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

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

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

INTRODUCTION

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

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

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

SYSTEMATIC PALAEONTOLOGY

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

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

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

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

Currently recognized species

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

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

Sexual dimorphism in *Potamochoerus*

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

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

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

Table 1. Measurements of modern *Potamochoerus* skulls.

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

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

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

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

Kolpochoerus from Ahl al Oughlam

Kolpochoerus phacochoeroides (Thomas, 1884)

Sus phacochoeroides Thomas, 1884: 10

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

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

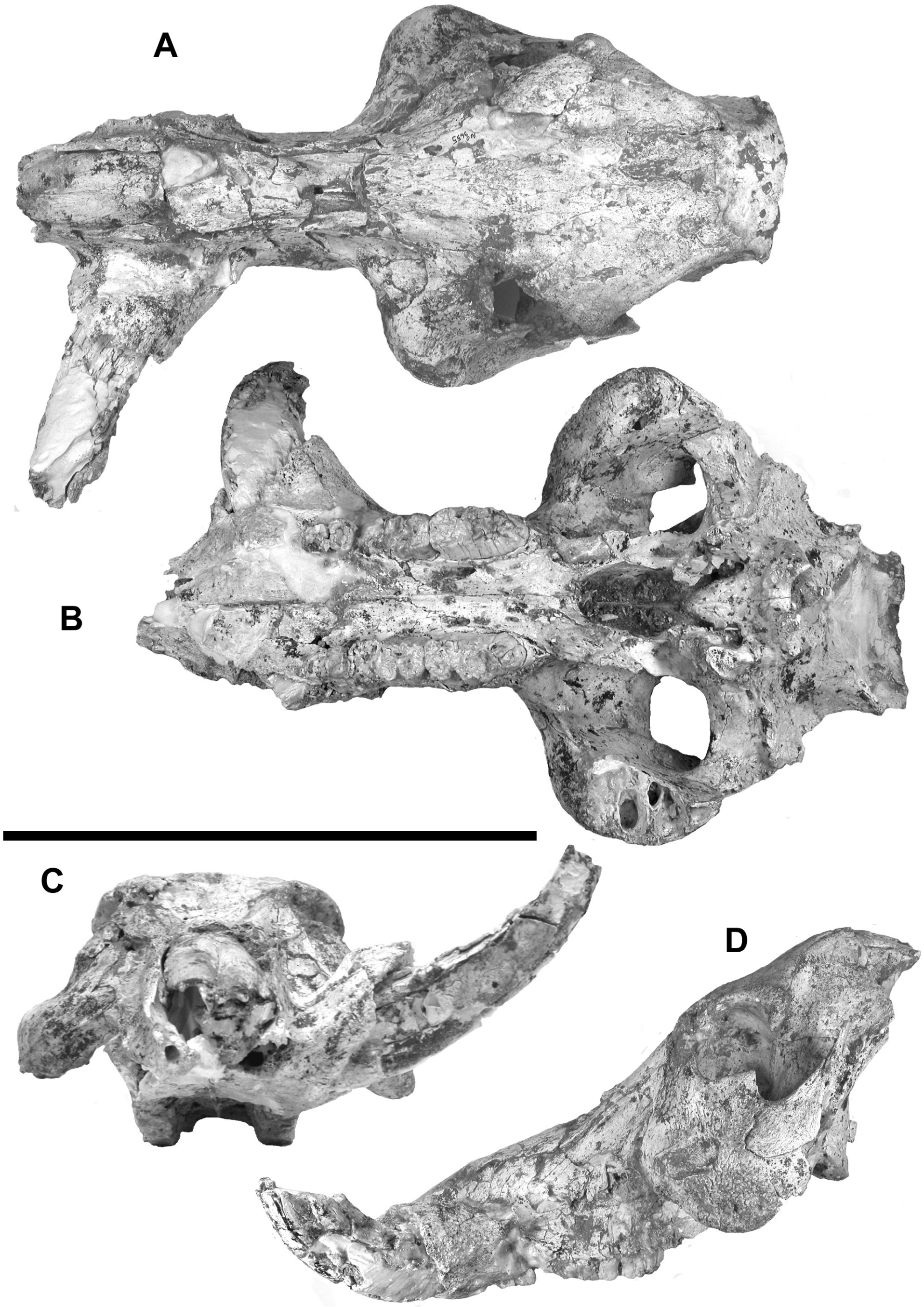

Figure 1. *Kolpochoerus phacochoeroides,* Ahl al Oughlam, AaO-3655. **A**, dorsal view; **B**, ventral view; **C**, anterior view; **D**, lateral view. Scale bar = 30 cm.

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

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

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

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

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

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

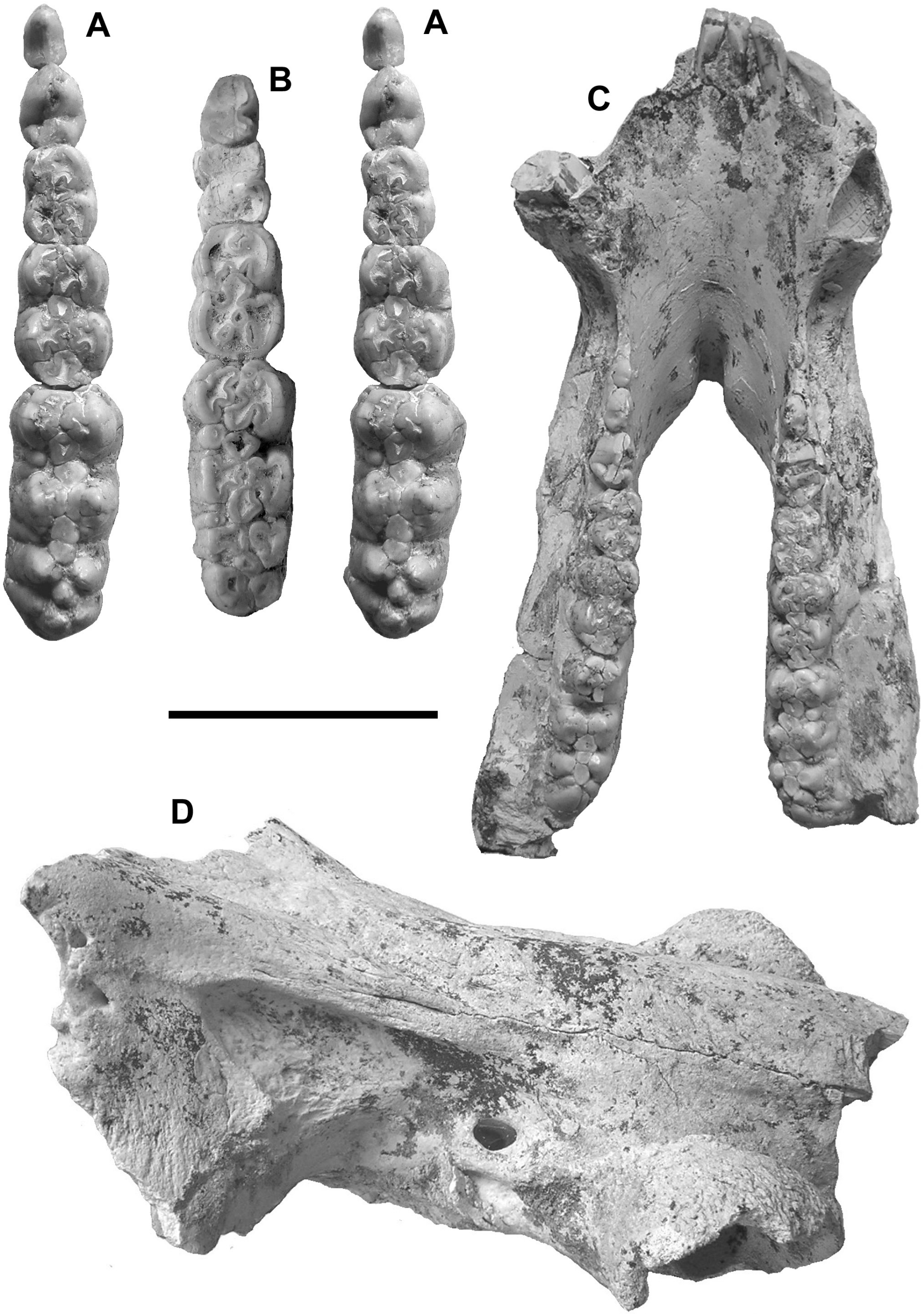

Figure 2. *Kolpochoerus phacochoeroides,* Ahl al Oughlam. **A**, AaO-141, p3–m3, occlusal view (stereo pair); **B**, AaO-2065, p4–m3, occlusal view; **C**, AaO-3478, dorsal view; **D**, AaO-4516, right antero-latero-dorsal view of muzzle. Scale bar = 5 cm for A, B; 7.5 cm for C, D.

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

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

Potamochoerus or even *K. afarensis.*

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

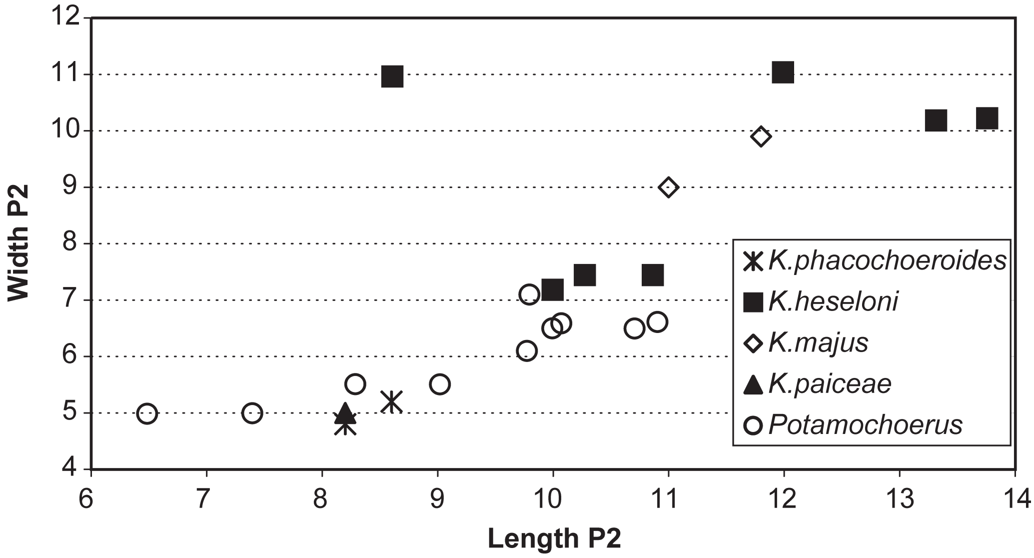

Figure 3. Plot of length *vs* width of *Kolpochoerus* upper second premolars. *Potamochoerus* from Fessaha (1999); *K. majus* from Geraads *et al.* (in press), *K. paiceae* and *K. heseloni* from Hendey & Cooke (1985).

lingual complex of cusps.

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

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

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

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

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

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

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

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

*Isolated teeth.

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

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

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

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

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

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

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

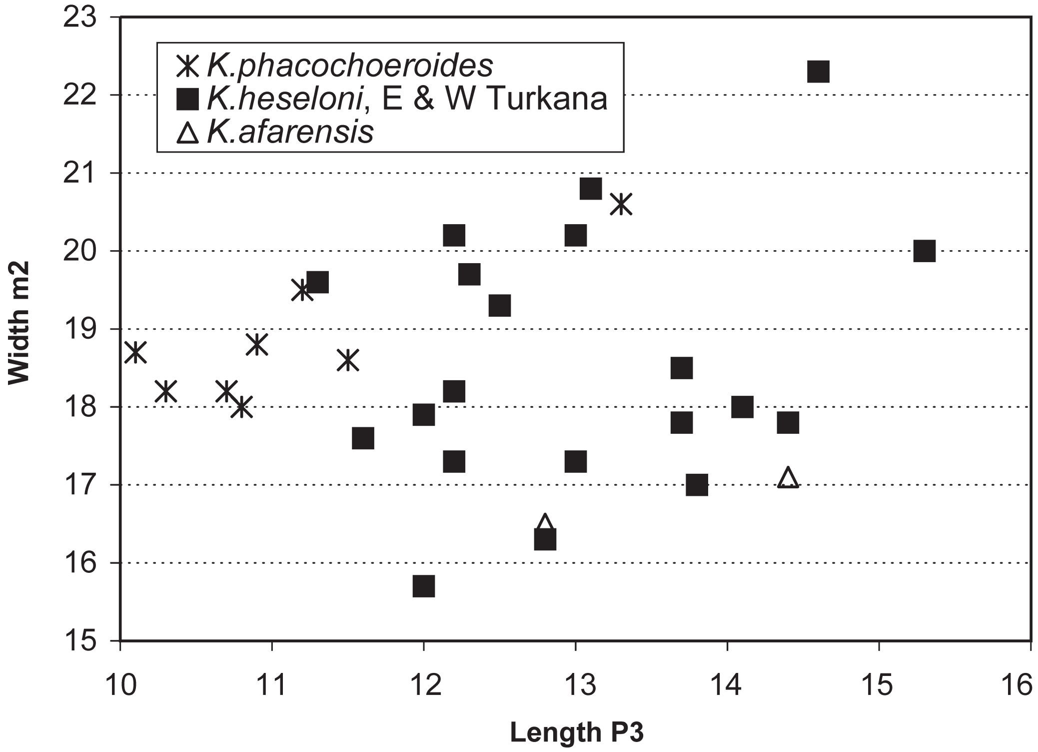

Figure 4. Plot of p3 length *vs* width of m2 (taken as a proxy for overall size) in *Kolpochoerus. K. afarensis* from Cooke (1978); *K. heseloni* from Harris (1983) and Harris *et al.* (1988).

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

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

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

Conclusion

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

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

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

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

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

*Isolated teeth.

Phylogeny of *Kolpochoerus*

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

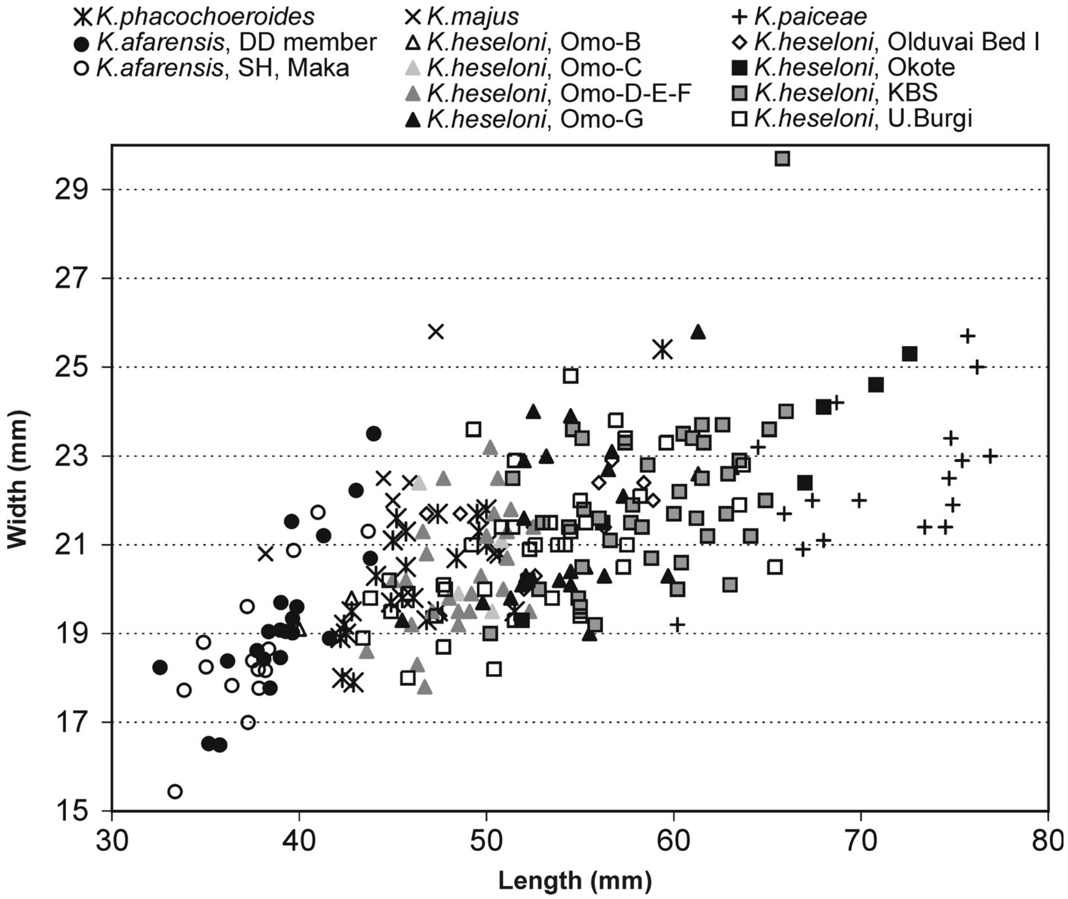

Figure 5. Plot of length *vs* width of *Kolpochoerus* lower third molars. *K. afarensis* from Hadar DD and SH members, *K. heseloni* from Omo Shungura members B-G, Olduvai, and Koobi Fora Formation members. Origin of data as for Figs 3 and 4, plus Cooke (1976) for Omo.

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

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

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

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

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

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

Quantitative characters were rather easily converted

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

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

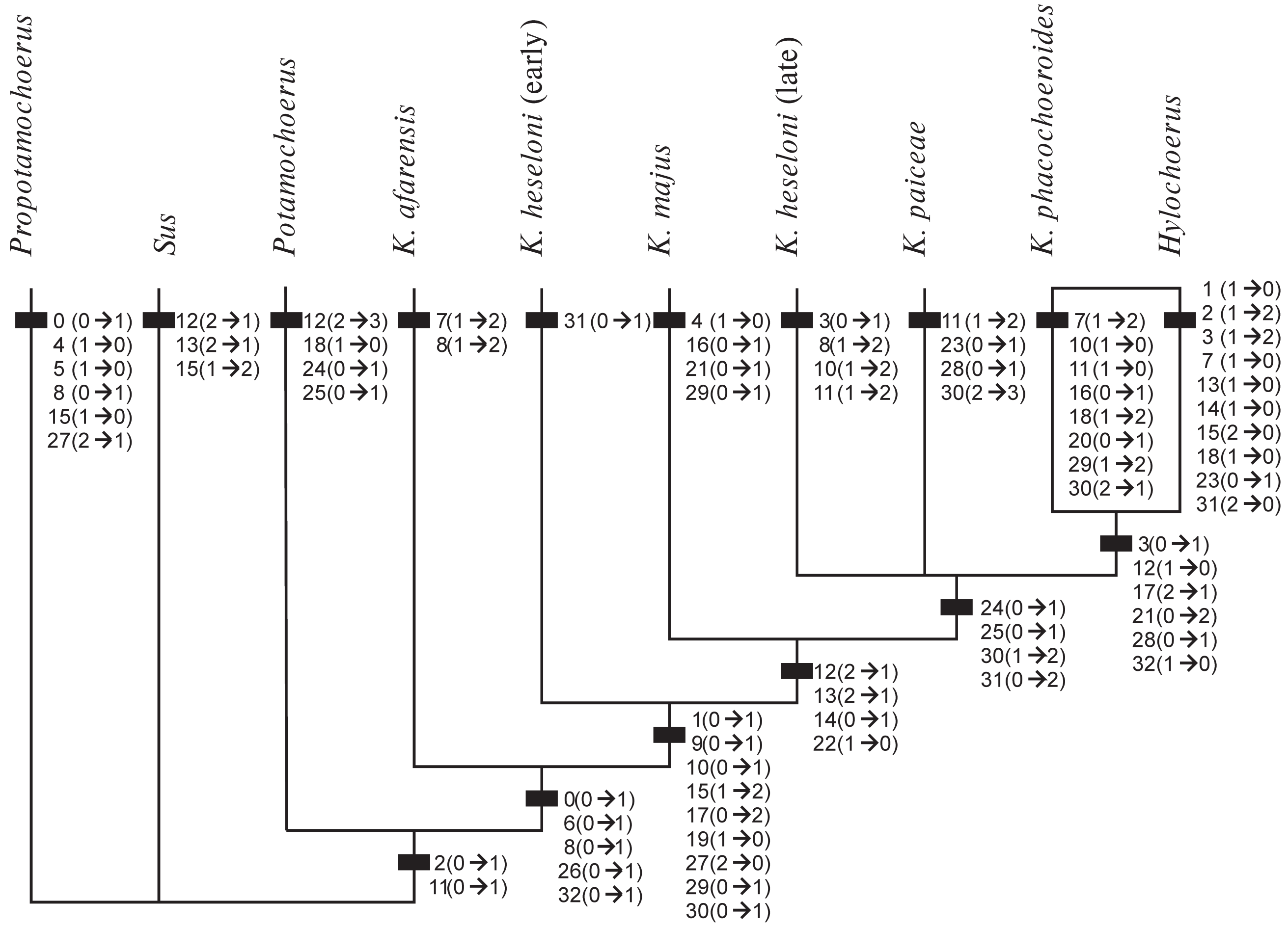

Figure 6. Cladogram of *Kolpochoerus* and related forms.

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

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

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

Table 12. Matrix used in the cladistic analysis.

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

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

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

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

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

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