                    |
| AaO-72                    | 99+                          | 86               | 100                |
| AaO-134                   | 74                           | 60               | 96                 |
| AaO-296                   | 72                           | 63               | 86+                |
| AaO-361                   |                              | 55               | 82                 |
| AaO-2065                  | 115                          | 93               | 105                |
| AaO-2240                  | 80                           | 64               | 80                 |
| AaO-3478                  | 110                          | 80               | 102                |
| <i>K. afarensis</i>       |                              |                  |                    |
| AL-134                    | 74                           | 60               | 96                 |
| AL-296                    | 72                           | 63               | 86+                |
| AL-361                    |                              | 55               | 82                 |
| <i>K. majus</i>           |                              |                  |                    |
| ASB-37                    | 111                          | 84               |                    |
| ASB-44                    | 113                          | 93               | 111                |
| ASB-172                   | 99+                          | 86               | 100-               |
| Bodo-255-2                | 139                          | 106              | 133                |
| <i>K. paiceae</i>         |                              |                  |                    |
| Elandsfontein 16675       | 102                          | 86               | 106                |
| Elandsfontein 20928       | 110                          | 95               | 106                |
| Skruverug                 | 93.5                         | 73.5             | 101                |
| <i>K. heseloni</i>        |                              |                  |                    |
| KNM-ER-432                | 118                          | 90               | 127                |
| KNM-ER-433                |                              | 78               | 115                |
| KNM-ER-946                | 131                          | 102              | 143                |
| KNM-ER-1314               | 102                          | 86               | 116                |
| KNM-ER-2701               | 73                           | 62               | 112                |
| KNM-ER-4304               | 117                          | 86               | 133                |
| Olduvai FLK               | 92                           | 73               | 115                |
| Olduvai MMK               | 136                          | 92               | 139                |
| Omo K11-71-114            | 80                           | 65               | 100                |
| Omo L635-1                | 84++                         | 65++             | 120?               |
| Omo L64-5                 | 112                          | 85               | 114                |
| Omo L895-2                | 95                           | 74               |                    |
| Omo O27_3-67              | 127?                         | 97               | 145                |
| Omo O75-69-4909           | 68                           | 54               | 103                |
| Omo O75N-71-127           |                              | 69               | 95                 |
| <i>Kolpochoerus</i> sp.   |                              |                  |                    |
| Ubeidiyeh                 |                              | 95               | 160?               |

TABLE 3 MEASUREMENTS OF THE MANDIBULAR SYMPHYSIS IN *KOLPOCHOERUS*

|          |   | antero-posterior | dorso-ventral |
|----------|---|------------------|---------------|
| AaO-8    | ○ | 33.5             | 26            |
| AaO-9    | ○ | 29.2             | 24            |
| AaO-23   | ○ | 34               | 25.5          |
| AaO-239  | ○ | 34               | 24            |
| AaO-267  | ○ | 58.5             | 39            |
| AaO-2000 | ○ | 28.2             | 25.5          |
| AaO-3656 | ○ | ca. 53           | ca. 40        |
| AaO-4456 | ○ | 61               | 40            |

TABLE 4. ANTERO-POSTERIOR AND DORSO-VENTRAL DIAMETERS OF *K. PHACOCHOEROIDES* UPPER CANINES

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

TABLE 5. MEASUREMENTS OF *K. PHACOCHOEROIDES* UPPER TOOTH SERIES

| Isolated teeth | P3   |      |          | P4   |      |
|----------------|------|------|----------|------|------|
|                | A-P  | TR   |          | A-P  | TR   |
| AaO-3482       | 11.3 | 10.2 | AaO-1382 | 10.5 | 13.1 |
| AaO-3511       | 11.3 | 10.8 | AaO-3152 | 11   | 12   |
| AaO-4369       | 11.3 | 11.3 | AaO-3560 | 11.2 | 14.2 |
| AaO-4355       | 11.5 | 11.2 | AaO-3562 | 11.2 | 13.4 |
| AaO-3563       | 11.8 | 11.1 | AaO-1484 | 11.3 | 14   |
| AaO-1381       | 12   | 11.5 | AaO-4351 | 11.4 | 13.2 |
| AaO-4409       | 12.2 | 11.4 | AaO-4358 | 11.4 | 13.6 |
| AaO-919        | 12.3 | 12.8 | AaO-4097 | 11.6 | 13.8 |
| AaO-4096       | 12.3 | 11.4 | AaO-4346 | 11.7 | 13.5 |
| AaO-4347       | 12.3 | 11.3 | AaO-1490 | 12   | 14.2 |
| AaO-4350       | 12.3 | 11.7 | AaO-4403 | 12.1 | 14.8 |
| AaO-3513       | 12.4 | 11.6 | AaO-4356 | 12.2 | 14.3 |
| AaO-3512       | 12.5 | 11   | AaO-1380 | 12.4 | 15   |
| AaO-3564       | 12.5 | 11.7 | AaO-918  | 12.6 | 15.4 |
| AaO-350        | 12.6 | 10.6 | AaO-55   | 12.7 | 14.7 |
| AaO-349        | 12.7 | 11   | AaO-53   | 12.8 | 14.4 |
| AaO-1493       | 12.7 | 11.3 | AaO-56   | 12.8 | 14.8 |
| AaO-3149       | 12.7 | 13   | AaO-57   | 12.8 | 13.8 |
| AaO-4406       | 12.9 | 12.5 | AaO-2599 | 12.8 | 14.3 |
| AaO-58         | 13   | 11.6 | AaO-54   | 12.9 | 15.2 |
| AaO-1494       | 13   | 14   | AaO-1482 | 13   | 16.7 |
| AaO-2600       | 13   | 13   | AaO-4407 | 13   | 16.8 |
| AaO-351        | 13.3 | 10.3 | AaO-2598 | 13.1 | 15   |
|                | M1   |      | AaO-3565 | 13.2 | 16.7 |
|                | A-P  | TR   | AaO-3558 | 14.3 | 17   |
| AaO-4094       | 15.8 | 16   | AaO-3147 | 14.5 | 16.1 |
| AaO-3578       | 16   | 14   |          | M3   |      |
| AaO-3504       | 16.1 | 15   |          | A-P  | TR   |
| AaO-4364       | 16.3 | 15.9 | AaO-906  | 37.6 | 23   |
| AaO-2594       | 16.5 | 13.1 | AaO-3589 | 37.8 | 21.2 |
| AaO-3577       | 16.6 | 14.3 | AaO-1462 | 38.5 | 24.9 |
| AaO-3561       | 16.7 | 13.5 | AaO-3502 | 40   | 22.1 |
| AaO-3567       | 16.7 | 15.1 | AaO-4400 | 40   | 22.1 |
| AaO-924        | 16.9 | 15   | AaO-3583 | 40   | 23.1 |
| AaO-2089       | 16.9 | 15.8 | AaO-4087 | 41.5 | 21.3 |
| AaO-928        | 17.1 | 15   | AaO-1479 | 41.5 | 25   |
| AaO-42         | 17.2 | 16   | AaO-1388 | 41.7 | 23.5 |
| AaO-26         | 17.5 | 14.8 | AaO-4088 | 41.8 | 23.2 |
| AaO-2054       | 17.8 | 15.7 | AaO-3586 | 42.2 | 21.6 |
|                | M2   |      | AaO-1478 | 43.1 | 23.5 |
|                | A-P  | TR   | AaO-4090 | 44.2 | 23   |
| AaO-4353       | 20.5 | 20   | AaO-3519 | 45   | 23.1 |
| AaO-4092       | 21.3 | 20.5 | AaO-3480 | 45.8 | 24.2 |
| AaO-1489       | 21.5 | 21.8 | AaO-2587 | 46   | 23.1 |
| AaO-4093       | 21.7 | 20.7 | AaO-4341 | 46.4 | 24.5 |
| AaO-2592       | 21.8 | 17.5 | AaO-3581 | 46.8 | 24.5 |
| AaO-3481       | 22   | 21.1 | AaO-2586 | 47.4 | 25   |
| AaO-4343       | 22   | 21.1 | AaO-1411 | 47.6 | 25.4 |
| AaO-2590       | 22.3 | 20   | AaO-2585 | 48.5 | 24.6 |
| AaO-2591       | 22.3 | 18.2 | AaO-3580 | 49.5 | 27.7 |
| AaO-4401       | 22.8 | 21.8 | AaO-3521 | 52.5 | 25.7 |
| AaO-40         | 23.1 | 21.3 |          |      |      |
| AaO-2589       | 24   | 21.8 |          |      |      |

TABLE 6. MEASUREMENTS OF *K. PHACOCHOEROIDES* UPPER CHEEK TEETH

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

TABLE 7. MEASUREMENTS OF *K. PHACOCHOEROIDES* LOWER CANINES

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

TABLE 8. MEASUREMENTS OF *K. PHACOCHOEROIDES* LOWER TOOTH SERIES

| isolated<br>teeth |      |      |          |      |      |
|-------------------|------|------|----------|------|------|
|                   |      |      | p3       | m2   |      |
| AaO-3510          | 10.3 | 7.9  | AaO-3570 | 22   | 18.3 |
| AaO-3503          | 10.6 | 7.8  | AaO-3582 | 22   | 18.1 |
| AaO-1483          | 10.8 | 9.2  | AaO-3568 | 22.4 | 16.8 |
| AaO-1414          | 10.9 | 8.4  | AaO-353  | 23   | 16.9 |
| AaO-3532          | 11.3 | 8.5  | AaO-913  | 23.5 | 19.5 |
| AaO-3161          | 14   | 11.9 | AaO-3505 | 23.7 | 17.8 |
| AaO-4359          | 15   | 11.4 | AaO-3571 | 24.5 | 19.6 |
|                   |      |      |          |      |      |
|                   |      |      | p4       |      |      |
| AaO-2610          | 13.2 | 10.5 | AaO-4402 | 24.5 | 18.1 |
| AaO-4098          | 13.2 | 11.1 | AaO-914  | 25.1 | 19.1 |
| AaO-2595          | 13.3 | 11.3 | AaO-4352 | 25.2 | 18   |
|                   |      |      | AaO-1491 | 25.5 | 20.2 |
| AaO-1495          | 13.5 | 11.3 |          |      |      |
|                   |      |      | m3       |      |      |
| AaO-2596          | 14   | 11.2 | AaO-352  | 42.2 | 18.9 |
| AaO-3577          | 14.1 | 11.5 | AaO-3584 | 42.3 | 18   |
| AaO-106           | 14.3 | 9    | AaO-3509 | 42.4 | 19.2 |
| AaO-2597          | 14.3 | 12.2 | AaO-3516 | 42.8 | 19.5 |
| AaO-1481          | 14.5 | 12.3 | AaO-3588 | 42.9 | 17.9 |
| AaO-3569          | 14.6 | 11.7 | AaO-1461 | 44.9 | 19.7 |
| AaO-3522          | 14.7 | 11.4 | AaO-1404 | 45   | 21.1 |
| AaO-3160          | 15.8 | 13.5 | AaO-2588 | 45.2 | 21.6 |
|                   |      |      |          |      |      |
|                   |      |      | m1       |      |      |
| AaO-314           | 15.5 |      | AaO-904  | 45.5 | 19.8 |
| AaO-3566          | 15.6 | 12.7 | AaO-3587 | 45.7 | 21.3 |
| AaO-922           | 15.9 | 12.5 | AaO-4404 | 45.7 | 20.5 |
| AaO-4348          | 15.9 | 13   | AaO-4405 | 46.8 | 19.3 |
| AaO-908           | 16   | 12.8 | AaO-1488 | 47.4 | 19.5 |
| AaO-1492          | 16.3 | 12.6 | AaO-903  | 48.4 | 20.7 |
| AaO-3523          | 16.6 | 12.4 | AaO-1465 | 49.5 | 21.7 |
| AaO-25            | 16.7 | 12.5 | AaO-1463 | 50   | 21.8 |
| AaO-1486          | 16.9 | 13.3 | AaO-3585 | 50   | 21   |
| AaO-920           | 17   | 13.4 | AaO-4086 | 59.4 | 25.4 |
| AaO-4344          | 17.3 | 13.9 |          |      |      |
| AaO-4354          | 17.8 | 13.9 |          |      |      |

TABLE 9. MEASUREMENTS OF *K. PHACOCHOEROIDES* LOWER CHEEK TEETH

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

TABLE 10. MEASUREMENTS OF *K. PHACOCHOEROIDES* METAPODIALS

|    |  |               |                        |                |             |
|----|--|---------------|------------------------|----------------|-------------|
| 0  | <b>cranial profile</b>                     | straight      | concave                |                |             |
| 1  | <b>parietal profile</b>                    | straight      | convex                 |                |             |
| 2  | <b>forehead</b>                            | narrow        | broad                  | very broad     |             |
| 3  | <b>forehead transverse profile</b>         | convex        | slightly concave       | deeply concave |             |
| 4  | <b>position of orbit</b>                   | middle of M3  | back of M3             |                |             |
| 5  | <b>level of zygomatic arch</b>             | M1            | M3                     |                |             |
| 6  | <b>zygomatic shelf</b>                     | low           | deep                   |                |             |
| 7  | <b>orientation of zygomatic arch</b>       | transverse    | slightly drooping      | drooping       |             |
| 8  | <b>pneumatization</b>                      | weak          | strong                 | very strong    |             |
| 9  | <b>snout muscle scars</b>                  | well-marked   | reduced                |                |             |
| 10 | <b>ante-canine part</b>                    | short         | medium                 | long           |             |
| 11 | <b>position of P2 relative to C</b>        | behind        | much behind            | far behind     |             |
| 12 | <b>supra-C flange</b>                      | almost absent | weak                   | strong         | very strong |
| 13 | <b>snout section</b>                       | rounded       | squarish               | square         |             |
| 14 | <b>auditory bulla</b>                      | large         | small                  |                |             |
| 15 | <b>auditory duct</b>                       | horizontal    | oblique                | very oblique   |             |
| 16 | <b>width of occipital crest</b>            | narrow        | broad                  |                |             |
| 17 | <b>position of condyle above tooth-row</b> | low           | high                   | very high      |             |
| 18 | <b>height of occipital</b>                 | low           | high                   | very high      |             |
| 19 | <b>upper canine section</b>                | trifoliate    | other                  |                |             |
| 20 | <b>enamel on upper canine</b>              | present       | absent                 |                |             |
| 21 | <b>I1</b>                                  | large         | small                  | very small     |             |
| 22 | <b>lingual cingulum on I1-I2</b>           | absent        | present                |                |             |
| 23 | <b>I3</b>                                  | present       | much reduced or absent |                |             |
| 24 | <b>P/p1</b>                                | normal        | reduced                |                |             |
| 25 | <b>P/p2</b>                                | normal        | reduced                |                |             |
| 26 | <b>P3 antero-lingual cusp</b>              | absent        | weak                   |                |             |
| 27 | <b>section of lower canine</b>             | verrucose     | intermediate           | scrofic        |             |
| 28 | <b>p3-p4</b>                               | long          | shortened              |                |             |
| 29 | <b>size of upper canine</b>                | small         | medium                 | large          |             |
| 30 | <b>length of m3/M3</b>                     | short         | medium                 | long           | very long   |
| 31 | <b>shape of tubercles</b>                  | simple        | more complex           | very complex   |             |
| 32 | <b>between 2nd and 3rd pairs of m3</b>     | one pillar    | two pillars            |                |             |

TABLE 11. CHARACTER LIST AND STATES USED IN THE CLADISTIC ANALYSIS



|                            | <b>1</b>   |            |            | <b>1 2</b> |          |  | <b>2 3 3</b> |          |          |
|----------------------------|------------|------------|------------|------------|----------|--|--------------|----------|----------|
|                            | <b>0</b>   | <b>9</b>   | <b>0</b>   | <b>9</b>   | <b>0</b> |  | <b>9</b>     | <b>0</b> | <b>2</b> |
| <i>K.phacochoeroides</i>   | 1111111211 | 0001121120 | 1200111012 | 120        |          |  |              |          |          |
| <i>K.majus</i>             | 1110011111 | 1111121210 | 0100001002 | 101        |          |  |              |          |          |
| <i>K.heselsoni</i> (early) | 1110111111 | 1122?20210 | 0??0??1001 | 111        |          |  |              |          |          |
| <i>K.heselsoni</i> (late)  | 1111111121 | 2211?20210 | 00?0?11001 | 221        |          |  |              |          |          |
| <i>K.paiceae</i>           | 111011???? | 12?11202?0 | 00?111101? | 321        |          |  |              |          |          |
| <i>K.afarensis</i>         | 1?101?1220 | ?1?20??0?? | 0??00?1200 | 001        |          |  |              |          |          |
| <i>Potamochoerus</i>       | 0010110100 | 0132010001 | 0010110200 | 000        |          |  |              |          |          |
| <i>Hylochoerus</i>         | 1022111011 | 1100000100 | 02?111?011 | 200        |          |  |              |          |          |
| <i>Propotamochoerus</i>    | 1000000110 | 0022?00011 | 0010000100 | 000        |          |  |              |          |          |
| <i>Sus</i>                 | 0000110100 | 0011020011 | 0010000?00 | 000        |          |  |              |          |          |

TABLE 12. MATRIX USED IN THE CLADISTIC ANALYSIS