

Pliocene suids from Musaitu and Dermenji, Moldova: implications for understanding the origin of African *Kolpochoerus* Van Hoepen & Van Hoepen, 1932

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ABSTRACT

Early Pliocene suids of Europe are generally rare and poorly preserved, but some exceptional fossils have been found at Roussillon, France, Villafranca d'Asti, Italy, and Kvabebi, Georgia. We here describe and interpret an almost complete skull of a small suid from Musaitu and a mandible fragment from Dermenji, Moldova, which add precious information to the data base concerning these small European Pliocene suids, here attributed to *Dasychoerus arvernensis* (Croizet & Jobert, 1828). The Moldovan fossils provide an important biogeographic link between the Western European and Asian Plio-Pleistocene suines. The Musaitu skull, in particular, shows the elongated snout, enlarged canine flanges, pneumatized zygomatic arch and low slung incisor row characteristic of the genus *Dasychoerus* Gray, 1873. This species is important because it represents the group from which the African *Kolpochoerus* Van Hoepen & Van Hoepen, 1932 lineage probably emerged. The latter group is useful for biochronology because, having arrived in Africa, where it has been called *Kolpochoerus deheinzeleni* Brunet & White, 2001 (in fact a junior synonym of *Dasychoerus arvernensis*) it evolved rapidly in dimensions and dental morphology. During the Pliocene the genus *Dasychoerus*, already adapted to tropical and sub-tropical climates, was widespread in mid-latitude Eurasia and Africa, but when much of mid-latitude Eurasia became boreal during the Plio-Pleistocene, the range of *Dasychoerus* shrank equatorwards, giving way to boreally adapted *Sus scrofa* Linnaeus, 1758 over much of its former territory, leaving a disjunct distribution of its descendants in Africa (*Hylochoerus* Thomas, 1904, possibly *Potamochoerus* Gray, 1854) and the tropical islands of the Far East (*Dasychoerus*).

KEY WORDS

Moldova,
Pliocene,
Suidae,
Dasychoerus,
Kolpochoerus,
Evolution,
Palaeobiogeography.

RÉSUMÉ

Les Suidés pliocènes de Musaitu et Dermenji, Moldavie : implications pour la compréhension de l'origine du Kolpochoerus Van Hoepen & Van Hoepen, 1932 d'Afrique.

Les suidés du Pliocène inférieur d'Europe sont généralement rares et mal préservés, néanmoins des fossiles exceptionnels ont été retrouvés à Roussillon en France, à Villafranca d'Asti en Italie et à Kvabebi en Géorgie. Nous décrivons et interprétons un crâne presque complet d'un petit suidé de Musaitu et un fragment de mandibule de Dermenji en Moldavie, attribués à *Dasychoerus arvernensis* (Croizet & Jobert, 1828). Ces fossiles ajoutent des informations précieuses à la connaissance des petits suidés européens pliocènes. Les fossiles moldaves constituent un lien biogéographique important entre les suinés plio-pléistocènes de l'Europe occidentale et ceux de l'Asie. En particulier, le crâne de Musaitu présente les caractéristiques du genre *Dasychoerus* Gray, 1873 : un museau allongé, des canines au rebord évasé, une arcade zygomatique pneumatisée et une rangée incisive basse. Cette espèce est importante car elle représente le groupe duquel la lignée africaine *Kolpochoerus* Van Hoepen & Van Hoepen, 1932 a probablement émergée. Ce dernier groupe est utile en biochronologie, parce qu'étant arrivé en Afrique où il a été nommé *Kolpochoerus deheinzeli* Brunet & White, 2001 (en fait un synonyme de *Dasychoerus arvernensis*) ses dimensions et sa morphologie dentaire ont rapidement évolué. Au cours du Pliocène, le genre *Dasychoerus*, déjà adapté aux climats tropicaux et subtropicaux, était largement répandu aux latitudes moyennes d'Eurasie et d'Afrique, mais quand les latitudes moyennes eurasiennes devinrent boréales durant le Plio-Pléistocène, son extension géographique s'est réduite vers l'équateur, laissant la place à *Sus scrofa* Linnaeus, 1758 sur une grande partie de son ancien territoire et conduisant à une répartition disjointe de ses descendants en Afrique (*Hylochoerus* Thomas, 1904, probablement *Potamochoerus* Gray, 1854) et dans les îles tropicales (*Dasychoerus*).

MOTS CLÉS

Moldavie,
Pliocène,
Suidae,
Dasychoerus,
Kolpochoerus,
évolution,
Paléobiogéographie.

INTRODUCTION

For well over a century, the origins of the African Plio-Pleistocene suid lineages remained obscure, with various authors either proposing that they emerged from a “hypothetical *Sus*-like ancestor” (Cooke & Wilkinson 1978) or simply not attempting to propose an ancestor, a history summarised by Pickford (2012, 2013a). Recently, Pickford (2012) observed that the most primitive described species of *Kolpochoerus* Van Hoepen & Van Hoepen, 1932 (*K. deheinzeli* Brunet & White, 2001) is morphometrically so close to the type material of *Dasychoerus arvernensis* (Croizet & Jobert, 1828) and other European specimens attributed to this taxon (and to *Sus minor* Depéret, 1890, another synonym of *Dasychoerus arvernensis*), that the African form should be transferred to this species. The species *Kolpochoerus millensis* Haile-Selassie & Simpson, 2012, is closely related to *Dasychoerus arvernensis*, the morphology and dimensions of its third molars overlapping those of *D. arvernensis*, but with several larger individuals. These suid species share a number of other characters including thickened mandibular bodies, low slung lower incisors, pneumatized zygomatic arches and well developed supra-canine flanges (at least in males) among others. The somewhat larger species *Kolpochoerus afarensis* Cooke, 1978 is likely a continuation of this trend towards increase in body dimensions, although some authors see in this species the origin of the *Potamochoerus* lineage (Bishop 2010; Souron *et al.* 2013).

Having arrived in Africa by dispersal from Eurasia, *Dasychoerus natrunensis* Pickford, 2012, and/or *Dasychoerus arvernensis* underwent rapid evolution in dimensions to give rise to *Kolpochoerus millensis* Haile-Selassie & Simpson, 2012, and *Kolpochoerus afarensis* Cooke, 1978, and the lineage then ex-

perienced rapid morphological and dimensional evolution of the skull and dentition to give rise to several taxa including *Kolpochoerus olduvaiensis* (Leakey, 1942), *Kolpochoerus majus* (Hopwood, 1934), *Kolpochoerus phacochoeroides* (Thomas, 1884), *Kolpochoerus paiceae* (Broom, 1931), *Kolpochoerus heseloni* (Leakey, 1943), *Kolpochoerus cookei* Brunet & White, 2001, and *Kolpochoerus phillipi* Souron, Boissérie & White, 2013 some of which developed high crowned cheek teeth. The extant genus *Hylochoerus* Thomas, 1904 (the Giant Forest Hog) probably descended from this same immigrant group.

Having diversified in Africa some kolpochoeres returned to the Middle East and Asia including *Kolpochoerus evronensis* (Haas, 1970) to Israel and *Kolpochoerus falconeri* (Lydekker, 1884) and *Kolpochoerus cautleyi* (Pilgrim, 1926) to Indo-Pakistan. The status of *Sus lydekkeri* Zdansky, 1928 (Young 1932; Dong 2008) from Choukoutien, China, needs further investigation, as its third molars and some skull characters (supra-canine flange) show resemblances to those of some species of *Kolpochoerus*, such as *K. phacochoeroides* (Thomas, 1884) *K. majus* (Hopwood, 1934), and *K. phillipi*.

Thus, any increase in knowledge about the Eurasian group from which the African *Kolpochoerus*, could have evolved, is to be welcomed.

During the Pliocene and early Pleistocene, within the confines of Europe, *Dasychoerus arvernensis* underwent evolution notably in dimensions, culminating in the large suine *Dasychoerus strozzi* (Meneghini, 1862) (Forsyth-Major 1881).

It is not beyond the realms of possibility that *Dasychoerus* Gray, 1873, could be the group from which the genus *Potamochoerus* Gray, 1854, descended – fossils of *Kolpochoerus* and *Dasychoerus* have on occasion been attributed to *Potamochoerus* (Cooke 1978; Arribas & Garrido 2008; Bishop 2010). Souron

et al. (2013) indicated that *Potamochoerus* was the sister group of *Kolpochoerus* + *Hylochoerus*, with *Sus scrofa* Linnaeus, 1758 more distantly related. These authors classified the species *K. afarensis* in *Potamochoerus*, a suggestion that echoes back to the identifications of Cooke (1978) and Bishop (2010).

In Asia, a similar scenario played out, with small species of *Dasychoerus*, close in dimensions and morphology to *Dasychoerus arvernensis*, evolving into larger species such as *Dasychoerus macrognathus* Dubois, 1908, and *Dasychoerus brachygnathus* Dubois, 1908 (Hardjasmita 1987) and the extant species *Dasychoerus verrucosus* (Müller & Schlegel, 1845) and *Dasychoerus celebensis* (Müller & Schlegel, 1845) (Pickford 2013a–c). The strange suid from the Celebes; *Celebochoerus heekereni* Hooijer, 1948 (Hooijer 1954, 1969, 1972; Suyono 2009) could well be a descendent of this same small *Dasychoerus arvernensis* as could some of the Chinese Plio-Pleistocene suids including “*Sus*” *australis* Han, 1987 (Pickford 2013b).

In the Siwaliks of Indo-Pakistan, there are several Pliocene species of suines which probably also belong to *Dasychoerus arvernensis*, including *Sus hysudricus* Falconer & Cautley, 1846, (not to be confused with *Propotamochoerus hysudricus* (Stehlin, 1899–1900)), *Dicoryphochoerus durandi* Pilgrim, 1926, and *Sus bakeri* Pilgrim, 1926.

In contrast, the origin of the species “*Sus*” *provincialis* Blainville, 1847 (Gervais 1850) probably predated the radiative process of *Dasychoerus*–*Kolpochoerus*, and it may have given rise to what in Africa are known as metridiochoeres and phacochoeres (Pickford 2012, 2013d).

MATERIAL AND METHODS

Dental nomenclature is based on the approaches of Hünemann (1968) and Pickford (1988, 2013d). Tooth types are abbreviated to single letters of the alphabet (i – incisor, c – canine, p – premolar, m – molar). Upper teeth are identified by capital letters (I, C, P, M) followed by a number representing the meristic position, followed by a forward slash representing the occlusal surface (i.e. the number is above the occlusal surface, therefore an upper tooth eg M1/ – first upper molar). Lower teeth are identified by lower case letters (i, c, p, m) followed by the forward slash and then by the number (ie the number is beneath the occlusal surface, therefore a lower tooth, e.g., p/3 – third lower premolar). Deciduous cheek teeth are identified by the letter “d” or “D”. Osteological terms are from Sisson & Grossman (1953) and facial musculature terminology is from Ewer (1958).

Place names in Moldova have been spelled in various ways in relation to the history of this part of what used to be called Central Bessarabia (Bessarabie Meridionale). Transliterations of the names from the Cyrillic vary from author to author, in large measure reflecting the mother tongue of the person doing the transliteration. We here use the original spellings of place names based on Romanian, but provide recent equivalents encountered in the literature (see Fig. 1): Carbolia–Karbolliya; Chisinau–Kishinev; Ialpug–Yalpug; Cogâlnic–Kogilnic; Cuchiurgan–Kuchurgan; Nistru–Dneister.

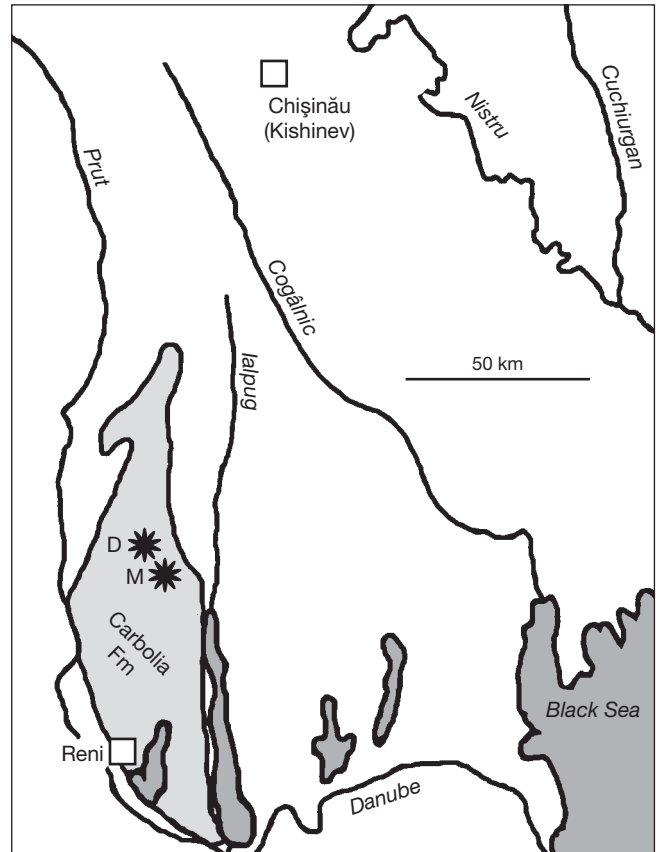


Fig. 1. — Map of southwestern Moldova and part of Ukraine, showing the distribution of the fluvatile Carbolia Formation and the fossiliferous sites of Dermenji (D) and Musaitu (M). Map modified from Pevzner *et al.* 1996.

ABBREVIATIONS

The fossils examined during this study are housed at the following institutions or collections.

BEL	Belohdelie, Ethiopia;
BGSK	British Geological Survey, Keyworth;
CCECL	Centre de Conservation et d'Études des Collections, Lyon;
FSL	Faculty of Science, Lyon;
IM	Ipswich Museum;
KB	Kossom Bougoudi, Chad;
MC	Mine Capeni;
MCFFMIZASM	Musée des Complexes faunistiques fossiles de Moldova, Institut de Zoologie, Académie des Sciences de Moldavie;
MCNM	Museo Nacional de Ciencias Naturales, Madrid;
MGPOT	Museum of Geology and Palaeontology, University of Turin;
MIL	Milia Museum;
MNHN	Muséum national d'Histoire naturelle, Paris;
MPV	Museum Palaeontology Valencia;
MSG	Museum Sf. Gheorghe;
NHMB	Naturhistorisches Museum, Basel;
NHMUK	Natural History Museum, United Kingdom, London;
NME	National Museum of Ethiopia, Addis Ababa;
NMENHM	National Museum of Ethnography and Natural History of Moldova;
NWHCM	Norwich Castle Museum;
OCO	Orrorin Community Organisation;
PIMUZ	Palaeontology Institute Museum, University of Zürich;
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden;
YORYM	York, Yorkshire Museum.

GEOLOGICAL CONTEXT

The Musaitu and Dermenji fossil localities occur within the fluvial Carbolia Formation of southwestern Moldova (Fig. 1). The Musaitu deposits were first mentioned by Khomenko (1914) who recorded the presence of the suid *?Sus provincialis*. The suid skull described herein was collected by the late Aleksandru Lungu, well known vertebrate palaeontologist based at the Tiraspol State University, Kishinev (Lungu & Rzebiak-Kowalska 2011). Written on the palate are the words “*Potamochoerus provincialis* Gervais”, and “Musaitu, sr. Pliocene” (transliteration of the Cyrillic script).

The Musaitu skull is dark brown and has pale rusty carbonate concretions stuck to it, notably on the front of the palate in the incisive region and partly obscuring the left M3/ and left palatine bone. The nasal cavity is full of the same type of carbonate sediment. These preservation characteristics indicate the likelihood that the fossil came from the basal beds of the Carbolia Formation (also spelled Karboliya) which comprise red weathered loam endowed with numerous carbonate concretions (Khubca 1982; Nadachowski *et al.* 2006) overlying Pontian sands.

Aleksandrova (1989) correlated the older of the Musaitu faunal elements to the base of MN 15, being equivalent to part “A” of the fourfold subdivision of the Moldavian Faunal Assemblage (Complex). Vangengeim *et al.* (1995, 1998) correlated the site of Musaitu to MN 15 (Musaitu 5 at *c.* 3.8 Ma, Musaitu 7 *c.* 3.6 Ma) on the basis of the fauna (*Dicerorhinus* sp., *Paracamelus alexeevi* Khavesson, 1950, *?Loribos* sp.) and the small mammals. Pevzner *et al.* (1996) listed two levels Musaitu 5 and Musaitu 7 (respectively 5 and 7 km from Musaitu Village), the former correlated to the base of MN 15, the latter near the top. The age range calculated by these authors for Musaitu was 5–3.8 (+ 0.05–0.04) Ma. Pevzner *et al.* (2001) positioned Musaitu 5 at 4.2 Ma. Vangengeim *et al.* (2005) put Musaitu 5 at 4.1 Ma. These age estimates are not contradicted by the palaeomagnetic correlations proposed by the same authors.

Nadachowski *et al.* (2006) listed faunal contents from different levels within the 45-metre thick post-Pontian beds at Musaitu. The lower parts correlating to the Moldavian Mammal Complex yielded *Promimomys moldavicus* Kormos, 1932, *Promimomys stehlini* Kormos, 1931, *Proochotona eximia* Khomenko, 1914, *Proochotona gigas* Argyropulo & Pidoplitshka, 1939, *Alilepus* cf. *lascarevi*, and the lowermost parts yielded *Pliomys kowalskii* Shewtschenko, 1965, *Hipparion* sp., *Paracamelus* sp., *Stephanorhinus* sp., *Talpa minor* Freudentberg, 1914, Spalacidae Gray, 1821 and Cricetidae Fischer, 1817 (Khubca 1982). The uppermost part of the outcrops yielded Leporidae Fischer, 1817, Ochotonidae Thomas, 1897, Castoridae Hemprich, 1820, *Nannospalax* sp., *Pliomys kowalskii* and *Promimomys moldavicus*. Large mammals from the Musaitu badlands comprise *Vulpes* sp., *Mammuth borsoni* (Hays, 1834), *Anancus* ex gr. *arvernensis* (Croizet & Jobert, 1828), *Hipparion* sp., *Stephanorhinus megarhinus* De Christol, 1835, *Paracamelus alexeevi* Khavesson, 1950, Cervinae Goldfuss, 1820, and *Parabos boodon* Gervais, 1853. The very highest levels of the deposits yielded *Talpa* sp., *Pliopetaurista moldaviensis* Baranova & Konkova, 1974, *Apodemus dominans* Kretzoi, 1959, *Pliomys* sp., and Cervinae.

SYSTEMATIC PALAEONTOLOGY

Family SUIDAE Gray, 1821

Genus *Dasychoerus* Gray, 1873

GENERIC DIAGNOSIS. — Suinae with verrucosic male lower canines, relatively narrow parietal region of the skull slightly convex transversely; gently undulating dorsal skull profile; widely diverging zygomatic arches tending to be broader in the middle than at the rear, zygoma inflated; laterally expanded nasals; large and rugose supra-canine flange (in males, more gracile in females), elongated rostrum; thickened mandibular body (pachygnathy Arambourg 1947) (modified and extended from descriptions in Azzaroli 1954 and Berdondini 1992).

TYPE SPECIES. — *Sus verrucosus* Müller & Schlegel, 1845.

Dasychoerus arvernensis (Croizet & Jobert, 1828)

Aper arvernensis Croizet & Jobert, 1828: 157–160, pl. XIII, figs 3–5.

Sus provincialis var. *minor* Depéret, 1890: 84–88, pl. V, figs 12–14.

Sus minor – Tobien 1951: 79–83; 1952: 191; Hünemann 1971: 213–222.

Sus arvernensis arvernensis – Guérin & Faure 1985: 22; Guérin *et al.* 1998: 442.

Sus arvernensis minor – Guérin & Faure 1985: 443–447.

For additional synonymy of the species see Fejfar (1964) and Hünemann (1971).

TYPE LOCALITY. — Les Étouaires, Perrier, France.

AGE OF TYPE LOCALITY. — MN 16, Lower Villafranchian (3.9–3.4 Ma, Bout, 1968, 3.6–2.4 Ma, Steininger *et al.* 1990).

HOLOTYPE. — Specimen MNHN.F.PET2005 labelled “Étouaires”, comprising associated juvenile left maxilla containing D2/-D4/ and M1/ and a left mandible fragment and symphysis containing d/2-d/4 and m/1 in occlusion on both sides, and the germ of the left m/2 and p/4 in crypto (illustrated in mirror image by Croizet & Jobert [1828], and Blainville [1847] which has caused confusion about which side the specimens came from [Guérin & Tsoukala 2013]). The symphyseal fragment which fits onto the left mandible contains parts of the left and right canines in situ (verrucosic male morphology) and the left i/2 in crypt (partly exposed by damage to the symphysis). The right mandible containing the d/2-d/4 and m/1 belongs to the same individual (Figs 2–6).

DIAGNOSIS

Small species of *Dasychoerus*, length M1/, 14.2–18 mm; length M2/, 18.5–22 mm; length M3/, 24.6–29.4 mm; length m/1, 14.7–18 mm; length m/2, 18–24 mm; length m/3, 28.3–33.3 mm.

Note on nomenclature and lectotypes of *Sus minor* Guérin & Faure (1985), Guérin *et al.* (1998) and Guérin & Tsoukala (2013) retained two subspecies *Sus arvernensis arvernensis* (Croizet & Jobert, 1828) and *Sus arvernensis minor* (Depéret, 1890) for these small Plio-Pleistocene European suids. Guérin *et al.* (1998) separated these two

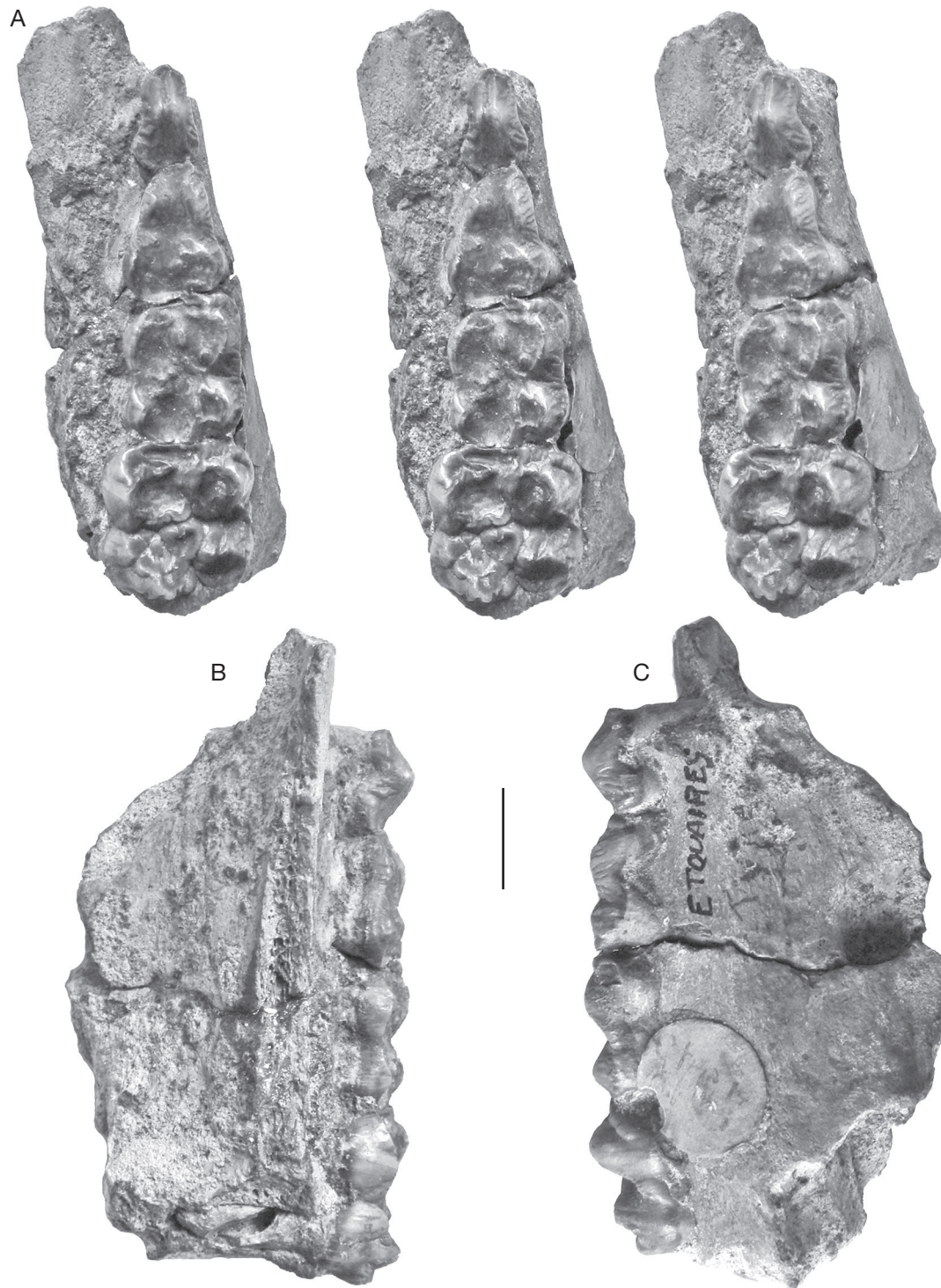


FIG. 2. — Left maxilla containing D2/-D4/ and M1/, part of the holotype of *Dasychoerus arvernensis* (Croizet & Jobert, 1828), from Les Étouaires, Perrier, France (MNHN.F.PET2005, specimen labelled “Étouaires”): **A**, stereo triplet of the occlusal view; **B**, lingual view; **C**, buccal view. Scale bar: 10 mm.

subspecies on the basis of the smaller dimensions of *Sus arvernensis minor*, and its relatively long premolars, narrower molars of simpler construction with fewer accessory tubercles. However, our own analysis of the dimensions and morphology of the teeth from the two type localities, Les Étouaires and Roussillon indicate significant morphometric overlap between the two subspecies. In this study, we

therefore treat all the material as a single unit at the species level, rather than continue to deal with two subspecies.

Azzaroli (1954, 1975) considered that *Sus arvernensis* was a “*nomen dubium*”, and wrote that it could possibly be a synonym of *Sus minor*, in which case *Sus arvernensis* would be the valid name. Hünemann (1971) considered the name *Sus arvernensis* to be invalid due to the incomplete preservation of the type specimen

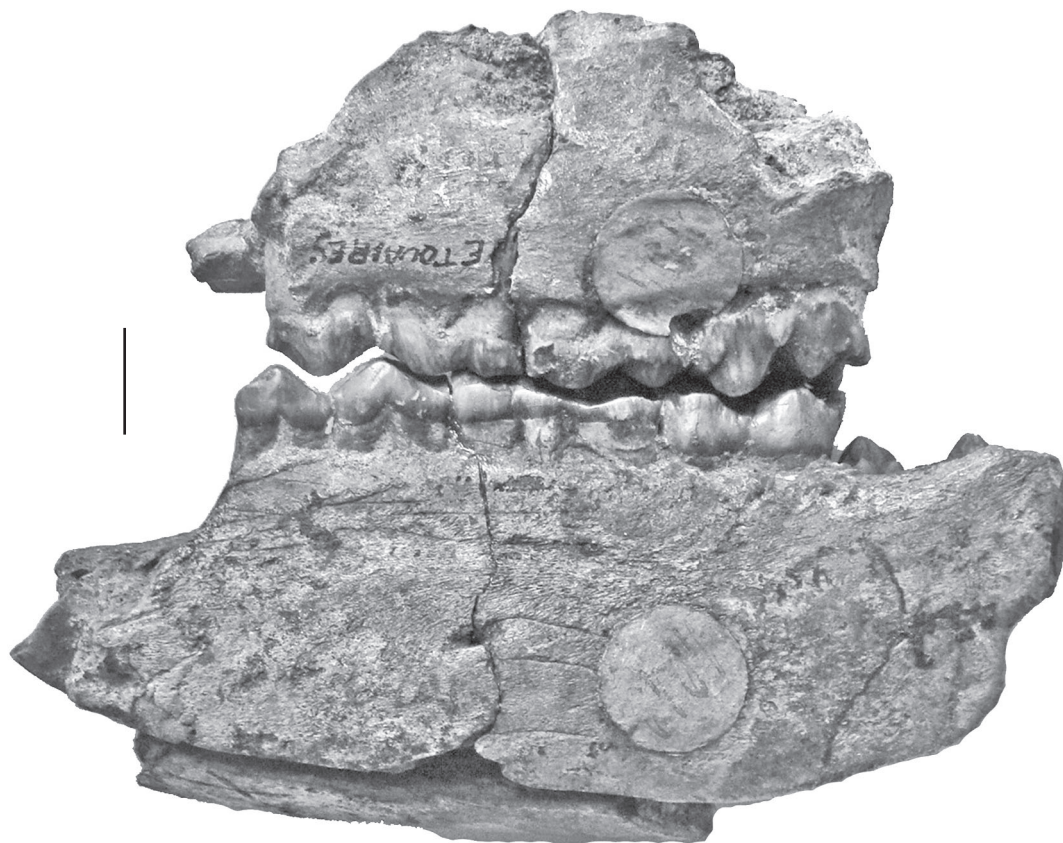


FIG. 3. — Buccal view of left maxilla and mandible containing mixed dentitions in occlusal relationship, parts of the holotype of *Dasyschoerus arvernensis* (Croizet & Jobert, 1828) from Les Étouaires, Perrier, France (MNHN.F.PET2005, specimen labelled “Étouaires”), figured in reverse by these authors and by Blainville (1847). Scale bar: 10 mm.

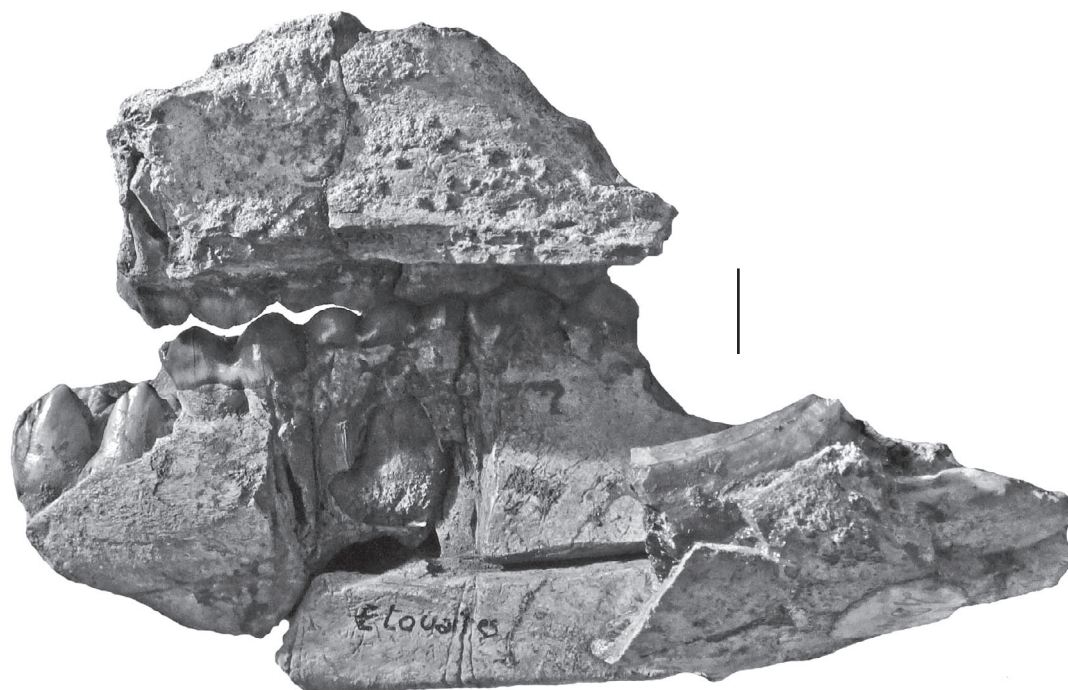


FIG. 4. — Holotype of *Dasyschoerus arvernensis* (Croizet & Jobert, 1828) from Les Étouaires, Perrier, France (MNHN.F.PET2005, specimen labelled “Étouaires”), viewed from the lingual side with the left maxilla, mandibular symphysis and left mandible articulated in occlusal relationship. The bone beneath the d/4 has been cut away to expose the p/4. Note also the verrucosic male canines, and the forward sloping incisors, located well beneath the level of the occlusal surface of the cheek teeth. Scale bar: 10 mm.

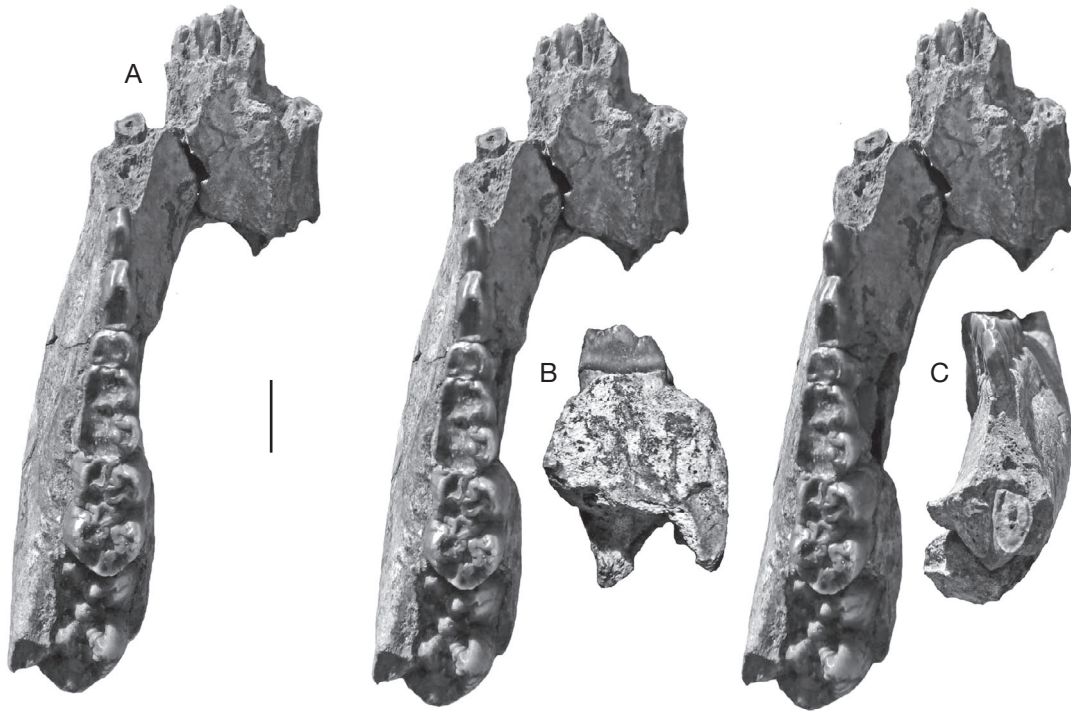


FIG. 5. — Left mandible and symphysis of the holotype of *Dasychoerus arvernensis* (Croizet & Jobert, 1828) from Les Étouaires, Perrier, France (MNHN.F.PET2005, specimen labelled “Étouaires”): **A**, stereo triplet of the occlusal view; **B**, view of the rear of the right mandible behind the m/1 to show the thickened mandibular ramus, expressed already in this juvenile individual; **C**, anterior view of left mandible to show verrucosic section of the male canine. Scale bar: 10 mm.

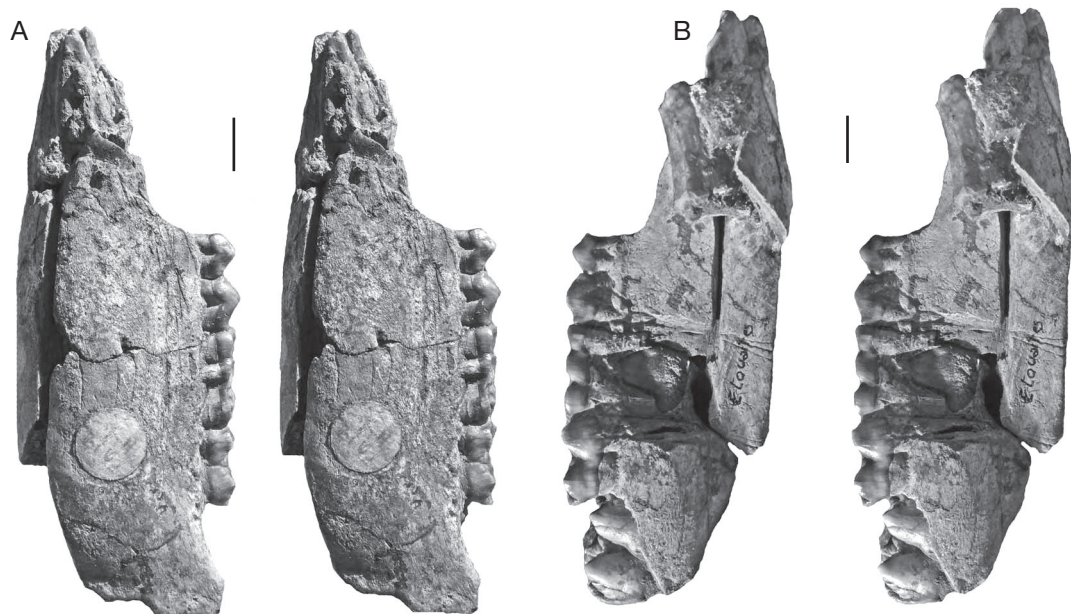


FIG. 6. — Left mandible of the holotype of *Dasychoerus arvernensis* (Croizet & Jobert, 1828) from les Étouaires, Perrier, France (MNHN.F.PET2005, specimen labelled “Étouaires”): **A**, stereo buccal view; **B**, stereo lingual view. Note the very low incisors relative to the cheek tooth occlusal surface. Scale bars: 10 mm.

(he agreed that *Sus arvernensis* and *Sus minor* were synonyms, but opted to support *Sus minor* even though this goes against the rule of priority). However, the type specimen of the former species is one of the more informative fossil suid specimens described, comprising associated upper and lower jaws, with well preserved elements of the deciduous and permanent cheek dentition, plus parts of both lower canines, and is thus more

informative than the lectotype of *Sus minor* (CCECL Pp 195) which comprises a mandible fragment with p/2-m/2.

There is an unusual situation concerning the type specimen of *Sus minor* which has caused confusion to the extent that different specimens have been used by different authors as reference specimens. Four separate fossils have been proposed either as lectotypes or as syntypes. Azzaroli

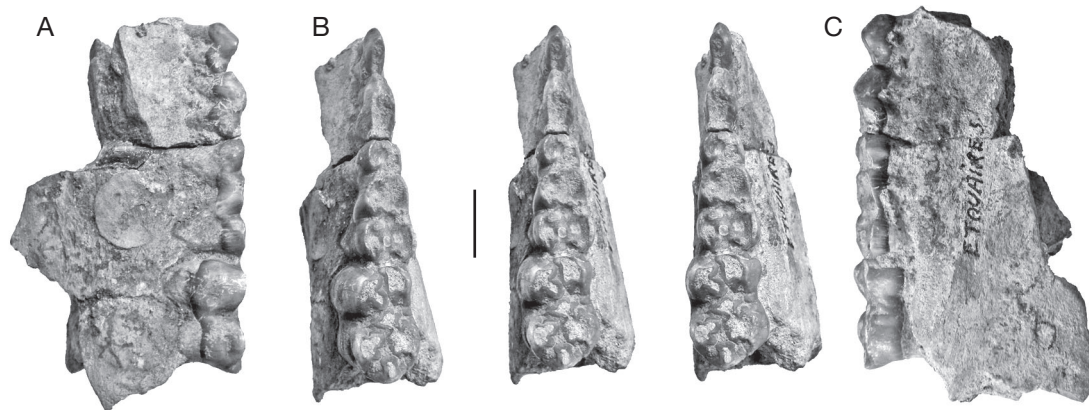


FIG. 7. — Right mandible containing d/2-m/1 of *Dasychoerus arvernensis* (Croizet & Jobert, 1828) from Les Étouaires, part of the holotype (<http://coldb.mnhn.fr/CatalogNumber/MNHN/F/PET2005>, specimen labelled “Étouaires”): A, lingual view; B, stereo triplet of the occlusal view; C, buccal view. Scale bar: 10 mm

(1954: 58 and caption to pl. 1; fig. 6a, b) employed the term “lectotype” for the left mandible figured by Depéret (1890: pl. V, fig. 13). This is the earliest nomination of a type specimen for *Sus minor* and thus is the valid one. It is the specimen comprising a left mandible with unerupted (but mechanically exposed) p/2-p/4 and m/1-m/2 in occlusion, curated at the CCECL under number Pp 195. Azzaroli (1975) reiterated the nomination but made an erroneous reference (erroneous citation of figure as Azzaroli 1954: pl. V, fig. 11, 11a).

Fejfar (1964) seemingly unaware of Azzaroli’s (1954) prior selection of a lectotype, nominated a different specimen as lectotype, a left lower jaw containing m/2 and m/3 *in situ*, according to him figured by Depéret (1890: 85, 86, pl. V, fig. 12). However, figure 12 on the cited plate is an image of a left M3/, the mandible with two molars being figure 14 of the same plate.

Guérin *et al.* (1998) wrote that the syntypes (sic) of *Sus minor* consist of “an almost complete palate and a last upper molar”. These specimens from Roussillon, which comprise a left maxilla with the cheek dentition running from P3/-M3/, and an isolated M3/, the former of which was attributed in the first instance to *Sus arvernensis* by Depéret (1885: pl. V, fig. 1).

Thus various authors have employed four different specimens to typify *Sus minor*, and this has undoubtedly caused some fluidity in the interpretations that flowed from the choice of type material. The first nominated, and therefore the valid lectotype of *Sus minor* is the mandible nominated by Azzaroli (1954) “CCECL Pp 195”.

In order to clarify the situation, the type materials of *Dasychoerus arvernensis* (Figs 2-7) and “*Sus*” *minor* (Fig. 8) are illustrated. The holotype of *Dasychoerus arvernensis* possesses the following teeth *in situ* in the maxilla and mandible – left and right i/1, left i/2, parts of the left and right male canines (the tip of the left canine has gone missing since it was illustrated by Croizet & Jobert [1828]), left D2/-D4/, M1/, left d/2-d/4, m/1-m/2, p/4 in crypt, right d/2-d/4, m/1, p/4 in crypt. The lectotype of “*Sus*” *minor* is a left mandible containing p/2-p/4, m/1-m/2.

DESCRIPTION

Musaitu suid skull

The Pliocene deposits at Musaitu, Moldova, yielded a remarkable skull of *Dasychoerus arvernensis* rivalling in completeness the material from Roussillon, France (Azzaroli 1975; Berdondini 1992) (Figs 9-14). The skull is notable for the narrow posterior cranial table, forming a narrow crest distally somewhat in the style of *Euhys barbatus* (Müller, 1838) (Gray 1868) and narrower than is usually the case in *Dasychoerus verrucosus*. The morphology of the brain case appears to be close to that of the Kvabebi suid described by Vekua (1972) although distortion of the latter specimen renders detailed comparisons difficult. A difference from the Kvabebi skull is the slightly convex longitudinal dorsal profile of the Musaitu skull, which is dished in the Kvabebi specimen (perhaps enhanced by crushing).

In lateral view the slightly convex dorsal transverse profile of the skull is evident, with a low swelling between the supra-orbital grooves in front of the supra-orbital foramina. The dorsal longitudinal profile of the nasals is very gently concave, almost flat. Although the anterior ends of the nasals are broken off, and the rear of the braincase is damaged, it is evident that the splanchnocranium was much longer than the neurocranium, as measured from the anterior margin of the orbit (Azzaroli 1954). The orbit lies behind the level of the upper third molar and is high on the face, bordered anteriorly by the lacrimal in which there are two prominent foramina. The post-orbital process ends in a sharp point above the mid-height of the orbit. In front of the orbit there is a well developed fossa for the origin of the *levator rostri* snout musculature (Ewer 1958). This fossa has a clear dorsal margin which leads forwards to the region above the canines, implying a well developed rooting habit in this species. The facial crest that separates the origin of the *levator rostri* from that of the *dilator naris lateralis* and the *depressor rostri* terminates short of the infra-orbital foramen. The infra-orbital foramen is large and lies at mid-height of the snout above the P4/-M1/. Above and just behind the canine alveolus there is a canine flange with a smooth concave dorsal surface over which passed the tendons for

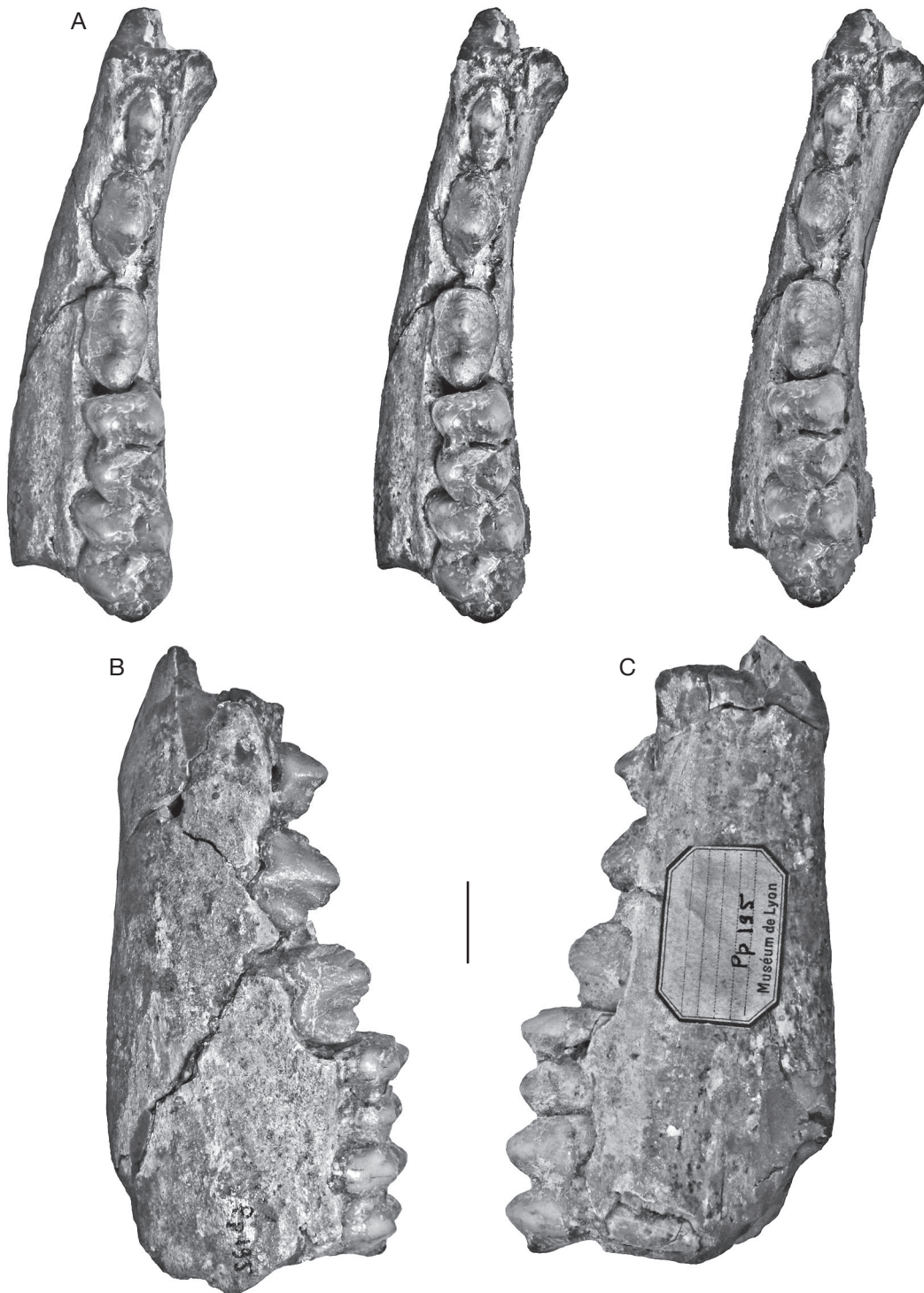


FIG. 8. — Left mandible containing p/2-m/2, from Perpignan, France (CCECL Pp 195), lectotype of “*Sus*” *minor* (Depéret, 1890) (Azzaroli 1954): **A**, stereo triplet of the occlusal view (note the thickness of the mandible despite the juvenile status of the jaw; **B**, buccal view; **C**, lingual view. Scale bar: 10 mm.

the snout musculature. At the canine level, the ventral part of the snout descends beneath the occlusal surface of the cheek teeth. The canine is inserted at the anterior ventral end of the supra-canine flange.

In dorsal view, the skull is observed to be long and narrow, broadest at the post-orbital processes, narrowing sharply distally, and narrowing more gently anteriorly. The

infra-orbital foramina emerge from the skull roof in line with the front of the orbits, and the supra-orbital grooves follow a slightly curved course anteriorly along the dorsal surface of the skull, first approaching each other, and then running sub-parallel to each other. The temporal crests approach each other distally but do not form a true sagittal crest. The degree of narrowing of the braincase distally is



FIG. 9. — Skull of *Dasychoeerus arvernensis* (Croizet & Jobert, 1828) from Musaitu, Moldova, right lateral view. Note the downward bend of the ventral part of the snout in front of the alveoli of P1/ (separated from the P2/ by a short diastema) and the relatively thin supra-canine flange above and behind the canine alveolus. Also of note is the slightly convex dorsal transverse profile of the skull in front of, and above, the orbits, and the absence of dishing of the dorsal longitudinal profile of the skull. Scale bar: 10 cm.



FIG. 10. — Skull of *Dasychoeerus arvernensis* (Croizet & Jobert, 1828) from Musaitu, Moldova, dorsal view. Note the temporal crests that approach each other distally almost forming a sagittal crest. Scale bar: 10 cm.

comparable to that seen in *Euhys barbatus*. It is narrower than is usually the case in *Dasychoeerus verrucosus* (Forsyth-Major 1897) and *Sus scrofa*, and quite similar to the fossil South African form *Potamochoeroides hypsodon* Dale, 1948 (Pickford 2013b). The zygomatic arches are broken, but the root of the right one suggests that it departs from the face at an angle of *c.* 45° with its anterior end above the M2/, just behind the infra-orbital foramen.

The supra-canine flange projects from the face above and behind the canine alveolus, its dimensions and that of the canine alveolus suggest that this was probably a juvenile male in which the flange had not grown to its fully mature form. The dimensions of the canine root support this diagnosis. The snout is rectangular in section, with almost vertical sides.

In palatal view, the lingual edges of the two cheek tooth rows are sub-parallel. The teeth are well preserved with the P2/-M3/ forming a closed series separated by a short diastema from the P1/, represented by two alveoli just behind

the canine alveoli which contain remnants of the root of the canine. The front parts of the palatines are broken so no information can be provided about the incisors. The supra-canine flange is positioned such that the canines emerged from its anterior end, and its rear margin is opposite the P2/. The individual was a young adult at the time of death, as revealed by the fact that M3/ is not completely erupted but the cusp apices of the anterior loph have reached the same level as the occlusal surface of the teeth in front of it. The posterior choanae open up a short distance behind the rear of the M3/s. The basicranial area of the skull is badly damaged.

In anterior view, the section of the snout is visible where the anterior part has broken off. This shows that the lateral walls of the rostrum are vertical, the nasal cavity is comprised of two lobes, a large one dorsally and a smaller one ventrally. The dorsal surface of the rostrum shows a low ridge in the midline.

In posterior view, the nuchal zone is observed to be tall and relatively narrow. The basicranium is broken.

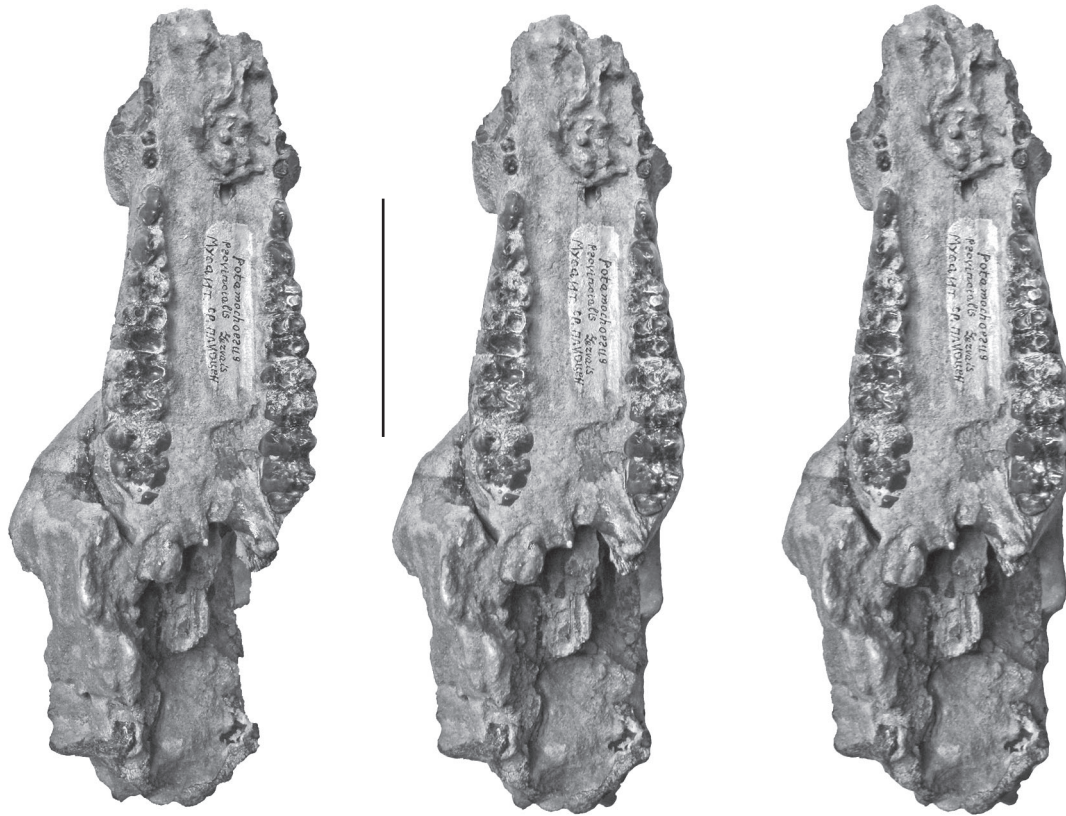


FIG. 11. — Skull of *Dasychoerus arvernensis* (Croizet & Jobert, 1828) from Musaitu, Moldova, stereo triplet ventral view. Note in particular the canine flanges, the short diastema between the P1/ and the P2/ and the position of the posterior choanae behind the M3/s. Scale bar: 10 cm.

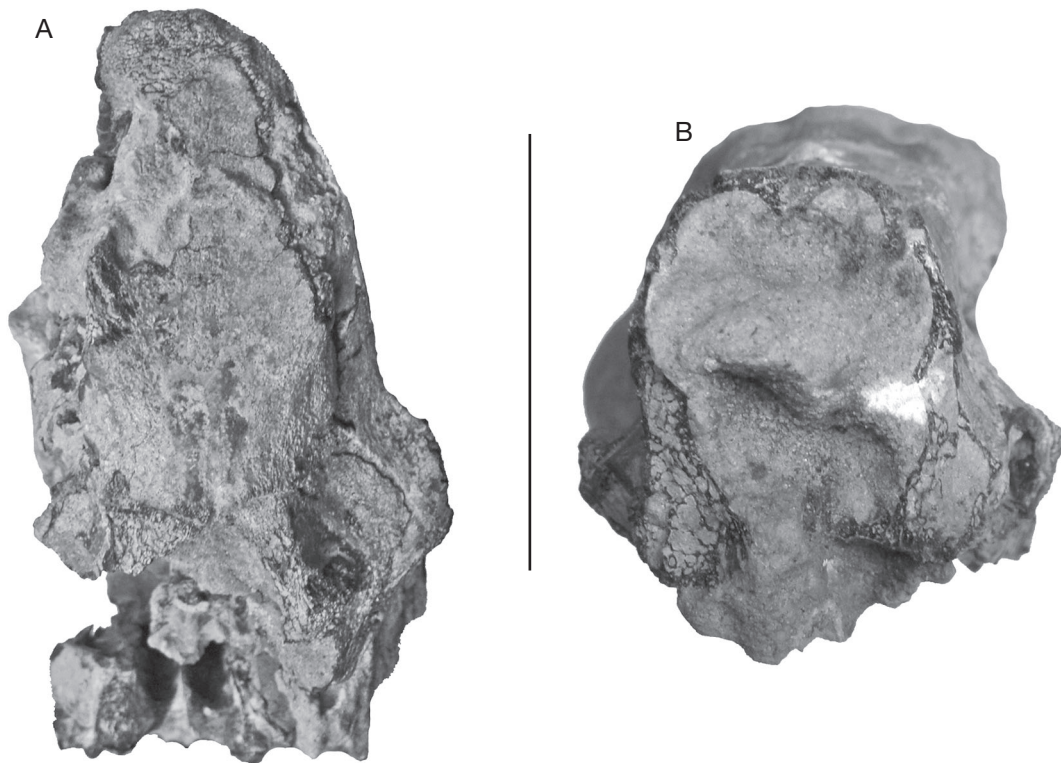


FIG. 12. — Skull of *Dasychoerus arvernensis* (Croizet & Jobert, 1828) from Musaitu, Moldova: **A**, posterior view showing the tall, narrow surface for attachment of the nuchal musculature; **B**, anterior view showing vertical lateral walls of the snout and the carbonate-rich sediment infilling the nasal cavity. Note the ridged dorsal profile of the rostrum, and the indentations in the sides of the nasal cavity dividing it into broader upper and narrower lower parts, the latter floored by the palate. Note also the large concretion obscuring the palate. Scale bar: 5 cm.

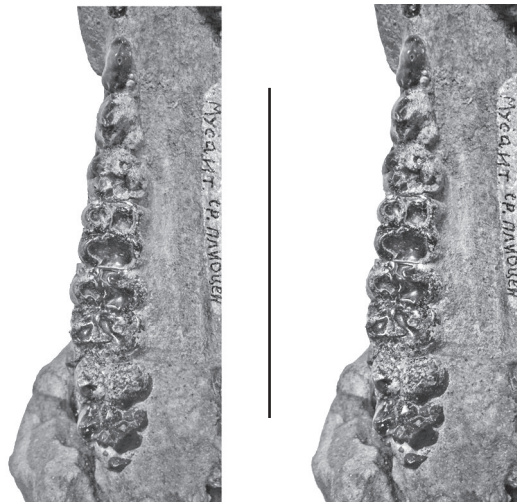


FIG. 13. — Right cheek teeth of the skull of *Dasychœrus arvernensis* (Croizet & Jobert, 1828) from Musaitu, Moldova, stereo occlusal view. Scale bar: 10 cm.

Dentition

P1. The P1/ is missing on both sides but it had two roots. It is positioned just behind the canine alveolus and slightly lingual to the inner edge of the canine alveolus.

P2. The P2/ is subtriangular in occlusal outline, with rounded apices of the triangle. The main cusp is somewhat anterior to the midline of the tooth. It has a precrista that descends towards a small mesial cusplet, and a prominent, swollen post-crista that forms a separate cusplet distally. There is a slight incision in the postcrista which separates the main cusp from the distal one. Disto-lingually, there is a small cingular cusplet separated from the rest of the crown by the distal fovea. Thus the rear of the tooth is broader than the front half.

P3. The P3/ has a broad triangular occlusal outline. It is constructed along the same lines as the P2/ but all the structures are better defined and larger. Thus the mesial cusplet at the anterior end of the precrista is more prominent and has cingular folds extending medially and laterally from it for a short distance, but not reaching the buccal side of the crown. The distal cusplet on the buccal side is larger and is better separated from the main cusp by lingual and buccal grooves. The distal fovea is broader than in the P2/ and the disto-lingual cusplet is larger, connected to a low cingulum that extends along the lingual base of the crown.

P4. The P4/ is tricuspid, and rectangular in occlusal outline. There are two buccal cusps, the posterior one as tall as the main cusp but mesio-distally smaller than it. These two cusps are separated from each other on the buccal side by a prominent vertical groove that reaches almost to the cervix. There is a prominent protocone on the lingual side of the tooth, connected to cingula that extend anteriorly and posteriorly to join the mesial and distal cingula respectively. There is a sagittal cusplet on the lingual side of the paracone, but there is none on the lingual side of the metacone.

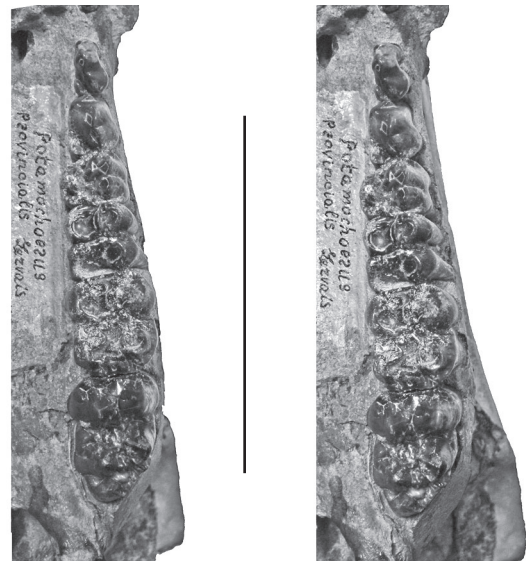


FIG. 14. — Left cheek teeth of the skull of *Dasychœrus arvernensis* (Croizet & Jobert, 1828) from Musaitu, Moldova, stereo occlusal view. Scale bar: 10 cm.

M1/ and M2/. The M1/ is deeply worn. The M2/ is also heavily worn, but shows four main cusps arranged in two lophs with a prominent median accessory cusplet blocking the median transverse valley. There are well formed mesial and distal cingula and there is a remnant of a lingual cingulum in the lingual end of the median transverse valley.

M3. The M3/s are lightly worn and show all the main structures well. This tooth has four main cusps and anterior, median and posterior accessory cusplets, as in the M2/ (the usual basic morphology found in suids) but in addition, at the rear of the crown, there is a small talon comprised of a low, pointed cusp slightly to the lingual side of the midline of the crown. The mesial cingulum is beaded and ends before reaching the buccal or lingual part of the crown. It ends lingually at a small cingular cusplet attached to the mesio-lingual corner of the protocone. The lingual end of the median transverse valley shows a low cingular remnant, and there are cingular beads of enamel at the lingual and buccal ends of the valley between the rear loph and the talonid of the tooth. The Fürchen are shallow apically but clearly discernible, especially towards the bases of the main cusps where they are deeper and broader.

Dermenji mandible

A mandible fragment from Dermenji curated at the Musée des Complexes Faunistiques Fossiles de Moldova, Institut de Zoologie, Académie des Sciences de Moldova, comprises the rear part of the right ramus containing m/2 and m/3 in medium wear (Fig. 15). The m/2 has four main cusps arranged in two lophs with clear anterior, median and posterior accessory cusplets in the midline of the crown. The two lophs are wide apart. The two anterior lophs of the m/3 have the same basic structure as the m/2, but in addition, there is a prominent talonid cusp behind

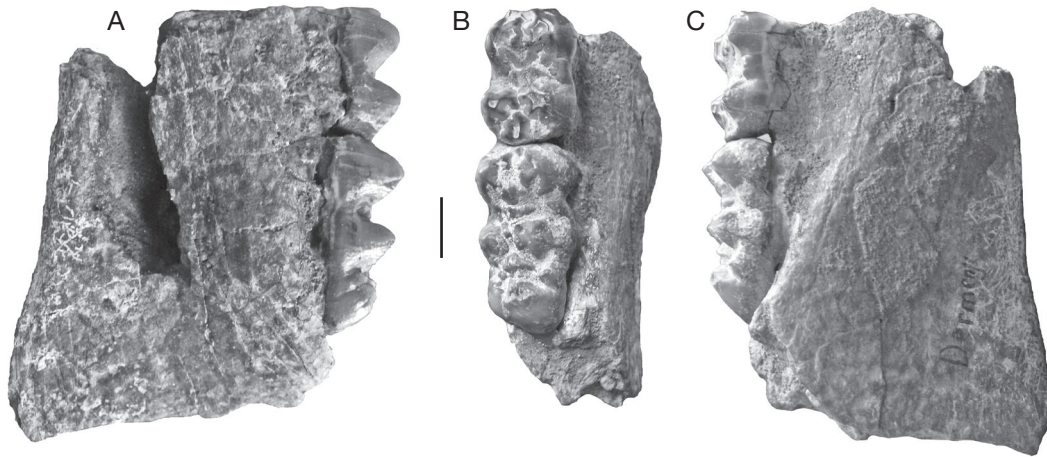


FIG. 15. — Right mandible of *Dasychoerus arvernensis* (Croizet & Jobert, 1828) from Dermenji, Moldova: **A**, lingual view; **B**, occlusal view; **C**, buccal view. Scale bar: 10 mm.

the posterior accessory cusplet in the centre-line of the crown. The teeth in this specimen resemble those from Gödöllő, Hungary (Mottl 1939) and Perpignan, France (Depéret 1890).

Metric analysis

Appendices 1 (Europe) and 2 (Africa) provide measurements of the teeth used in the metric analysis.

The dental metrics of the Musaitu and Dermenji suids show close correspondence with material of *Dasychoerus arvernensis* from other localities in Europe (Figs 16–19). The specimens are smaller than the suids from Kvabebi, Georgia (Vekua 1972) although there are some morphological resemblances in the skulls from Musaitu and Kvabebi, such as the presence of a narrow cranial table distally, almost forming a sagittal crest, and well developed supracanine flange. However, the dorsal surface of the Kvabebi skull has a dished profile in lateral view, and the specimen from Musaitu is slightly convex, almost straight. The Kvabebi specimen is distorted, and this may have altered the profile, but even so, the difference seems to be important. Similar dishing of the skull occurs in the African genus *Kolpochoerus*, and it could be that the Kvabebi morphology represents an intermediate stage between *Dasychoerus arvernensis* as exemplified by the almost straight, slightly convex condition seen not only in the Musaitu skull but also in the material from Roussillon and Villafranca d'Asti (Azzaroli 1954, 1975; Berdondini 1992) and the dished condition observed in *Kolpochoerus*.

The Kvabebi suid (Vekua 1972) has thickened mandibular rami, as do specimens from Roussillon and Villafranca d'Asti (Figs 20, 21), and the same condition occurs in *Kolpochoerus*. There can be little doubt that the African kolpochoeres, *Dasychoerus arvernensis* and the Kvabebi suid are closely related members of a lineage or clade.

The larger of the specimens attributed to *Kolpochoerus millensis* are similar in size to the suid from Kvabebi, Georgia (Vekua 1972) (Figs 22, 23).

The upper and lower third molars attributed to the Ethiopian species *Kolpochoerus millensis* (Haile-Selassie & Simpson 2012) have a somewhat greater range of length variation than the closely related taxon *Dasychoerus arvernensis*. Many of the former specimens fall within the range of variation of the latter species but there are a few more elongated teeth. Whether this is related to a real increase in variability of the length of the teeth, or whether it is due to the mixing of two closely related taxa needs to be examined. The authors did not provide measurements of the other cheek teeth of *Kolpochoerus millensis*, so it is not possible to determine whether they too show an increase in variability over the situation in *Dasychoerus arvernensis*. It is clear however, that the larger of the specimens attributed to *Kolpochoerus millensis* overlap in length dimensions with the Kvabebi suid, although the latter material has broader third molars than *K. millensis*.

Boreal, sub-tropical and tropical suids

As in other artiodactyl groups there are suids adapted to high latitudes and others to low latitudes. A major difference between these groups concerns the timing of reproduction related to seasonal changes in climate. Boreal taxa time their reproduction to winter-summer cycles whereas more tropical lineages time their reproduction to wet season – dry season cycles. The metabolic triggers for reproductive activity differ between the groups, in high latitudes the hormonal changes are linked to variations in day length which are highly predictable. The Wild Boar (*Sus scrofa*) times its reproductive cycle such that litters are born in spring (MacDonald 2001) whereas in the tropics suid reproduction is linked to changes in humidity which are much more variable in timing, partly due to the El Niño phenomenon. In the humid tropics where the seasons are not marked, reproduction may occur all the year round, but where there is marked dry-wet cyclicity, birth is usually timed to occur near the beginning of the wet season, but with marked variability due to vagaries in the onset of the different seasons.

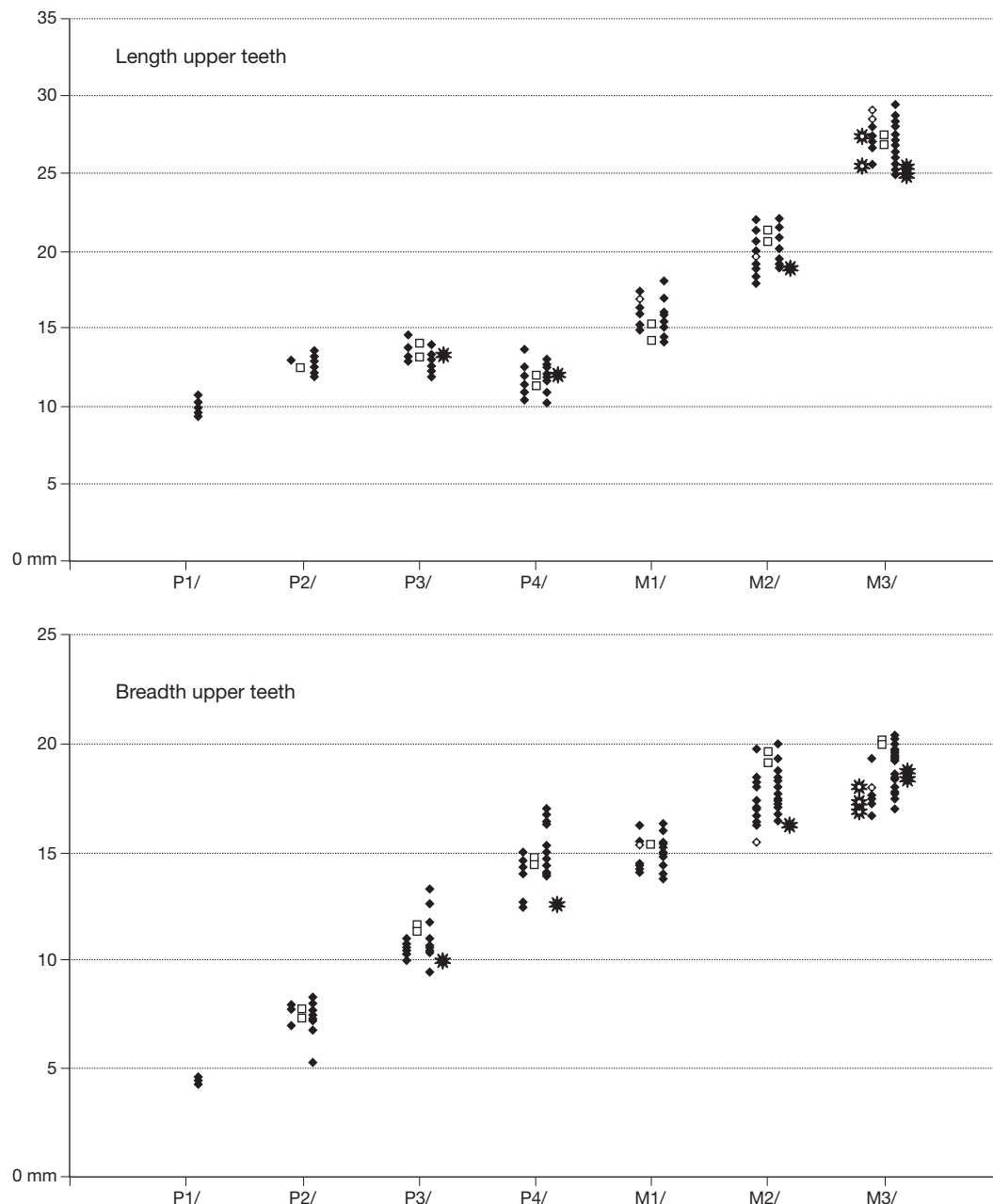


FIG. 16. — Length and breadth plots of the upper cheek teeth of *Dasychoerus arvernensis* (Croizet & Jobert, 1828) from Europe and Africa. In the midline (□) are the measurements of the teeth in the Musaitu skull. To the left are measurements of teeth from Les Étouaires (◊) and Roussillon (Perpignan) (◆) and to the right are measurements of teeth from Afyonkarahisar, Alcoy, Autrey, Auvergne, Bra, Çalta, Capeni, Dinar Akçakoy, Gödöllő, Hajnacka, Herbolzheim, Ivanovce, Milia, Trévoux, Virgis, and Villafranca d'Asti (see Appendix 1 for data sources). Further to the right are specimens from Ethiopia (★) and further to the left are specimens from Chad (✱) (Appendix 2).

This translates into divergent controls of reproductive behaviour in *Sus* Linnaeus, 1758 and *Dasychoerus*, the Wild Boar (*Sus scrofa*) being adapted to boreal environments with marked day length changes through the year, whereas the more tropical Warty Pigs (*Dasychoerus*) and their relatives the Wart Hog (*Phacochoerus* Cuvier, 1826) the Red River Hog (*Potamochoerus*) and the Forest Hog (*Hylochoerus*) are adapted to tropical environments where day length changes are not as marked as they are at high latitudes. Thus not only do reproductive parameters link *Dasychoerus*, *Phacochoerus*, *Potamochoerus* and *Hylochoerus*, to the exclusion of *Sus*, but

so do the presence of warts, lower canine morphology (verrucosic), style of intraspecific combat during the rutting season among others (MacDonald 2001). The definition of verrucosic canines is based on the sub-equal dimensions of the lingual and labial enamel-covered surfaces of the tooth. In scrofic canines the labial surface is appreciably shorter than the lingual surface. The distal, enamel-free surface can be broad or narrow in both types. Of course, the measurements should be taken on the unworn part of the tooth, because wear can give a false scrofic section to a verrucosic underlying morphology. By these criteria, the canines of *Potamochoerus* are verrucosic.

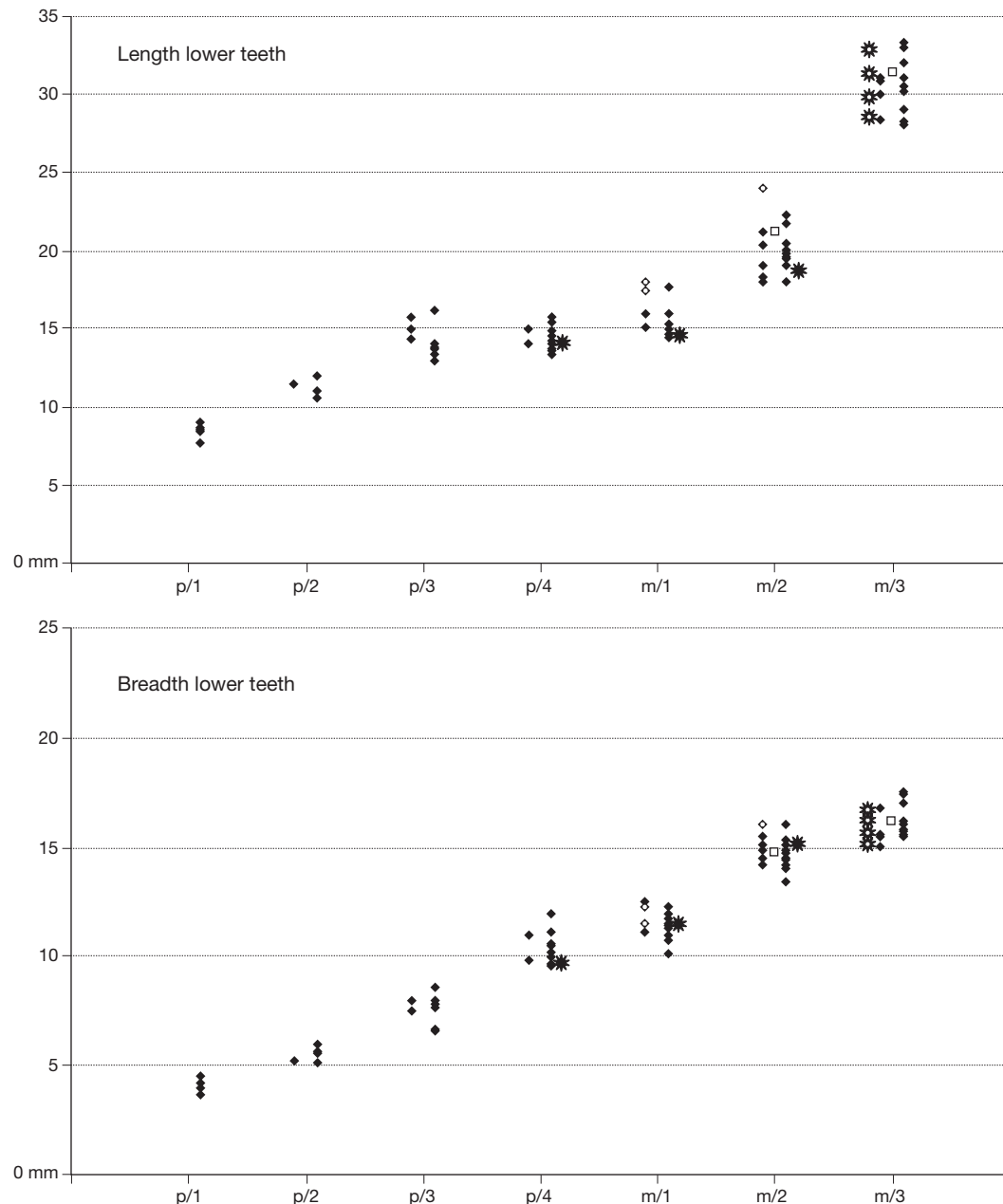


FIG. 17. — Length and breadth plots of the lower cheek teeth of *Dasychœrus arvernensis* (Croizet & Jobert, 1828) from Europe. In the midline (□) are the measurements of the teeth in the Dermenji mandible. To the left are measurements of teeth from Les Étouaires (◊) and Roussillon (Perpignan) (◆) and to the right are measurements of teeth from Afyonkarahisar, Alcoy, Autrey, Auvergne, Bra, Çalta, Capeni, Dinar Akçakoy, Gödöllő, Hajnacka, Herbolzheim, Ivanovce, Milia, Trévoux, Virgis, and Villafranca d'Asti (see Appendix 1 for data sources). Further to the right are specimens from Ethiopia (✱) and further to the left are specimens from Chad (✱) (Appendix 2).

Reproductive potential of *Suidae*

Species of *Sus* (*sensu lato*) differ from most other artiodactyls by their reproductive potential. They are the only group to give birth to several offspring at a time (litters range from one to twelve in *Sus*) (Table 1). Other suids tend to give birth to fewer offspring (one to six in *Porcula* Hodgson, 1847 and one to two in *Babryrousa* Perry, 1811, usually two in *Phacochoerus* (but as many as four have been observed by the senior author), and perhaps two in *Hylochoerus*). Peccaries usually give birth to fewer offspring (one to four, usually two) and most other artiodactyls only one or two offspring at a time. Given that in

Sus scrofa sexual maturity is attained at 18 months, gestation is 115 days and life span ranges from 15 to 20 years, a sow that starts breeding at an age of two years may leave behind an astonishing number of descendents, especially if she breeds twice each year (White 1788).

Rates of evolution

A consequence of having large litters and relatively short generation times (Table 1) is that evolution seems to have occurred more slowly when compared with other artiodactyls which have only one or two offspring per pregnancy and

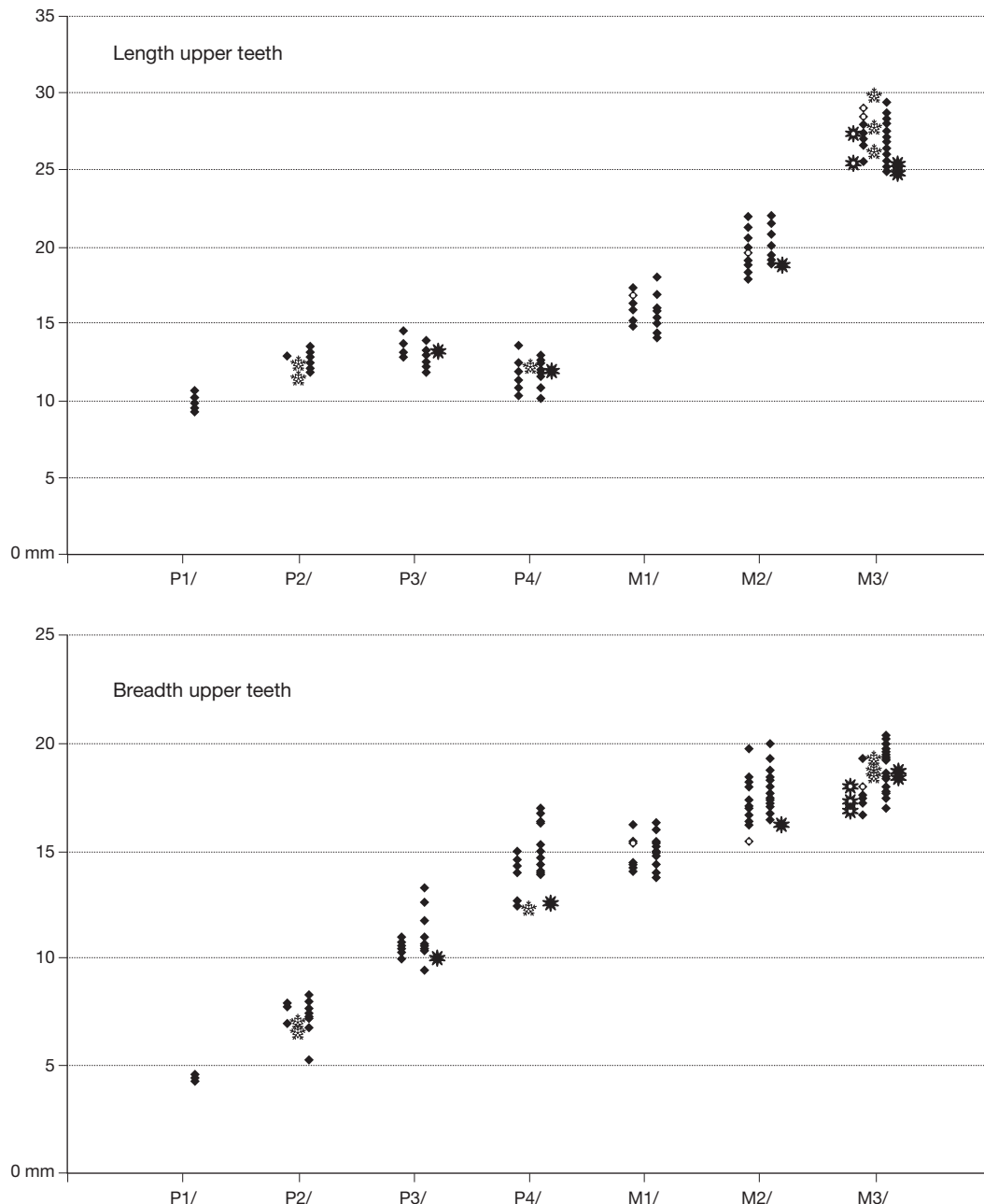


FIG. 18. — Length and breadth of upper cheek teeth of *Dasychœrus arvernensis* (Croizet & Jobert, 1828) from Europe and Africa (Mabaget Formation, Tugen Hills, Kenya). Symbols are the same as in Figures 16 and 17, except that the hollow snowflake symbol (*) in the middle line refers to the fossils from Mabaget.

successive pregnancies more spaced apart. Suids with fewer offspring per pregnancy and longer gestation periods, such as *Phacochoerus* and *Hylochoerus*, appear, from their fossil record, to have evolved more rapidly than those lineages that have larger numbers of offspring (*Sus scrofa*, for example). The same probably applies to *Babyrousa*, which departs greatly from the basic suid grundplan as exemplified by *Sus*. Possessing warts, the babyrousa may be more closely related to *Dasychœrus* than to other suids.

There is debate about the possibility of a link between rates of evolution and reproductive strategies (K-strategy, r-strategy) in mammals, with evolution often occurring more rapidly in

K-strategists such as proboscideans, than in r-strategists such as many rodent taxa. However, some K-strategists, including rhinocerotids, underwent slow evolution. For this reason, rates of evolution in suines requires further study, but at present, the fossil record seems to support the notion that r-strategists such as *Sus scrofa* evolved more slowly than K-strategists such as *Phacochoerus*.

PHYLOGENY

Molecular evidence

Molecular techniques have thrown some light on relationships among extant suid lineages, although the results are actively debated without any firm consensus emerging from

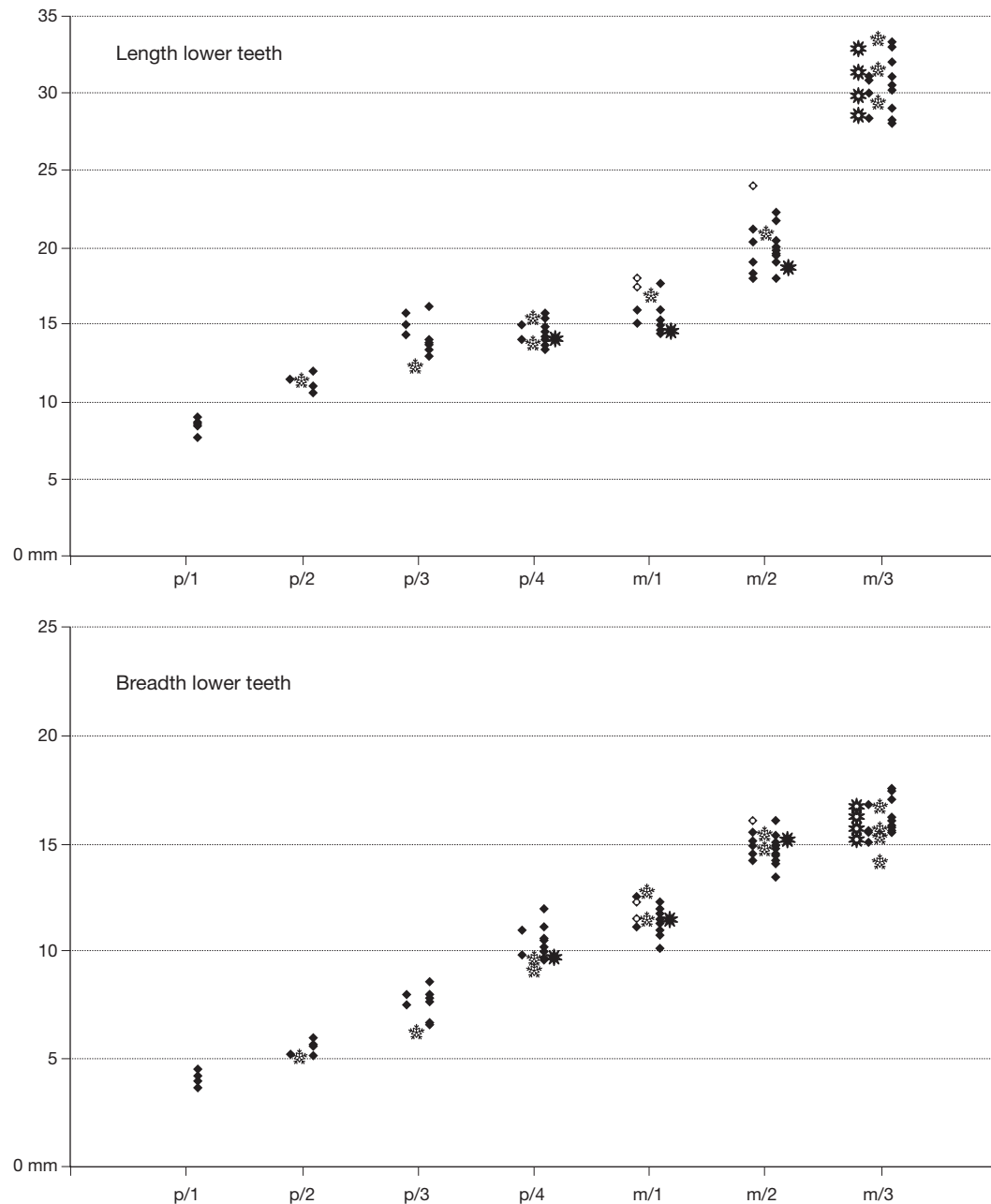


FIG. 19. — Length and breadth of lower cheek teeth of *Dasychœrus arvernensis* (Croizet & Jobert, 1828) from Europe and Africa (Mabaget Formation, Tugen Hills, Kenya). Symbols are the same as in Figures 16 and 17, except that the hollow snowflake symbol (*) in the middle line refers to the fossils from Mabaget.

the studies (Wu *et al.* 2006; Funk *et al.* 2007; Gongora *et al.* 2010; Frantz *et al.* 2013). The genus *Porcula*, for example, was for many years included in the genus *Sus* as a sister taxon of *Sus scrofa* (sometimes as a subgenus *Porcula* [Herre 1962]) with other species of *Sus* more distantly related. *Porcula* is now considered by some researchers (Funk *et al.* 2007) to represent a genus distinct from *Sus*, which means that some of the other species traditionally included in the genus *Sus* need to be reclassified into a separate genus or genera. From a morphological perspective two or three subgroups have been commonly recognised among the species hitherto included in *Sus* (Groves 1981, 1997;

Groves & Grubb 1993): 1) non-warty pigs (*Sus scrofa* and *Porcula salvania* Hodgson, 1847); and 2) warty pigs (all other species of “*Sus*”). Subdivision on the basis of lower canine morphology yields almost the same categories except that the “warty” subgroup is capable of further subdivision into two clusters: 2a) the *philippensis* group; and 2b) the *verrucosus* group. “*Sus*” *philippensis* poses particular problems because it is a “warty” pig, whereas some molecular analyses suggest closer affinities to *Sus scrofa* than to the other warty pigs (Funk *et al.* 2007). Warts occur in the African warthog, indicating possible phylogenetic links with the “warty” pigs, and so does the Giant Forest Hog



FIG. 20. — Mandible of *Dasychoerus arvernensis* (Croizet & Jobert, 1828) from Villafranca d'Asti, Italy (NHMB VI 144), showing thick mandibular bodies, one of the defining characteristics of the genus *Dasychoerus* Gray, 1873. Scale bar: 10 mm.

(*Hylochoerus*) (Ewer 1970). The bush pig (*Potamochoerus*) has thickened skin patches on the face (Ewer 1958) and some authors (MacDonald 2001) report that males have

these structures. This suggests that the presence of facial warts represents a derived (autapomorphic) feature of the group.



FIG. 21. — Left lateral view of male mandible of *Dasychoeus arvernensis* (Croizet & Jobert, 1828) from Villafranca d'Asti, Italy (NHMB VI 144), showing the procumbent incisors well beneath the level of the cheek teeth. Note the disproportionately small and low p/2 relative to p/3, a feature also found in *Potamochoerus* Gray, 1854. Scale bar: 10 mm.

On the basis of whole-genome analyses, Frantz *et al.* (2013) recognised a deep split between *Sus verrucosus* and *Sus scrofa*. Their cladogram shows a single specimen of “*Sus scrofa*” plotting within the clade comprising *Sus verrucosus* + *Sus barbatus* Müller, 1838 + *Sus celebensis* Müller & Schlegel, 1845, and this is the subspecies *Sus scrofa vittatus* Boie, 1828 (Müller & Schlegel 1845), from Sumatra, a tropical island form long ago considered by some authors (Lydekker 1915) (possibly in the basis of misidentified specimens – see Forsyth-Major [1897]) to be specifically distinct from boreal populations of *Sus scrofa*. This raises questions about the taxonomic affinities of *Sus scrofa vittatus* – is it really a subspecies of *Sus scrofa*? Old literature refers this species to the genus *Aulacochoerus* Gray, 1873, of which it is the type species. However, there has been confusion about which specimens belong to “*Sus*” *vittatus*, who the author of the species name was (Boie 1828 or Müller & Schlegel 1845) and where the type material came from (Java or Sumatra). According to Mees (1957) the lectotype of *Sus vittatus* is the skeleton numbered RMNH 13508, and the type locality is Tjikao aan de Tjitaroem, West Java, but according to Hardjasmita (1987) the holotype is a skull from Padang, Sumatra (RMNH Ost “d” in image page 51, but erroneously cited as Ost “c” in the text). Forsyth-Major (1897) re-identified four of the six skulls that Gray (1873) attributed to *Aulacochoerus vittatus* – NHMUK 1362f as a juvenile *Sus verrucosus*, NHMUK 1362c and 1362d as *Sus verrucosus amboinensis* (Forsyth-major, 1897) and NHMUK 1362g as *Sus verrucosus celebensis*. Thus from its inception, the concept of the genus *Aulacochoerus* was based on misidentifications of at least four out of six skulls.

In summary, recent molecular biology studies of suids indicate that the so-called Warty Pigs (*Dasychoeus*) and Bearded Pig (*Euhys*) are more closely related to each other, than any of them are to the Wild Boar (*Sus scrofa*) (Gongora *et al.* 2010; Frantz *et al.* 2013) or to *Phacochoerus* (the outgroup in the study by Frantz *et al.* 2013). On the basis of the fossil record, Pickford (2013e) postulated that the Wart Hog lineage (*Phacochoerus*) split from the Warty Pig lineage (*Dasychoeus*) during the Late Miocene which would accord with the molecular data.

TABLE 1. — Summary of life history and morphological variables of some species of extant suids. –, data not available.

Taxon	Body weight (kg)	Gestation period (days)	Mammae (pairs)	Longevity (years)
<i>Sus scrofa</i> Linnaeus, 1758	50-200	115	6	15-20
<i>Porcula salvania</i> Hodgson, 1847	6-9	100	3	10-12
<i>Euhys barbatus</i> (Müller, 1838)	140	120	–	–
<i>Dasychoeus verrucosus</i> (Müller & Schlegel, 1845)	185	120	6	14
<i>Dasychoeus celebensis</i> (Müller & Schlegel, 1845)	50-350	–	6	–
<i>Hylochoerus meinertzhageni</i> Thomas, 1904	130-275	149-154	3	–
<i>Phacochoerus aethiopicus</i> (Pallas, 1767)	50-100	170-175	2	12-15
<i>Babyrousa babyrussa</i> Rafinesque, 1815	90	125-150	1	24
<i>Potamochoerus porcus</i> (Linnaeus, 1758)	50-120	127	3	10-15

Fossil evidence

The morphometric resemblances between European and African *Dasychoeus arvernensis*, the Kvabebi suid, and *Kolpochoerus phillipi* are flagrant. The Kvabebi suid has pachygnathous mandibles, the dorsal profile of the skull is moderately dished, the lower incisors are well beneath the occlusal surface of the cheek teeth, and the lateral edges of the supra-canine flanges project upwards, all features observed in species of *Kolpochoerus*. Souron *et al.* (2013) listed two of these characters as unambiguous synapomorphies of the group comprising *Potamochoerus*, *Hylochoerus* and *Kolpochoerus*. The lateral extent of the zygomatic arches cannot be determined in the Kvabebi skull, due to damage, but what remains appears to be pneumatized. A dished cranial profile is listed by these authors as a synapomorphy of *Hylochoerus* and *Kolpochoerus*, but such a morphology also occurs in the Kvabebi skull. Furthermore,

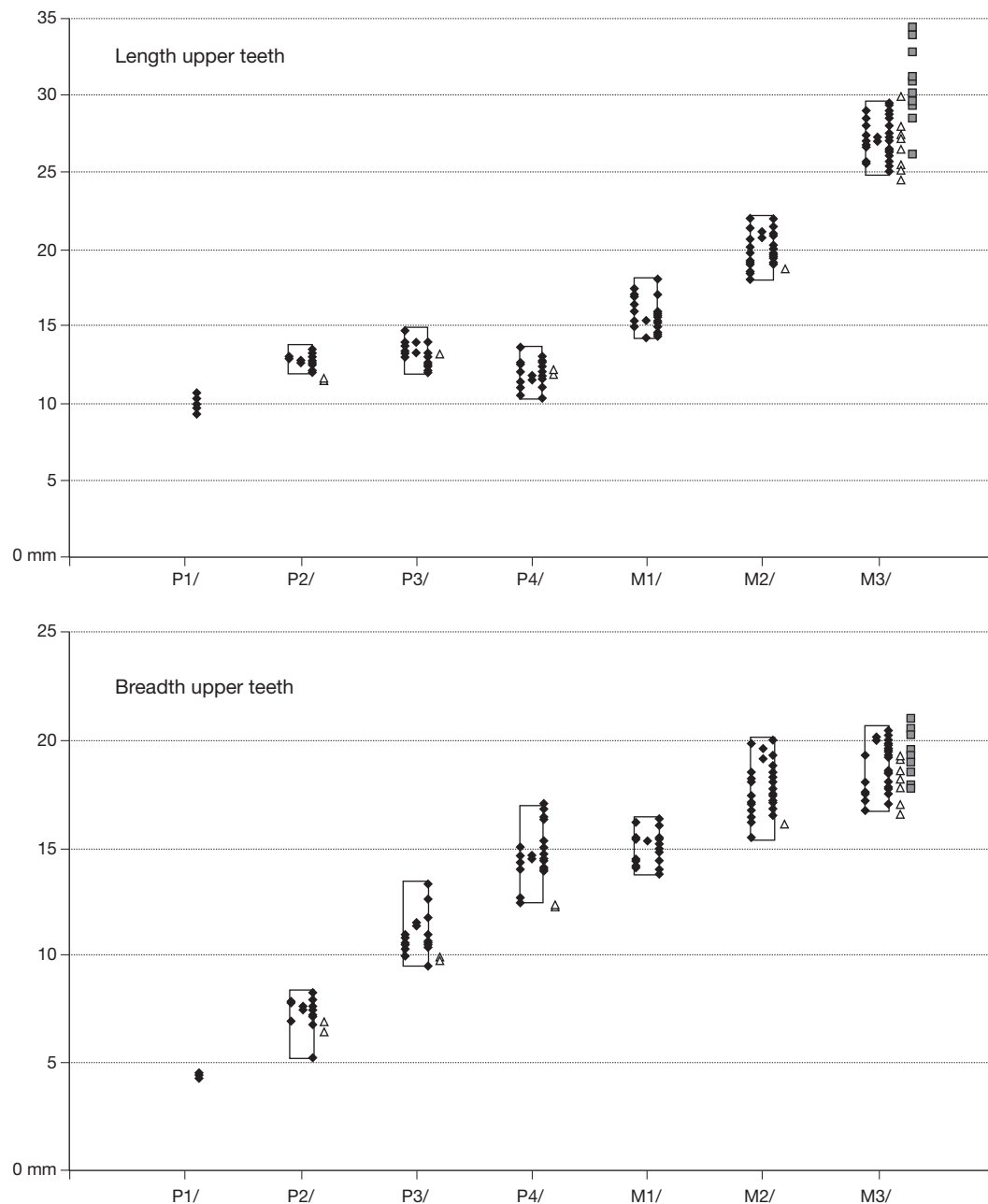


FIG. 22. — Comparison of dimensions of the upper cheek teeth of *Dasychoerus arvernensis* (Croizet & Jobert, 1828) from Europe (◆) and African fossils attributed to the same species (previously as *Kolpochoerus deheinzellini* Brunet & White, 2001 [Δ]) and the fossils attributed to *Kolpochoerus millensis* Haile-Selassie & Simpson, 2012 (■) in the right hand column (measurements of only the M3/ are available, Haile-Selassie & Simpson 2012).

Dasychoerus arvernensis and the Kvabebi suid have procumbent lower incisors that are positioned well beneath the level of the occlusal surface of the cheek teeth. The latter character was listed by Souron *et al.*, (2013) as a potential synapomorphy of *Kolpochoerus*. Because of all this, it is concluded that *Dasychoerus arvernensis* and the Kvabebi suid are closely related to *Kolpochoerus*, *Potamochoerus* and *Hylochoerus*.

The importance of *Dasychoerus arvernensis*

The fossil suids from Ethiopia and Chad previously attributed to *Kolpochoerus deheinzellini* by Brunet & White in 2001, are

so similar to material of *Dasychoerus arvernensis*, that Pickford (2012) proposed that the two species were synonymous, with *Dasychoerus arvernensis* (Croizet & Jobert, 1828) having priority over *Kolpochoerus deheinzellini* Brunet & White, 2001. The metric analysis (Figs 16, 17) indicates how close the African and European material is, as does the morphology of the cheek teeth. The fact that the African and European fossils span the same time range strengthens the taxonomic conclusions, otherwise one would need to explain how Lower Pliocene suids from Africa and Europe which are morphometrically compatible with each other and which occurred

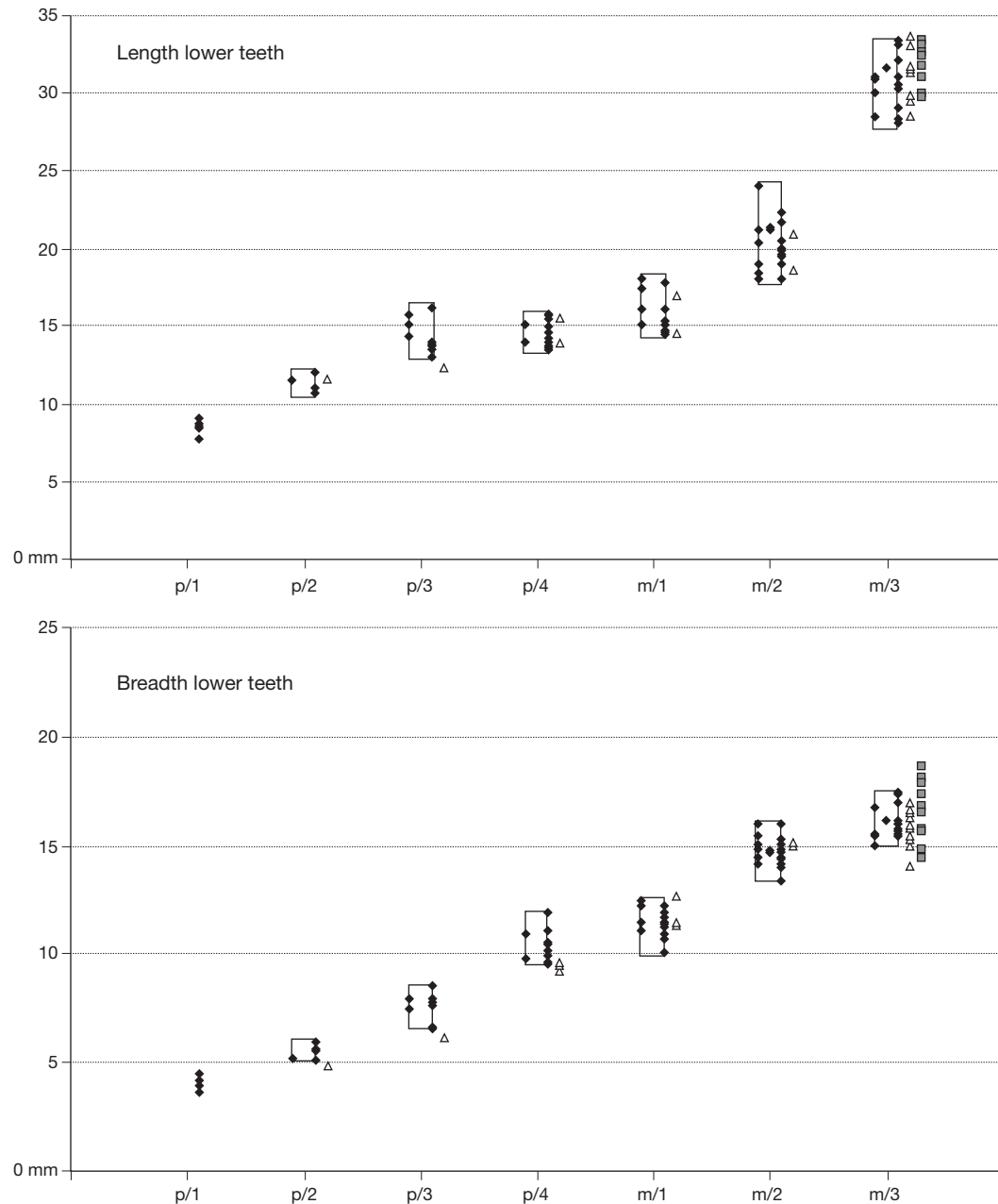


FIG. 23. — Comparison of dimensions of the lower cheek teeth of *Dasychœrus arvernensis* (Croizet & Jobert, 1828) from Europe (◆) and African fossils attributed to the same species (previously as *Kolpochoerus deheinzeli* Brunet & White, 2001 [Δ]) and the fossils attributed to *Kolpochoerus millensis* Haile-Selassie & Simpson, 2012 (■) in the right hand column (measurements of only the m/3 are available, Haile-Selassie & Simpson 2012).

as contemporaries, could belong to two distinct genera. Furthermore, such a decision would once again leave the African kolpochoeres without an ancestral group which runs against the almost universally accepted scenario that their ancestors must have dispersed into Africa from Eurasia during the basal Pliocene (Cooke & Wilkinson 1978; Pickford 2012).

BIOGEOGRAPHY OF EXTANT AND EXTINCT SUIDAE AND DISTRIBUTION OF DASYCHOERUS SPECIES

As a consequence of their high potential for demographic increase, extant suid species are capable of rapidly expand-

ing their range, and the same appears to have been the case in the past. The fossil record reveals that suids were often in the vanguard of mammalian lineages dispersing to newly available territory, as for example when passage between two continents, or between continents and islands, became possible (Pickford 1993). Feral pigs have often expanded rapidly into suitable environments, even when subjected to human intervention (hunting, trapping) aimed at reducing or controlling their populations.

Today confined to Java and the Celebes (and some nearby islands [Forsyth-Major 1897]), the genus *Dasychœrus* was

extremely widespread during the Pliocene, a period during which a diversity of mammals and other vertebrates spread widely over mid-latitude Eurasia which was tropical to sub-tropical at the time. Among the dispersals from the Far East to Europe were the tapir, the panda, the peafowl, bunodont otters, some bovids, hyaenids, giraffids, rhinocerotids, camels and monkeys, some of which managed to disperse southwards into Africa, such as some bovids, bunodont otters and other carnivores, *Dasychoerus*, the pea-fowl, giraffids and camels (Pickford 2012).

The poor Pliocene record in Peninsular India and the Iranian-Arabian corridor represents a void in our knowledge. A similar fossil void extends over much of Africa. Further palaeontological discoveries in these regions may fill some of the blank areas, but the overall picture that emerges is that the Far East, mid-latitude Eurasia and Africa were for a while (MN 14-MN 15: 6-3 Ma) part of a widespread tropical to subtropical biogeographic province over the extent of which dispersal by mammals was relatively easily accomplished. The high latitude limit of this palaeobiogeographic province was probably much as shown on the map (Fig. 24) (many fossil sites are known from this high latitude zone, but none have yielded *Dasychoerus*). Instead they contain proto-boreal taxa, including *Sus* sensu stricto (*Sus scrofa* and close relatives).

Dasychoerus has been found in Pliocene and Pleistocene deposits in Asia, Europe and Africa (Pickford 2012, 2013a, b) (Fig. 24). In Eurasia it has usually previously been identified as *Sus*, whereas in Africa early representatives of the genus were previously attributed to *Kolpochoerus* and/or *Potamochoerus*.

This paper recognises several species of the genus *Dasychoerus* in the fossil record, as well as the survival of at least two extant species, *Dasychoerus verrucosus* and *Dasychoerus celebensis* which, among extant suids, are most closely related to *Euhys barbatus* and more distantly related to *Sus scrofa* (Frantz *et al.* 2013).

At present *Dasychoerus* is restricted to the Island of Java (and small islands close to Java) (*D. verrucosus*) and Sulawesi (*D. celebensis*). However, the genus was widespread through Asia, Europe and Africa during the Pliocene and into the Pleistocene (Appendix 3). Hardjasmita (1987) reported that *Sus verrucosus* is also present in Malasia and Sumatra.

The small extinct species *Dasychoerus arvernensis* was the most widespread member of the genus, being common in Europe, Asia and Africa. The large extinct species *Dasychoerus stozzii* appears to have been confined to Europe and the Middle East, although Gallai (2007) thought that it might have spread to Africa to give rise to *Kolpochoerus*. The extinct Pleistocene species *Dasychoerus macrognathus* has been reported from Java, Myanmar and China, and it could represent the ancestor of the extant species *Dasychoerus verrucosus*.

Fossils attributed to *Dasychoerus* have been reported from many localities throughout the Old World (Appendix 3).

Origin of the *Kolpochoerus* lineage

Wherever its ultimate centre of origin is determined to have been (the Far East? – similar species are known from Java (Hardjasmita 1987), Myanmar (Pickford 2013b) and China (Han 1987; Pickford 2013b), as well as the Siwaliks of Indo-

Pakistan (Pickford 1988) – *Dasychoerus arvernensis* was in the right place (mid-latitude Eurasia) at the right time (basal Pliocene) to spread to Africa (Fig. 24) whereupon it gave rise to the *Kolpochoerus* and subsequently to the *Hylochoerus* lineage (Pickford 2013a, d) and possibly to *Potamochoerus* as well, an old idea (Cooke 1978; Bishop 2010), resurrected by Souron *et al.* (2013). The earliest record of this genus in Africa is *Dasychoerus natrunensis* Pickford, 2012, which either evolved into *Dasychoerus arvernensis*, or was replaced by a second wave of dispersal by the latter species – it did not change its generic status while entering the continent, but only later, when it was subjected to a variety of selective pressures which led to modifications in its dimensions (generally increasing in size), skull morphology (cranial dishing, expansion of the cranial table, swelling and drooping of the zygomatic arches) and dental morphology (increased hypsodonty, elongation of the third molars by addition of loph(id)s to the talon(id), hypertrophy of the canines, reduction of anterior cheek teeth).

Gallai (2006, 2007) postulated a slightly different scenario for the origin of *Kolpochoerus*, which he considered could be descended from *Sus arvernensis* via *Sus stozzii*. Whilst we agree that *Kolpochoerus afarensis* and *Dasychoerus stozzii* are related to each other and are comparable in dimensions and some details of morphology, we prefer to derive the genus *Kolpochoerus* earlier than is implied by the hypothesis of Gallai (2007). We estimate that the dichotomy between the *Dasychoerus arvernensis-stozzii* lineage on the one hand and the *Dasychoerus arvernensis-Kolpochoerus* lineage on the other occurred during the Pliocene *c.* 3.5 million years ago (Pickford 2012). Nevertheless, there could have been some gene flow among suid populations of Europe and Africa during the Lower Pliocene.

What the new interpretations of the fossil record reveal is that in mid-latitude Eurasia and Africa during the Plio-Pleistocene there was a widespread clade of suids related to the extant species *Dasychoerus verrucosus* which was adapted to tropical and sub-tropical regions which differed in several features from the Wild Boar (*Sus scrofa* and relatives) which is well adapted to boreal regions. During the Pleistocene the latter lineage populated mid-latitude regions formerly occupied by *Dasychoerus* species, either displacing *Dasychoerus* from its former more northern habitats, or simply moving in after *Dasychoerus* had died out in those regions consequent to climatic change (increased severity of Plio-Pleistocene cooling), with its descendants surviving only in the tropical parts of Asia, and in Africa.

CONCLUSIONS

Suid fossils from basal Pliocene deposits of Moldova provide fuel for the debate about the origin and affinities of European *Dasychoerus arvernensis* (Croizet & Jobert, 1828) and African *Kolpochoerus deheinzellini* Brunet & White, 2001, and related suids. It is likely that the two named taxa are synonymous (Pickford 2012). There is also a potential phylogenetic link to the the Kvabebi, Georgia, suid (Vekua 1972).

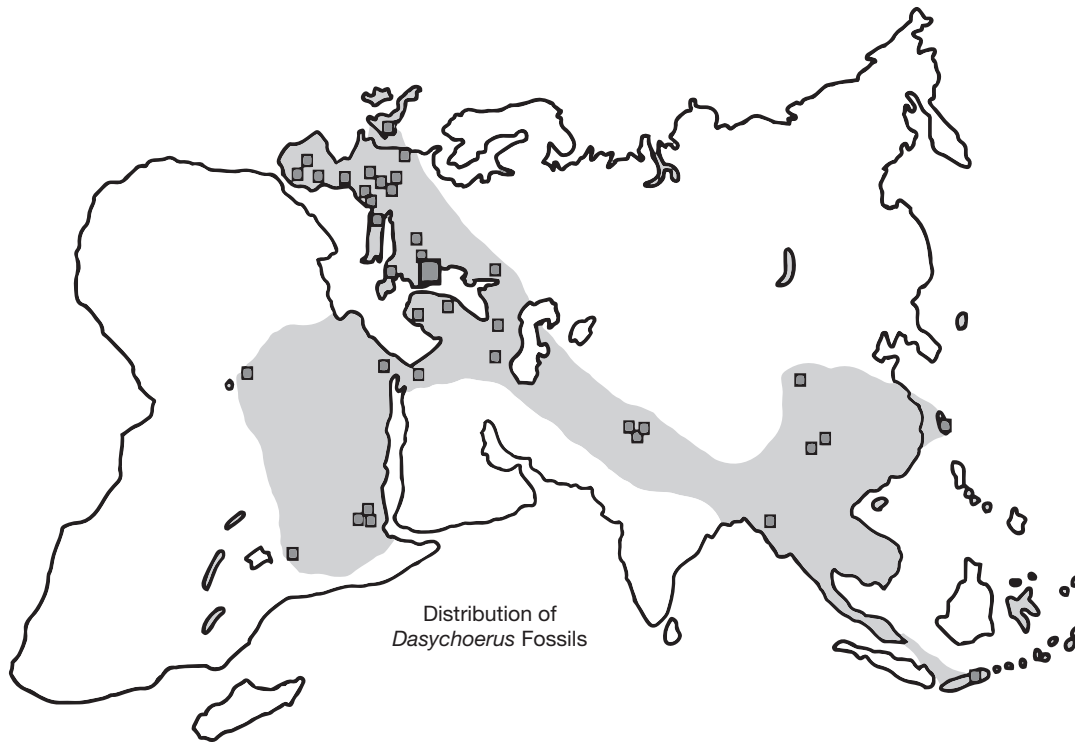


FIG. 24. — Map of the Old World showing the reconstructed Plio-Pleistocene distribution of *Dasychoerus* Gray, 1873 (grey zones) (fossil localities: squares). The large square west of the Black Sea localises Musaitu and Dermenji, Moldova.

The suids from Musaitu and Dermenji fit well with the correlations proposed previously (Pevzner *et al.* 1996, 2001; Nadachowski *et al.* 2006) more or less equivalent to the Ruscinian of France, – indeed, the Carbolia unit has been termed the Moldovan Ruscinian – and possibly a little earlier than the stratigraphic succession at Villafranca d’Asti in Italy that yielded *Dasychoerus arvernensis*. An age of c. 5–4 Ma for Musaitu would fit well with the other records of the species, not only in Europe, but also in Africa, where the same taxon has been described in Ethiopia and Chad under the name *Kolpochoerus deheinzellini*. In Ethiopia the range of the species is c. 5.2–3.8 Ma (Brunet & White 2001) which coincides closely with the estimated age span of the Moldovan Mammal Complex (Pevzner *et al.* 1996). The Kenyan material, from the Mabaget Formation in the Tugen Hills, spans the period around 5 Ma to 4.5 Ma (Pickford *et al.* 2009). The type material of *Dasychoerus arvernensis* from Les Étouaires, Perrier, France is dated between 3.9 and 3.1 Ma on the basis of age determinations of lava flows beneath and above the fossiliferous deposits (Bout 1968).

The *Phacochoerus* lineage is more likely to have descended from a distinct ancestor, “*Sus*” *provincialis* (Blainville, 1847), via *Potamochoeroides* Dale, 1948, from Makapansgat and Bolt’s Farm, South Africa (Bender 1992; Pickford 2012) thence to *Notochoerus* Broom, 1931 (Pickford 2013e) and onwards to *Metridiochoerus* Hopwood, 1926 (Pickford 2013a, d) and eventually to *Phacochoerus* Cuvier, 1826.

The similarities between the faunas from Musaitu and Dermenji on the one hand and coeval localities in south-

ern Europe on the other, indicate the former presence of a widespread biogeographic province extending from Spain in the west to Moldova and Ukraine in the east, and from the shores of the Mediterranean as far north as England, Hungary and Slovakia. This region evidently had biogeographic links to Indo-Pakistan, Myanmar, Java and China, because *Dasychoerus* was also widespread in those regions during the Plio-Pleistocene. During the Pliocene this biogeographic province had relatively open dispersal opportunities with Africa, with evidence of several lineages of mammals dispersing from north to south (among the suids, *Dasychoerus* entered Africa in latest Miocene to basal Pliocene times and evolved into the *Kolpochoerus* and *Hylochoerus* lineages) and vice versa (*Kolpochoerus*, having originated in Africa, dispersed to the Middle East and India, and possibly as far as China during the Late Pliocene and Early Pleistocene).

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APPENDICES

APPENDIX 1. — Measurements (in mm) of the teeth of *Dasychoerus arvernensis* (Croizet & Jobert, 1828) from Europe. Abbreviations: **B.**, Berdondini; **G.**, Guérin; **MDL**, mesio-distal length; **BLB**, bucco-lingual breadth; **lt**, left; **rt**, right; **ms**, manuscript; **est.**, estimated; **Own**, refers to the author's measurements and the year of acquisition.

Catalogue	Tooth	MDL	BLB	Locality, Country	Data source and comments
NHMB VI 144	c/1 lt	21.3	15	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 144	c/1 rt	21.6	15.4	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 184	c/1 rt	15.7	11.3	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 144	C1/ lt	22	18	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 144	C1/ rt	22.6	17	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 147	CI/ lt	22.3	17.3	Villafranca d'Asti, Italy	Own, 2012
MNHN.F.PET2005	d/2 lt	8.3	4	Les Étouaires, France	Own, 2011
MNHN.F.PET2005	d/2 rt	8.8	3.8	Les Étouaires, France	Own, 2011
MNHN.F.PET2005	d/3 lt	10.2	5.6	Les Étouaires, France	Own, 2011
MNHN.F.PET2005	d/3 rt	10.8	5.8	Les Étouaires, France	Own, 2011
MNHN.F.PET2005	d/4 lt	18.8	10	Les Étouaires, France	Own, 2011
MNHN.F.PET2005	d/4 rt	19	9.9	Les Étouaires, France	Own, 2011
MNHN.F.PET2005	D2/ lt	10.2	6.7	Les Étouaires, France	Own, 2011
MNHN.F.PET2005	D3/ lt	13	10.2	Les Étouaires, France	Own, 2011
MNHN.F.ACA313	D4/	16	14.5	Çalta, Turkey	Guérin <i>et al.</i> 1998
BGSK sans n° Boyton	D4/ lt	0	13	Red Crag (Boyton), England	Own, 2011
NHMB VI 8	D4/ lt	14	13	Villafranca d'Asti, Italy	Own, 2012
MNHN.F.PET2005	D4/ lt	14.2	12	Les Étouaires, France	Own, 2011
NHMB VI 144	i/1 lt	7.4	10.4	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 145	i/1 lt	6	11	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 144	i/1 rt	7	10.7	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 145	i/1 rt	6	0	Villafranca d'Asti, Italy	Own, 2012
CCECL Pp 199b	i/2 lt	8.7	12	Perpignan, France	Own, 2011
BGSK sans n° Boyton	i/2 lt	7.2	8.8	Red Crag (Boyton), England	Own, 2011
NHMB VI 144	i/2 lt	7	11.2	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 145	i/2 lt	6	11.6	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 144	i/2 rt	7.6	12.3	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 145	i/2 rt	6	11.8	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 145	i/3 rt	7	9.4	Villafranca d'Asti, Italy	Own, 2012
MNCN cast	I1/ lt	17.3	8.7	Alcoy, Spain	Own, 2011
NHMB VI 144	I1/ lt	10.5	13.7	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 144	I1/ rt	10.9	13.3	Villafranca d'Asti, Italy	Own, 2012
MSG P 136	p/1	8.5	4.5	Capeni, Romania	Samson <i>et al.</i> 1971
MC 12	p/1	8.6	4.2	Virghis, Romania	Samson <i>et al.</i> 1971
NHMB VI 178	p/1	8.7	3.7	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 145	p/1 rt	7.7	4	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 181	p/1 rt	9	4	Villafranca d'Asti, Italy	Own, 2012
MSG P 136	p/2	12	6	Capeni, Romania	Samson <i>et al.</i> 1971
NHMB VI 182	p/2 lt	10.6	5.7	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 144	p/2 lt	11	5.1	Villafranca d'Asti, Italy	Own, 2012; G. ms as 11 × 5
NHMB VI 145	p/2 lt	11	5.6	Villafranca d'Asti, Italy	Own, 2012; G. ms as 11 × 5
CCECL Pp 195	p/2 lt	11.5	5.2	Perpignan, France	Own, 2011
FSL 41 190	p/3 lt	15	7.5	Perpignan, France	Own, 2011; G. ms as 14.5 × 7.5; FSL 41 100
NHMB DP 8	p/3 lt	16.2	8.6	Herbolzheim (cast), Germany	Own, 2012
NHMB VI 145	p/3 lt	13.4	8	Villafranca d'Asti, Italy	Own, 2012; G. ms as 14 × 8
NHMB VI 176	p/3 lt	13.8	7.8	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 144	p/3 lt	14	6.6	Villafranca d'Asti, Italy	Own, 2012; G. ms as 14 × 6.5
NHMB VI 17	p/3 lt	14	7.7	Villafranca d'Asti, Italy	Own, 2012
CCECL Pp 195	p/3 lt	14.3	0	Perpignan, France	Own, 2011; G. ms 15 × 7.5
CCECL Pp 2601	p/3 rt	15.7	8	Perpignan, France	Own, 2011; G. ms as 15 × 8
NHMB VI 145	p/3 rt	13	7.7	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 144	p/3 rt	13.7	6.7	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 172	p/3 rt	14	8	Villafranca d'Asti, Italy	Own, 2012
Coll Aymard	p/4	15	11	Perpignan, France	G. ms
PIMUZ A/V 2347	p/4 lt	14.6	10.5	Dinar Akçakoy, Turkey	Own, 2014
NHMB VI 144	p/4 lt	13.7	9.6	Villafranca d'Asti, Italy	Own, 2012; G. ms as 14 × 9.5
NHMB VI 145	p/4 lt	14	10.6	Villafranca d'Asti, Italy	Own, 2012; G. ms as 14.5 × 10
NHMB VI 17	p/4 lt	14.2	10.2	Villafranca d'Asti, Italy	Own, 2012
CCECL Pp 195	p/4 lt	14	9.8	Perpignan, France	Own, 2011; G. ms 14.5 × 10
MCNM	p/4 rt	15.4	12	Alcoy, Spain	Own, 2011
NHMB DP 7	p/4 rt	15.7	11.1	Herbolzheim (cast), Germany	Own, 2012
NHMB VI 144	p/4 rt	13.4	9.7	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 145	p/4 rt	13.6	10.5	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 173	p/4 rt	14.9	10	Villafranca d'Asti, Italy	Own, 2012
YORYM 2011.1119	p/4 rt	15.5	10.4	Red Crag (Boyton), England	Own, 2011
YORYM 2011.1101	p/4 rt	13.8	10.2	Red Crag, England	Own, 2011
IM 31 Walford coll.	p/4 rt	14.9	10	Red Crag, England	Own, 2011

APPENDIX 1. — Continuation.

Catalogue	Tooth	MDL	BLB	Locality, Country	Data source and comments
YORYM 2011.1105	p/4 rt	15.5	10	Red Crag, England	Own, 2011
MCNM	m/1 lt	17.7	12.3	Alcoy, Spain	Own, 2011
PIMUZ A/V 2347	m/1 lt	14.4	10.7	Dinar Akçakoy, Turkey	Own, 2014
NHMB VI 145	m/1 lt	14.4	11	Villafranca d'Asti, Italy	Own, 2012; G. ms as 14.5 × 11.5; B. 1992 as 14 × 12
NHMB VI 144	m/1 lt	15	11.7	Villafranca d'Asti, Italy	Own, 2012; G. ms as 15.5 × 11.5; B. 1992 as 14 × 12
NHMB VI 17	m/1 lt	15	0	Villafranca d'Asti, Italy	Own, 2012; G. ms as 14 × 0; B. 1992 as 13 × 12
YORYM 2011.1123	m/1 lt	0	11.7	Red Crag, England	Own, 2011
MNHN.F.PET2006	m/1 lt	17.4	12.3	Les Étouaires, France	Own, 2011; G. ms 18 × 13
CCECL Pp 195	m/1 lt	15.1	11.1	Perpignan, France	Own, 2011; G. ms 15.5 × 11
FSL 41 098	m/1 rt	16	11.5	Perpignan, France	Own, 2011; G. ms 16 × 11
MPV S/S Alcoy	m/1 rt	15	10.1	Alcoy, Spain (cast)	Own, 2011
FSL 40 151	m/1 rt	15.3	11.3	Montpellier, France	Own, 2011; G. ms 15 × 11.5
NHMB VI 144	m/1 rt	14.5	12	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 145	m/1 rt	14.7	11.5	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 170	m/1 rt	16	11.4	Villafranca d'Asti, Italy	Own, 2012
BGSK sans n° Boyton	m/1 rt	0	11.2	Red Crag (Boyton), England	Own, 2011
NHMUK M 44049	m/1 rt	15.6	10.9	Red Crag, England	Own, 2011
YORYM 2011.1114	m/1 rt	16.4	11.2	Red Crag, England	Own, 2011
MNHN.F.PET2005	m/1 rt	18	12.5	Les Étouaires, France	G. ms
NHMB Rss 70	m/2	18	14.5	Perpignan (Roussillon), France	G. ms
Ivanovce 6513c	m/2	19.5	15.1	Ivanovce, Slovakia	Hünemann, 1971
FSL 41 097	m/2 lt	20.3	15.1	Perpignan, France	Own, 2011; G. ms 20 × 15
CCECL Pp 196	m/2 lt	21.2	15.5	Perpignan, France	Own, 2011; G. ms 21.5 × 15.5
NMENHM	m/2 lt	21.2	14.7	Dermenji, Moldova	Own, 2011
MCNM	m/2 lt	20	14.9	Alcoy, Spain	Own, 2011
PIMUZ A/V 2347	m/2 lt	19.6	14	Dinar Akçakoy, Turkey	Own, 2014
OB 5903	m/2 lt	22.3	16	Gödöllő, Hungary	Mottl 1939 as <i>P. provincialis minor</i>
NHMB VI 17	m/2 lt	18	15	Villafranca d'Asti, Italy	Own, 2012; G. ms as 18.5 × 14.5; B. 1992 as 18 × 17
NHMB VI 145	m/2 lt	19.5	14.7	Villafranca d'Asti, Italy	Own, 2012; G. ms as 19 × 15, B. 1992 as 19 × 15
NHMB VI 144	m/2 lt	19.8	15	Villafranca d'Asti, Italy	Own, 2012; G. ms as 19 × 15, B. 1992 as 18 × 15
NHMUK M 5224	m/2 lt	17.8	13.8	Red Crag, England	Own, 2011
NHMUK M 44693	m/2 lt	19.7	14.8	Red Crag, England	Own, 2011
YORYM 2011.1104	m/2 lt	21.3	14	Red Crag, England	Own, 2011
MNHN.F.PET2005	m/2 lt	24	16	Les Étouaires, France	Own, 2011; G. ms as 25 × 17
CCECL Pp 195	m/2 lt	18.3	14.2	Perpignan, France	Own, 2011; G. ms 19 × 14.5
NHMB Perp	m/2 rt	19	14.9	Perpignan, France	Own, 2012
NMENHM	m/2 rt	21.3	14.8	Dermenji, Moldova	Own, 2011
PIMUZ A/V 2347	m/2 rt	19.5	14.4	Dinar Akçakoy, Turkey	Own, 2014
NHMB DP 7	m/2 rt	21.7	14.2	Herbolzheim (cast), Germany	Own, 2012
MIL 696	m/2 rt	20	14.5	Milia, Greece	Guérin & Tsoukala 2013 as left
FSL 40 151	m/2 rt	19.6	13.4	Montpellier, France	Own, 2011; G. ms 21 × 15
NHMB VI 145	m/2 rt	19	15.3	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 144	m/2 rt	20	15	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 169	m/2 rt	20.4	14.4	Villafranca d'Asti, Italy	Own, 2012
NWHCM FC 2912	m/2 rt	21	14.2	Red Crag, England	Own, 2011
YORYM 2005.174.2.2	m/2 rt	22.7	16	Red Crag, England	Own, 2011
NHMB Rss 70	m/3	30	15	Perpignan (Roussillon), France	G. ms
Coll Aymard	m/3	30.5	17	Auvergne, France	G. ms
MSG P 136	m/3	31	0	Capeni, Romania	Samson <i>et al.</i> 1971
OB 5903	m/3	33.3	17.5	Gödöllő, Hungary	Mottl 1939; Fejfar 1964 as <i>P. provincialis minor</i>
Hajnacka 3983	m/3	33	17	Hajnacka, Slovakia	Hünemann 1971 est.
MC 12	m/3	32	16	Virghis, Romania	Samson <i>et al.</i> 1971
CCECL Pp 196	m/3 lt	30.8	16.8	Perpignan, France	Own, 2011; G. ms 31 × 17
MPV 186 ALA 4c cast	m/3 lt	30.2	15.8	Alcoy, Spain	Own, 2011
PIMUZ A/V 2347	m/3 lt	0	15.5	Dinar Akçakoy, Turkey	Own, 2014
NHMB VI 17	m/3 lt	28	0	Villafranca d'Asti, Italy	Own, 2012; G. ms as 30.5 × 0; B. 1992 as 27 × 15
NHMB VI 168	m/3 lt	28.3	15.5	Villafranca d'Asti, Italy	Own, 2012; G. ms as 28.5 × 15.5
NHMB VI 144	m/3 lt	32	17	Villafranca d'Asti, Italy	Own, 2012; G. ms as 30 × 17; B. 1992 as 28 × 16
YORYM 2005.174.1.2	m/3 lt	32.4	17.4	Red Crag (Boyton), England	Own, 2011
YORYM 2011.1127	m/3 lt	0	14.4	Red Crag, England	Own, 2011
IM 3 (72)	m/3 lt	28.3	15.9	Red Crag, England	Own, 2011

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Catalogue	Tooth	MDL	BLB	Locality, Country	Data source and comments
NHMuK M 9594	m/3 lt	29.1	15.4	Red Crag, England	Own, 2011; G. ms as 29 × 15
IM 15 Walford coll.	m/3 lt	30.7	16	Red Crag, England	Own, 2011
YORYM 2011.1121	m/3 lt	30.9	15.5	Red Crag, England	Own, 2011
NHMuK M 9149	m/3 lt	31	16	Red Crag, England	Own, 2011
YORYM 2011.1102	m/3 lt	32.2	17	Red Crag, England	Own, 2011
YORYM 2005.174.1.1	m/3 lt	33.9	17.7	Red Crag, England	Own, 2011
CCECL Pp 197	m/3 rt	28.4	15.5	Perpignan, France	Own, 2011; G. ms 29 × 15.5
NHMB Perp	m/3 rt	31	15.6	Perpignan, France	Own, 2012
NMENHM	m/3 rt	31.5	16.2	Dermenji, Moldova	Own, 2011
MCNM	m/3 rt	32	0	Alcoy, Spain	Own, 2011
PIMUZ A/V 2347	m/3 rt	0	15.6	Dinar Akçakoy, Turkey	Own, 2014
FSL 40 151	m/3 rt	29	16.2	Montpellier, France	Own, 2011; G. ms 31 × 15.5
NHMB VI 171	m/3 rt	0	15.7	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 145	m/3 rt	30.5	17.4	Villafranca d'Asti, Italy	Own, 2012; G. ms as 30.5 × 17.5; B. 1992 as 30 × 17
NHMB VI 144	m/3 rt	32	17	Villafranca d'Asti, Italy	Own, 2012
BGSK 1989	m/3 rt	0	14	Red Crag (Boyton), England	Own, 2011
BGSK sans n° Boyton	m/3 rt	0	15	Red Crag (Boyton), England	Own, 2011
BGSK 7311	m/3 rt	31.4	17.5	Red Crag (Waldringfield), England	Own, 2011
BGSK 483574 XVI/5/2/48	m/3 rt	29.3	14.7	Red Crag (Woodbridge), England	Own, 2011
NHMuK M 9148	m/3 rt	29.7	16	Red Crag, England	Own, 2011
NHMuK M 46574	m/3 rt	30.6	15.8	Red Crag, England	Own, 2011; G. ms as 29 × 15
NHMuK M 3782	m/3 rt	31.4	16.7	Red Crag, England	Own, 2011; G. ms as 31 × 16.5
FSL 40 154	m/3 rt	36.3	15.7	Montpellier, France	Own, 2011; extra pair of cusps
NHMB VI 146	P1/ lt	9.3	4.5	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 147	P1/ lt	10.7	4.6	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 21	P1/ rt	9.7	4.6	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 180	P1/ rt	9.9	4.3	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 22	P1/ rt	10.3	4.3	Villafranca d'Asti, Italy	Own, 2012
NHMB Rss 70	P2/	13	7	Perpignan (Roussillon), France	G. ms
PIMUZ A/V 2358	P2/ lt	12.2	7.3	Afyonkarahisar, Turkey	Own, 2014
NMENHM	P2/ lt	12.6	7.5	Musaitu, Moldova	Own, 2011
NHMB Perp	P2/ lt	12.9	7.9	Perpignan, France	Own, 2012
CCECL Br 87	P2/ lt	13	7.2	Trévoux (Reyrieux), France	Own, 2011; G. ms as 12.5 × 7.5
NHMB VI 179	P2/ lt	12	6.8	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 20	P2/ lt	12.5	7.7	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 144	P2/ lt	12.7	5.3	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 146	P2/ lt	13.2	8.3	Villafranca d'Asti, Italy	Own, 2012
MCNM	P2/ rt	13.5	0	Alcoy, Spain	Own, 2011
NMENHM	P2/ rt	12.7	7.7	Musaitu Moldova	Own, 2011
NHMB Perp	P2/ rt	13	7.8	Perpignan, France	Own, 2012
CCECL Br 87	P2/ rt	12.7	7.2	Trévoux (Reyrieux), France	Own, 2011
NHMB VI 144	P2/ rt	12.2	7.5	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 177	P2/ rt	12.5	7.5	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 18	P2/ rt	12.6	8	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 183	P2/ rt	12.7	7.2	Villafranca d'Asti, Italy	Own, 2012
NHMB Rss 70	P3/	14	11	Perpignan (Roussillon), France	G. ms
NMENHM	P3/ lt	13.2	11.4	Musaitu, Moldova	Own, 2011
CCECL Pp 198	P3/ lt	13	10.3	Perpignan (Citadelle), France	Own, 2011; G. ms 13 × 10.5
NHMB Perp	P3/ lt	13.7	10.5	Perpignan, France	Own, 2012
CCECL Pp 200	P3/ lt	14.7	10.6	Perpignan, France	Own, 2012; G. ms as 14 × 12
Piedrabuena	P3/ lt	14	9.5	Piedrabuena, Spain	Mazo & Torres 1990 as right
CCECL Br 87	P3/ lt	13	10.5	Trévoux (Reyrieux), France	Own, 2011; G. ms as 13.5 × 10.5
NHMB VI 144	P3/ lt	12	10.6	Villafranca d'Asti, Italy	Own, 2012; G. ms as 13 × 10.5
NHMB VI 19	P3/ lt	12.5	11	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 146	P3/ lt	12.6	12.6	Villafranca d'Asti, Italy	Own, 2012; G. ms as 14 × 12.5
NHMB VI 174	P3/ lt	12.6	10.6	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 158	P3/ lt	13	11.8	Villafranca d'Asti, Italy	Own, 2012
BGSK 483566 XVI/5/2/103	P3/ lt	13	10	Red Crag (Boyton), England	Own, 2011
YORYM 2005.173.4	P3/ lt	13.5	10.8	Red Crag, England	Own, 2011
NMENHM	P3/ rt	14	11.5	Musaitu, Moldova	Own, 2011
NHMB Perp	P3/ rt	13.3	10.8	Perpignan, France	Own, 2012
CCECL Pp 198	P3/ rt	13.4	10	Perpignan, France	Depéret 1885 as left (now missing)
CCECL Br 87	P3/ rt	13.3	10.7	Trévoux (Reyrieux), France	Own, 2011
NHMB VI 1	P3/ rt	12.2	13.3	Villafranca d'Asti, Italy	Own, 2012; G. ms as 14 × 13
NHMB VI 161	P3/ rt	12.4	11	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 144	P3/ rt	13	10.4	Villafranca d'Asti, Italy	Own, 2012

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Catalogue	Tooth	MDL	BLB	Locality, Country	Data source and comments
NHMB VI 175	P3/ rt	13	11	Villafranca d'Asti, Italy	Own, 2012
NHMB Rss 62	P4/	10.5	14	Perpignan (Roussillon), France	G. ms
NHMB Rss 70	P4/	12	14	Perpignan (Roussillon), France	G. ms
NHMB VI 10	P4/	12.6	0	Villafranca d'Asti, Italy	Own, 2012
NHMB DP 6	P4/ lt	12.4	14.1	Herbolzheim (cast), Germany	Own, 2012
NMENHM	P4/ lt	11.5	14.5	Musaitu, Moldova	Own, 2011
CCECL Pp 198	P4/ lt	12.6	12.5	Perpignan (Citadelle), France	Own, 2011; G. ms 12.6 × 12.5
NHMB Perp	P4/ lt	11.4	14.6	Perpignan, France	Own, 2012
FSL 40 945	P4/ lt	13.6	14.3	Perpignan, France	Own, 2011; G. ms as 13.5 × 14 FSL 3084
Piedrabuena	P4/ lt	10.3	14	Piedrabuena, Spain	Mazo & Torres 1990 as right
CCECL Br 87	P4/ lt	11	14.4	Trévoux (Reyrieux), France	Own, 2011; G. ms as 11.5 × 15
NHMB VI 157	P4/ lt	11	14	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 146	P4/ lt	11.6	16.4	Villafranca d'Asti, Italy	Own, 2012; G. ms as 11.5 × 16.5
NHMB VI 160	P4/ lt	11.8	14.5	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 2	P4/ lt	11.9	15.3	Villafranca d'Asti, Italy	Own, 2012; G. ms as 12 × 15
NHMB VI 144	P4/ lt	12	14.4	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 9	P4/ lt	12.7	17	Villafranca d'Asti, Italy	Own, 2012
MIL 205	P4/ rt	13	15	Milia, Greece	Guérin & Tsoukala 2013
NMENHM	P4/ rt	11.8	14.6	Musaitu, Moldova	Own, 2011
CCECL Pp 198	P4/ rt	11	12.7	Perpignan (Citadelle), France	Own, 2011; G. ms 11.5 × 13
NHMB Perp	P4/ rt	12	14.6	Perpignan, France	Own, 2012
NHMB RS 62	P4/ rt	12.5	15	Perpignan, France	Own, 2012; G. ms as 12 × 16
CCECL Br 87	P4/ rt	11.6	14.5	Trévoux (Reyrieux), France	Own, 2011
NHMB VI 144	P4/ rt	11	13.9	Villafranca d'Asti, Italy	Own, 2012; G. ms as 12 × 14
NHMB VI 1	P4/ rt	11	16.3	Villafranca d'Asti, Italy	Own, 2012; G. ms as 11.5 × 16
NHMB VI 159	P4/ rt	11.5	14.7	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 162	P4/ rt	12	14.7	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 3	P4/ rt	12	16.8	Villafranca d'Asti, Italy	Own, 2012
Hajnacka 35421	M1/	15.3	15.4	Hajnacka, Slovakia	Hünemann 1971
NHMB Rss 70	M1/	15	15.5	Perpignan (Roussillon), France	G. ms
NHMB Rss 62	M1/	17	15.5	Perpignan (Roussillon), France	G. ms
MCNM	M1/ lt	16	15.2	Alcoy, Spain	Own, 2011
NHMB DP 6	M1/ lt	0	14	Herbolzheim (cast), Germany	Own, 2012
NMENHM	M1/ lt	14.2	15.3	Musaitu, Moldova	Own, 2011
CCECL Pp 198	M1/ lt	15.3	14.1	Perpignan (Citadelle), France	Own, 2011; G. ms 15.5 × 14
NHMB Perp	M1/ lt	16	14.4	Perpignan, France	Own, 2012
Piedrabuena	M1/ lt	14.6	14	Piedrabuena, Spain	Mazo & Torres 1990 as right
CCECL Br 87	M1/ lt	15.6	15.5	Trévoux (Reyrieux), France	Own, 2011; Mazo & Torres 1990, 15.4 × 14.8; G. ms as 15.5 × 16
NHMB VI 2	M1/ lt	14.3	15.2	Villafranca d'Asti, Italy	Own, 2012; G. ms as 13.5 × 15.5; B. 1992 as 14 × 15
NHMB VI 144	M1/ lt	15	14.8	Villafranca d'Asti, Italy	Own, 2012; G. ms as 15.5 × 15; B. 1992 as 15 × 14
NHMB VI 146	M1/ lt	15.8	16	Villafranca d'Asti, Italy	Own, 2012; G. ms as 16 × 16; B. 1992 as 15 × 15
NHMB VI 154	M1/ lt	16	14.4	Villafranca d'Asti, Italy	Own, 2012
YORYM 2011.1124	M1/ lt	16.3	13.9	Red Crag, England	Own, 2011
IM 24 Walford coll.	M1/ lt	17.2	13.4	Red Crag, England	Own, 2011
MNHN.F.PET2006	M1/ lt	17.4	15.4	Les Étouaires, France	Own, 2011; G. ms as 17.5 × 16
MPV 186 ALA 46 cast	M1/ rt	15	13.8	Alcoy, Spain	Own, 2011
MIL 205	M1/ rt	18	15.5	Milia, Greece	Guérin & Tsoukala 2013
NMENHM	M1/ rt	15.3	15.3	Musaitu, Moldova	Own, 2011
CCECL Pp 198	M1/ rt	15.3	14.2	Perpignan (Citadelle), France	Own, 2011; G. ms 16 × 14; Mazo & Torres 1990 as 15.5 × 14.5
NHMB Perp	M1/ rt	16.4	14.5	Perpignan, France	Own, 2012
NHMB RS 62	M1/ rt	16.9	16.2	Perpignan, France	Own, 2012; G. ms as 17 × 16
CCECL Br 87	M1/ rt	15.7	16	Trévoux (Reyrieux), France	Own, 2011; Mazo & Torres 1990, 16.2 × 15
NHMB VI 155	M1/ rt	14.5	14.9	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 1	M1/ rt	15.2	16	Villafranca d'Asti, Italy	Own, 2012; G. ms as 15 × 16; B. 1992 as 15 × 16
NHMB VI 144	M1/ rt	15.2	15	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 153	M1/ rt	16	14.4	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 3	M1/ rt	17	16.3	Villafranca d'Asti, Italy	Own, 2012
YORYM 2011.1128	M1/ rt	0	14.4	Red Crag, England	Own, 2011
NHMYUK M 44695	M1/ rt	16.2	13.8	Red Crag, England	Own, 2011
YORYM 2011.1120	M1/ rt	16.4	14	Red Crag, England	Own, 2011
Ivanovce 6513d	M2/	19.5	18.3	Ivanovce, Slovakia	Hünemann 1971
NHMB Rss 107	M2/	18	16.2	Perpignan (Roussillon), France	Azzaroli 1954; Mazo & Torres 1990
NHMB Rss 70	M2/	19	18	Perpignan (Roussillon), France	G. ms

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Catalogue	Tooth	MDL	BLB	Locality, Country	Data source and comments
NHMB Rss fig, 2	M2/	20.1	17.4	Perpignan (Roussillon), France	Azzaroli 1954; Mazo & Torres 1990
NHMB Rss 62	M2/	20.6	18.5	Perpignan (Roussillon), France	Azzaroli 1954; Mazo & Torres 1990; G. ms as 21 × 18
MCNM	M2/ lt	19	17.4	Alcoy, Spain	Own, 2011
MCNM	M2/ lt	19.2	17.1	Alcoy, Spain	Own, 2011
MGPOT (MB TI 449)	M2/ lt	19.6	19.3	Bra (Piemont), Italy	Own, 2011; G. ms as 20 × 19.5; Dal Piaz 1930 as 20 × 19.4
NMENHM	M2/ lt	20.7	19.6	Musaitu, Moldova	Own, 2011
CCECL Pp 198	M2/ lt	19	16.7	Perpignan (Citadelle), France	Own, 2011; G. ms 20 × 17; Mazo & Torres 1990 as 20.5 × 16
NHMB Perp	M2/ lt	18.4	16.4	Perpignan, France	Own, 2012
FSL 41 096	M2/ lt	19.2	17.1	Perpignan, France	Own, 2011; G. ms as 20 × 17.5; FSL 3058
FSL 40 945	M2/ lt	22	19.8	Perpignan, France	Own, 2011
Piedrabuena	M2/ lt	19	17.7	Piedrabuena, Spain	Mazo & Torres 1990 as right
CCECL Br 87	M2/ lt	19.5	18.5	Trévoux (Reyrieux), France	Own, 2011; Mazo & Torres 1990, 19.5 × 12.9; G. ms as 21.5 × 19.5
NHMB VI 2	M2/ lt	19.4	17.7	Villafranca d'Asti, Italy	Own, 2012; G. ms as 20.5 × 18.5; B. 1992 as 19 × 18
NHMB VI 144	M2/ lt	20	18.5	Villafranca d'Asti, Italy	Own, 2012; G. ms as 20.5 × 18.5; B. 1992 as 19 × 18
NHMB VI 146	M2/ lt	20	18.5	Villafranca d'Asti, Italy	Own, 2012; G. ms as 20.5 × 18.5; B. 1992 as 20 × 18
NHMB VI 156	M2/ lt	20.8	17.2	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 152	M2/ lt	21	17.2	Villafranca d'Asti, Italy	Own, 2012
BGSK 21716	M2/ lt	19.3	15.4	Red Crag (Waldringfield) England	Own, 2011
YORYM 2011.1111	M2/ lt	21.6	17.8	Red Crag (Woodbridge) England	Own, 2011
NHMUK M 46009	M2/ lt	18.7	16.1	Red Crag, England	Own, 2011
NHMUK M 48961	M2/ lt	19.4	17.2	Red Crag, England	Own, 2011
YORYM 2005.174.2.3	M2/ lt	19.7	16.6	Red Crag, England	Own, 2011
NHMUK M 46691	M2/ lt	20.4	18	Red Crag, England	Own, 2011
YORYM 2011.1113	M2/ lt	21	19	Red Crag, England	Own, 2011
NHMUK M 9147	M2/ lt	22.6	19	Red Crag, England	Own, 2011
YORYM 2011.1122	M2/ lt	22.7	17.9	Red Crag, England	Own, 2011
MNHN.F.PET2006	M2/ lt	19.3	15.5	Les Étouaires, France	Own, 2011, G. ms as 20 × 16
MCNM	M2/ rt	0	16.5	Alcoy, Spain	Own, 2011
MCNM	M2/ rt	19.5	16.8	Alcoy, Spain	Own, 2011
MIL 205	M2/ rt	21.5	17.5	Milia, Greece	Guérin & Tsoukala 2013
NMENHM	M2/ rt	21.1	19.1	Musaitu, Moldova	Own, 2011
CCECL Pp 198	M2/ rt	19.8	16.4	Perpignan (Citadelle), France	Own, 2011; G. ms 20 × 17
NHMB Perp	M2/ rt	18.5	17	Perpignan, France	Own, 2012
NHMB RS 62	M2/ rt	21.4	18.2	Perpignan, France	Own, 2012; G. ms as 21 × 19
CCECL Br 87	M2/ rt	20.2	18.8	Trévoux (Reyrieux), France	Own, 2011; Mazo & Torres 1990, 19.7 × 18.7
NHMB VI 151	M2/ rt	19.6	17.1	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 144	M2/ rt	19.8	18	Villafranca d'Asti, Italy	Own, 2012
NHMB VI 1	M2/ rt	20	18.3	Villafranca d'Asti, Italy	Own, 2012; G. ms as 19.5 × 18.5; B. 1992 as 20 × 19
NHMB VI 3	M2/ rt	22	20	Villafranca d'Asti, Italy	Own, 2012
NHMUK M 46692	M2/ rt	20.3	16.7	Red Crag, England	Own, 2011
YORYM 2011.1125	M2/ rt	21.7	17.8	Red Crag, England	Own, 2011
MNHN.F.ACA314	M3/	28.5	17	Çalta, Turkey	Guérin <i>et al.</i> , 1998
MSG P 136	M3/	27.5	18.4	Capeni, Romania	Samson <i>et al.</i> 1971; Mottl 1939 as 28.5 × 19.5
Hajnacka 39831	M3/	25.4	18	Hajnacka, Slovakia	Hünemann 1971
NHMB Rss 70	M3/	28	18	Perpignan (Roussillon), France	G. ms
Museum Perpignan	M3/	0	17.5	Perpignan, France	G. ms
MCNM	M3/ lt	26.4	19.3	Alcoy, Spain	Own, 2011
MCNM	M3/ lt	29.4	18.6	Alcoy, Spain	Own, 2011
MGPOT (MB TI 449)	M3/ lt	27.2	19.5	Bra (Piemont), Italy	Own, 2011; G. ms as 27.2 × 19.15; Dal Piaz 1930 as 28 × 20
NMENHM	M3/ lt	27.3	20.1	Musaitu, Moldova	Own, 2011
CCECL Pp 198	M3/ lt	25.5	16.7	Perpignan (Citadelle), France	Own, 2011; G. ms 26 × 17; Mazo & Torres 1990 as 25 × 16
NHMB Perp	M3/ lt	26.7	17.2	Perpignan, France	Own, 2012
FSL 41 096	M3/ lt	27	19.3	Perpignan, France	Own, 2011; G. ms as 29 × 19; FSL 3058
FSL 214 215	M3/ lt	27.4	18	Perpignan, France	Own, 2011
Perpignan	M3/ lt	29	18	Perpignan, France	Depéret 1885
Piedrabuena	M3/ lt	27	18.5	Piedrabuena, Spain	Mazo & Torres 1990 as right
CCECL Br 87	M3/ lt	28	19.6	Trévoux (Reyrieux), France	Own, 2011; Mazo & Torres 1990, 28.4 × 20.1
NHMB VI 4	M3/ lt	26	17.5	Villafranca d'Asti, Italy	Own, 2012

APPENDIX 1. — Continuation.

Catalogue	Tooth	MDL	BLB	Locality, Country	Data source and comments
NHMB VI 144	M3/ lt	26	19.7	Villafranca d'Asti, Italy	Own, 2012; G. ms as 27 × 20; B. 1992 as 26 × 20
NHMB VI 146	M3/ lt	26	20	Villafranca d'Asti, Italy	Own, 2012; G. ms as 28 × 20
NHMB VI 2	M3/ lt	26	19.2	Villafranca d'Asti, Italy	Own, 2012; G. ms as 25 × 19; B. 1992 as 26 × 19
NHMB VI 5	M3/ lt	26	19.7	Villafranca d'Asti, Italy	Own, 2012; G. ms as 0 × 19.5
BGSK 7306	M3/ lt	26.7	18	Red Crag (Boyton), England	Own, 2011
IM 23 Walford coll.	M3/ lt	0	19.7	Red Crag, England	Own, 2011
IM 4 Walford coll.	M3/ lt	0	17.6	Red Crag, England	Own, 2011
NWHCM FC 2912	M3/ lt	0	20.5	Red Crag, England	Own, 2011
NHMUK M 46573	M3/ lt	25.7	18	Red Crag, England	Own, 2011
NHMUK M 3782	M3/ lt	27.2	17.1	Red Crag, England	Own, 2011; G. ms as 27 × 17
YORYM 2011.1103	M3/ lt	28.6	18.2	Red Crag, England	Own, 2011
IM 1930-176-19	M3/ lt	28.7	18	Red Crag, England	Own, 2011
IM 18 Walford coll.	M3/ lt	30.1	19.8	Red Crag, England	Own, 2011
MNHN.F.PET2007	M3/ lt	28.5	0	Les Étouaires, France	Own, 2011; G. ms as 27.5 × 0
MCNM 700 cast	M3/ rt	25.7	17.7	Alcoy, Spain	Own, 2011
MCNM	M3/ rt	29.3	18.4	Alcoy, Spain	Own, 2011
CCECL Br 54	M3/ rt	0	17.5	Autrey (Haute Savoie), France	Own, 2011
MIL 205	M3/ rt	29	17.7	Milia, Greece	Guérin & Tsoukala, 2013
NMENHM	M3/ rt	27	20	Musaitu, Moldova	Own, 2011
CCECL Pp 198	M3/ rt	25.6	17.6	Perpignan (Citadelle), France	Own, 2011; G. ms 25 × 17
NHMB Perp	M3/ rt	26.6	17.5	Perpignan, France	Own, 2012
CCECL Br 87	M3/ rt	28.7	20.2	Trévoux (Reyrieux), France	Own, 2011; Mazo & Torres, 1990, 28.6 × 19.8; G. ms as 30 × 20
NHMB VI 150	M3/ rt	25	17.8	Villafranca d'Asti, Italy	Own, 2012; G. ms as 25 × 17
NHMB VI 149	M3/ rt	26.3	19.4	Villafranca d'Asti, Italy	Own, 2012; G. ms as 27 × 19
NHMB VI 151	M3/ rt	26.4	18.4	Villafranca d'Asti, Italy	Own, 2012; G. ms as 27 × 19
NHMB VI 144	M3/ rt	26.5	19.8	Villafranca d'Asti, Italy	Own, 2012; G. ms as 26 × 16.5
NHMB VI 1	M3/ rt	28	20.4	Villafranca d'Asti, Italy	Own, 2012; G. ms as 28 × 21
FSL 40 152	M3/ rt	33	19.6	Montpellier, France	Own, 2011
BGSK 52457	M3/ rt	28	0	Red Crag (Boyton), England	Own, 2011
BGSK 21715	M3/ rt	0	18	Red Crag (Waldringfield), England	Own, 2011
BGSK 21718	M3/ rt	27	17.6	Red Crag (Waldringfield), England	Own, 2011
BGSK 483574 XVI/5/2/48	M3/ rt	26.4	17.3	Red Crag (Woodbridge), England	Own, 2011
NHMUK M 9146	M3/ rt	24.1	16.4	Red Crag, England	Own, 2011; G. ms as 26 × 16.5
NHMUK M 9146	M3/ rt	25.4	17.4	Red Crag, England	Own, 2011; G. ms as M 9148, 24.5 × 16
NHMUK M 21677	M3/ rt	27.2	19.4	Red Crag, England	Own, 2011; G. ms as 27 × 19
NHMUK M 9146	M3/ rt	27.2	17.4	Red Crag, England	Own, 2011; G. ms as 27 × 17
IM 10 Walford coll.	M3/ rt	27.8	19.2	Red Crag, England	Own, 2011
NWHCM FC 2912	M3/ rt	28	18.5	Red Crag, England	Own, 2011
YORYM 2011.1126	M3/ rt	28.6	18.1	Red Crag, England	Own, 2011
IM 1930-176-18	M3/ rt	29.1	18.7	Red Crag, England	Own, 2011
IM 12 Walford coll.	M3/ rt	29.5	19	Red Crag, England	Own, 2011
NHMUK M 39039	M3/ rt	29.5	17.9	Red Crag, England	Own, 2011; G. ms as 29 × 18
MNHN.F.PET2007	M3/ rt	28	18	Les Étouaires, France	G. ms

APPENDIX 2. — Measurements (in mm) of the teeth of *Dasychoerus arvernensis* (Croizet & Jobert, 1828) (ex *Kolpochoerus deheinzellini* Brunet & White, 2001) from Africa. Abbreviations: **MDL**, mesio-distal length; **BLB**, bucco-lingual breadth; **lt**, left; **rt**, right; **ms**, manuscript.

Catalogue	Tooth	MDL	BLB	Locality, Country	Data source and comments
NME ARA-VP 1/986	P3/ lt	13.2	9.8	Aramis, Ethiopia	Own, 2011
NME ARA-VP 1/986	P3/ rt	13.3	9.9	Aramis, Ethiopia	Own, 2011
NME ARA-VP 1/986	P4/ lt	12.0	12.4	Aramis, Ethiopia	Own, 2011
NME ARA-VP 1/986	M2/ lt	18.8	16.1	Aramis, Ethiopia	Own, 2011
NME ARA-VP 1/986	M3/ lt	24.6	18.6	Aramis, Ethiopia	Own, 2011; Brunet & White 2001, as 25.4 × 18.6
NME ARA-VP 1/986	M3/ rt	25.2	18.2	Aramis, Ethiopia	Brunet & White 2001 (holotype of <i>K. deheinzellini</i>)
NME URU-VP 1/10	p/4 lt	13.9	9.6	Awash, Ethiopia	Own, 2011
NME URU-VP 1/10	m/1 lt	14.5	11.4	Awash, Ethiopia	Own, 2011
NME URU-VP 1/10	m/2 lt	18.6	15.0	Awash, Ethiopia	Own, 2011
BEL VP-1/2	m/3 lt	33.0	16.3	Belohdelie, Ethiopia	Brunet & White 2001
KB 3-00-001	m/3 rt	28.5	15.0	Kossom Bougoudi, Chad	Brunet & White 2001
KB 3-97-383	m/3 lt	29.8	15.5	Kossom Bougoudi, Chad	Brunet & White 2001
KB 3-97-165	m/3 rt	31.3	15.3	Kossom Bougoudi, Chad	Brunet & White 2001
KB 4-97-184	m/3 lt	31.5	16.0	Kossom Bougoudi, Chad	Brunet & White 2001
KB 7-98-007	m/3 rt	33.0	16.6	Kossom Bougoudi, Chad	Brunet & White 2001
KB 4-97-185	M3/ rt	25.5	17.0	Kossom Bougoudi, Chad	Brunet & White 2001
KB 3-98-066	M3/ rt	27.3	16.6	Kossom Bougoudi, Chad	Brunet & White 2001
KB 97	M3/ rt	27.5	17.8	Kossom Bougoudi, Chad	Brunet & White 2001
KNM BC 1462	M3/ rt	28.0	18.6	KNM BC 1462	Tsujikawa, ms
OCO Bar 2074'05	p/4	13.9	9.3	OCO Bar 2074'05	Own, 2005
OCO Bar 2074'05	m/1 lt	0	11.5	OCO Bar 2074'05	Pickford <i>et al.</i> 2009
OCO 842'11	m/1 lt	17.0	12.7	OCO 842'11	Own, 2011
OCO Bar 2074'05	m/2 lt	20.9	15.2	OCO Bar 2074'05	Pickford <i>et al.</i> 2009
OCO Bar 2074'05	m/3 lt	31.6	15.9	OCO Bar 2074'05	Pickford <i>et al.</i> 2009
OCO 841'11	m/3 rt	33.6	16.7	OCO 841'11	Own, 2011
OCO Bar 4'06	M3/ rt	30.0	19.1	OCO Bar 4'06	Own, 2006
OCO Bar 1353'05	p/2 rt	11.6	4.9	OCO Bar 1353'05	Own, 2005
OCO Bar 1352'05	P2/ rt	11.8	6.5	OCO Bar 1352'05	Own, 2005
OCO Bar 59'05	M3/ lt	26.5	19.3	OCO Bar 59'05	Own, 2005
OCO Bar 853'05	D4/ rt	0	11.8	OCO Bar 853'05	Own, 2005
OCO 1523'11	P2/ lt	11.7	7.0	OCO 1523'11	Own, 2011
OCO 126'11	p/3 lt	12.3	6.2	OCO 126'11	Own, 2011
OCO 206'11	p/4 lt	15.5	9.7	OCO 206'11	Own, 2011
OCO 1522'11	m/3	0	15.3	OCO 1522'11	Own, 2011
OCO 1407'11	m/3 rt	29.5	14.1	OCO 1407'11	Own, 2011
OCO Bar 822'05	i/2 rt	5.5	4.7	OCO Bar 822'05	Own, 2005
OCO 1514'11	l2/ lt	12.2	7.3	OCO 1514'11	Own, 2011
OCO 125'11	l3/ lt	6.2	4.4	OCO 125'11	Own, 2011
OCO Bar 1060'05	P4/ lt	12.3	12.3	OCO Bar 1060'05	Own, 2005

APPENDIX 3. — Distribution of extinct species of *Dasychoerus* Gray, 1873 and other Plio-Pleistocene suids of mid-latitude Eurasia arranged by taxon and country.

Taxon	Country	Localities and references
<i>Dasychoerus arvernensis</i> (Croizet & Jobert, 1828)	France	Perrier les Étouaires (type locality, Croizet & Jobert 1828; Bout 1960; Pickford 2012); Cavaillé Brickyard (Perpignan, Serrat d'En Vacquer, Depéret 1890; Azzaroli 1954); Mas Bruno (St Estève, Guérin <i>et al.</i> 1998); Autrey (near Gray, Haute Saône, Depéret 1890; this paper); Vialette (Guérin <i>et al.</i> 1998); Trévoux-Reyrieux (Guérin <i>et al.</i> 1998); Sables marins de Montpellier (Pickford 2013c).
	Spain	Gorafe IV (Van der Made 1989); Piedrabuena (Mazo & Torres 1990); Alcoy (Golpe-Posse 1972; Van der Made & Belinchon 1991; Montoya <i>et al.</i> 2006).
	England	Red Crag (Lydekker 1885, 1886; Newton 1891; Guérin <i>et al.</i> 1998).
	Germany	Herbolzheim (Tobien 1951); Wölfersheim-Wetterau (Tobien 1952).
	Italy	Val di Pugna (Berdondini 1992; Gallai 2006); Barga, Pieve Fosciana, Triversa, Bra (Dal Piaz 1930); Villafranca d'Asti (Azzaroli 1954; Hürzeler 1967; Berdondini 1992); Collepardo (Anagni Basin, Gliozzi <i>et al.</i> 1997; Guérin & Tsoukala 2013); Roallo (Campanino <i>et al.</i> 1994; Guérin & Tsoukala 2013).
	Slovakia	Hajnacka (Fejfar 1961, 1964; Hünemann 1971); Ivanovce (Fejfar 1961; Hünemann 1971).
	Hungary	Gödöllő (Mottl 1939; Fejfar 1964).
	Romania	Baraolt Basin (Barot-Köpec); Capeni (Mottl 1939; Radulescu <i>et al.</i> 2003; Radulescu 2005); Virghis (Radulescu <i>et al.</i> 2003; Radulescu 2005)
	Moldova	Musaitu, Dermenji (this paper, Moldovan Faunal Complex, David <i>et al.</i> 1997)
	Bulgaria	Mussielevo (Spassov 2005)
	Greece	Milia (Guérin & Tsoukala 2013); Damatia? (Rhodes, Koufos 1986); Megalo Emvolon (Radulescu <i>et al.</i> 2003); Sesklo (Symeonidis 1992; Athanassiou 1996; Kostopoulos & Athanassiou 2003).
	Turkey	Afyon Dinar Akçakoy (Hünemann 1975); Çalta (Guérin <i>et al.</i> 1998); Afyon Karahisar (Sandiki-Garkin area, this paper).
	Ethiopia	Aramis (<i>Kolpochoerus deheinzeli</i> , Brunet & White 2001); Belohdelie (Brunet & White 2001); Sagantole (Brunet & White 2001); Galili (Kullmer <i>et al.</i> 2008; Haile-Selassie & Simpson 2012).
	Chad	Kossom Bougoudi (<i>Kolpochoerus deheinzeli</i> , Brunet & White 2001).
	Kenya	Mabaget Formation (Tugen Hills, Pickford <i>et al.</i> 2009; this paper).
	India	Sivalik Hills (many of the specimens attributed to <i>Sus hysudricus</i> Falconer & Cautley, 1846, belong to this species not to be confused with <i>Propotamochoerus hysudricus</i> [Stehlin 1899-1900; Pilgrim 1925, 1926]).
	China	Nanzhuanggou (Shanxi, Berdondini 1992).
	Taiwan	Qiding (<i>Sus houi</i> , Qi <i>et al.</i> 1999).
Non <i>Dasychorus arvernensis</i> (= <i>Hippopotamodon major</i>)	Greece	Servia (Tobien 1981).
<i>Dasychoerus natrunensis</i> Pickford, 2012	Egypt	Wadi Natrun , Egypt (Andrews 1902; Tobien 1936; Pickford 2012).
<i>Dasychoerus nanus</i> (<i>sondaari</i>) (Van der Made, 1988)	Italy	Capo Mannu (Capo Figari, Sardinia, Van der Made 1988, 1999; Gallai 2006, 2007).
	Ethiopia	Omo (<i>Kolpochoerus cookei</i> , Brunet & White 2001; Pickford 2012).
<i>Dasychoerus macrognathus</i> (Dubois, 1908)	Java	Kedungbrubus, Bangle, Ngandong (<i>Sus terhaari</i>); Bumiayu (<i>Sus stremmi</i>); Sumberkepuh, Kebonduren, Teguan (Hardjasasmita 1987).

APPENDIX 3. — Continuation.

Taxon	Country	Localities and references
<i>Dasychoerus macrognathus</i> (Dubois, 1908)	Myanmar	Naungkwe Taung (Pickford 2013b)
	China	Liucheng <i>Gigantopithecus</i> Cave (<i>Sus australis</i> , Han 1987); Bijashan Cave (Han <i>et al.</i> 1975).
	Taiwan	Qiding (Qi <i>et al.</i> 1999).
<i>Dasychoerus brachygnathus</i> (Dubois, 1908)	Java	Trinil, Kebonduren, Bangle, Kaligede, Teguan, Watualang (<i>Sus vatualangensis</i>) (Hardjasasmita 1987).
<i>Dasychoerus strozzi</i> (Meneghini, 1862)	Italy	Val d'Arno (Forsyth-Major 1881; Azzaroli 1954, 1975); Olivola (Azzaroli 1954, 1975); Brisighella (Gallai & Rook 2011); Quercia (Azzaroli 1954); Casino (Stehlin 1899-1900; this paper); Mugello (Faure & Guérin 1984).
	France	Montpellier (Sables marins de Montpellier, a composite unit, Fejfar 1964; Pickford 2013c); Senèze (Schaub 1943; Azzaroli 1954, 1975); Le Coupet? (Geraads <i>et al.</i> 1986; Faure 2004); Saint-Vallier (Faure 2004).
	Spain	Fonelas (<i>Potamochoerus magnus</i> , Arribas & Garrido 2008); Valdeganga (Van der Made & Moyà-Solà 1989).
	England	Red Crag (Owen 1856; Lydekker 1885, 1886; Newton 1891 (Nodule Bed); Stuart 1982; Guérin <i>et al.</i> 1998).
	Holland	Tegelen (Richarz 1921; Bernsen 1931; Schreuder 1945; Hooijer 1947; Van der Made & Moyà-Solà 1989).
	Greece	Gerakarou (Kostopoulos & Athanassiou 2003); Vassiloudi (Kostopoulos & Athanassiou 2003; Koufos 1986).
	Romania	Valea Graunceanului (Tetoiu) (Bolomey 1965; Faure 2004).
	Moldova	Khaprovian and Odessian Faunal Complexes (David <i>et al.</i> 1997).
	Russia	Khapry (Titov 2000).
	North Caucasus	Tamansk? (<i>Sus tamanensis</i> , Gromov & Baranova 1981; Geraads <i>et al.</i> 1986).
	Azerbaijan	Palan-Tyukan (Titov 2000; Kostopoulos & Athanassiou 2003).
	Israel	Oubeidiyeh (Geraads <i>et al.</i> 1986; Kostopoulos & Athanassiou 2003).
	Georgia	Kvabebi (Vekua 1972).
	Spain	? Corral de Lobato (this paper).
<i>Suidae incertae sedis</i> (taxon to which the Samos specimen attributed to <i>Postpotamochoerus "hyotherioides"</i> by Thenius 1950, belongs)	Moldova	Nikolskoe (Titov 2000, this paper).
	Macedonia	Kalnitsa (Geraads <i>et al.</i> 2008), Vozarci (Geraads <i>et al.</i> 2008).
	Bulgaria	Kalimantsi (Geraads <i>et al.</i> 2008).
	Greece	Maramena (Hellmund 1995; Geraads <i>et al.</i> 2008), Samos (Thenius 1950).
	England	Red Crag (Pickford 2013c).
<i>Potamochoerus provincialis</i> (Blainville, 1847)	France	Montpellier (Sables marins de Montpellier; Blainville 1847; Gervais 1850, 1859; Fejfar 1964; Pickford 2013c);
	Spain	Venta del Moro (Morales 1984);
	Italy	Casino (Gallai 2006), Brisighella (Gallai 2006);
	Romania	Malusteni (Athanasiu 1912 ; Simionescu 1930)
	Moldova	Carbolia Formation (Karboliya Beds of Pevzner <i>et al.</i> 1996) { Lucesti (Vangengeim <i>et al.</i> 1998); Pelinei (David <i>et al.</i> 1997)} = Moldovian Faunal Complex (David <i>et al.</i> 1997).
	Hungary	Hatvan (Gaal 1943; Hünemann 1975, identified the suid lower molar as <i>Sus minor</i> , but the tooth is too large to belong to this species, being compatible in dimensions to <i>Potamochoerus provincialis</i> from Montpellier)
	Russia	Kosiakino (Vangengeim <i>et al.</i> 1998).
	Turkey	Sinap Tepe 42 (Van der Made 2003).
	Hungary	Süttő (Janössy 1986; Guérin & Tsoukala 2013; = <i>Sus scrofa</i> according to Pazonyi <i>et al.</i> 2013).
Specimen of <i>Sus scrofa</i> Linnaeus, 1758, previously identified as <i>Sus arvernensis</i>	Hungary	