

Re-assessment of the suids from the Sables marins de Montpellier and selection of a lectotype for *Sus provincialis* Blainville, 1847

Martin PICKFORD

Muséum national d'Histoire naturelle, Département Histoire de la Terre,
UMR 7207 du CNRS,
case postale 38, 57 rue Cuvier, 75231 Paris cedex 05 (France)
pickford@mnhn.fr

Pickford M. 2013. — Re-assessment of the suids from the Sables marins de Montpellier and selection of a lectotype for *Sus provincialis* Blainville, 1847. *Geodiversitas* 35 (3): 655-689.
<http://dx.doi.org/10.5252/g2013n3a8>

ABSTRACT

Part of the problem of interpreting fossil suids has been the misplacement or loss of material described during the 19th Century, which makes comparisons difficult because usually only occlusal views of teeth were illustrated and the illustrations, although labelled as “natural size” often differ from the real dimensions, sometimes by as much as 10%. Some of the fossils attributed by Blainville (1847) and Gervais (1850, 1859) to *Sus provincialis* Blainville, 1847 are preserved at the University of Montpellier II (some are mislabelled due to the fact that several of the illustrations are reversed) and one original specimen and a set of casts is preserved at the Muséum national d'Histoire naturelle, Paris. Fossils found after Gervais' publications reveal that the deposits in the neighbourhood of Montpellier contain four species of suid, *Dasychoerus arvernensis* (Croizet & Jobert, 1828), *Dasychoerus* sp. from Kvabebi, “*Sus*” *provincialis* Blainville, 1847 and *Dasychoerus strozzii* (Meneghini, 1862) and that ever since Blainville's (1847) publication, as well as those of Gervais (1850, 1859) and above all the monograph of Stehlin (1899-1900) the concept of the species “*Sus*” *provincialis* has been based on a chimera of two taxa (“*Sus*” *provincialis* and *Dasychoerus strozzii*). In order to ensure stability of nomenclature, it is necessary to avoid nominating a lectotype that might belong either to *Dasychoerus arvernensis* or to *Dasychoerus strozzii*. For this to succeed a detailed revision of the Montpellier suids is necessary.

KEY WORDS

Suidae,
Pliocene,
Montpellier,
lectotype,
systematics,
biochronology,
lectotypification.

RÉSUMÉ

Révision des suidés des sables marins de Montpellier et désignation d'un lectotype pour Sus provincialis Blainville, 1847.

Une partie du problème lié à l'interprétation des suidés fossiles réside dans le fait que le matériel décrit au XIX^e siècle a été mal rangé dans les collections ou

MOTS CLÉS
Suidae,
Pliocène,
Montpellier,
lectotype,
systématique,
biochronologie,
lectotypification.

bien perdu. Les comparaisons s'avèrent donc difficiles car seules les vues occlusales des dents ont été illustrées; de plus les illustrations sensées être à la taille normale diffèrent souvent de la taille réelle et jusqu'à 10 % dans certains cas. Quelques fossiles attribués par Gervais (1850, 1859) à *Sus provincialis* Blainville, 1847 sont conservés à l'Université de Montpellier II (dont certains sont mal étiquetés car les illustrations ont été inversées). En outre, les collections du Muséum national d'Histoire naturelle à Paris renferment un spécimen original et des moulages. Les fossiles récoltés après les publications de Gervais suggèrent que quatre espèces de suidés sont présentes dans les dépôts de la région de Montpellier, *Dasychoerus arvernensis* (Croizet & Jobert, 1828), *Dasychoerus* sp. de Kvabebi, "*Sus*" *provincialis* et *Dasychoerus strozzii* (Meneghini, 1862), et montrent que depuis le début (Blainville 1847; Gervais 1850, 1859) et surtout après la monographie de Stehlin (1899-1900) le concept de *Sus provincialis* a été basé sur une chimère des deux derniers taxons. Pour assurer la stabilité de la nomenclature il faut éviter de désigner un lectotype qui pourrait appartenir soit à *Dasychoerus arvernensis* soit à *Dasychoerus strozzii*. La révision détaillée des suidés de Montpellier était donc nécessaire.

INTRODUCTION

Gervais (1850, 1859) described and illustrated seven fossils from Early Pliocene marine sands at Montpellier, France, which he attributed to the species *Sus provincialis* Blainville, 1847. As was the custom at the time he did not specify a holotype. However, Gervais' use of the species name is not the earliest, as the figures in Blainville (1847) to which Gervais refers are labelled *S. provincialis*. Blainville's (1847) mention of the species name has generally been considered to be a *nomen nudum*: all authors subsequent to Gervais (1859) have credited the species to Gervais and the year of availability as 1859. Rüttimeyer (1857) discussed the species, proving that the name was available before 1859. However, the ICZN (art. 12.2.7) is clear on the matter – the association of a Latin name with a figure is considered an indication and makes the name available if published before 1930. The name *Sus provincialis* was therefore erected by Blainville (1847) and not Gervais (1850) or Gervais (1859).

Two of the specimens from Montpellier figured by Blainville (1847) UM SM 460, right M3/; MNHN.F.MON13 mandible fragment contain-

ing m/2 and m/3 (but now without the mandible fragment and figured as though from the right side), are the same as the specimens figured by Gervais (1850: pl. 3, figs 2, 3 refigured in 1859). In addition, Blainville (1847) figured a deciduous upper molar, UM SM 394, left D4/ (as though from the right side) which was not figured by Gervais (1850, 1859).

Blainville's (1847) use of the species name appears to have been a case of pre-publication of another author's findings because Gervais (1850, 1859) mentioned that he communicated the illustrations and the original teeth to Blainville, and presumably felt that he and not Blainville (1847) should be regarded as the author of the species. Gervais himself used the name *Sus provincialis* in 1849 for a fossil from Cucuron, Vaucluse, that he reported was a new species, but in this instance the name is a *nomen nudum* as there is no description and no figure. The specimen was later named *Sus major* Gervais, 1850 of which it is the holotype.

Gervais (1850; 1859: 177) mentioned that Blainville (1847) considered the Montpellier teeth to be similar to those of *Sus larvatus* Cuvier, 1822 (i.e. *Potamochoerus larvatus* (Cuvier,

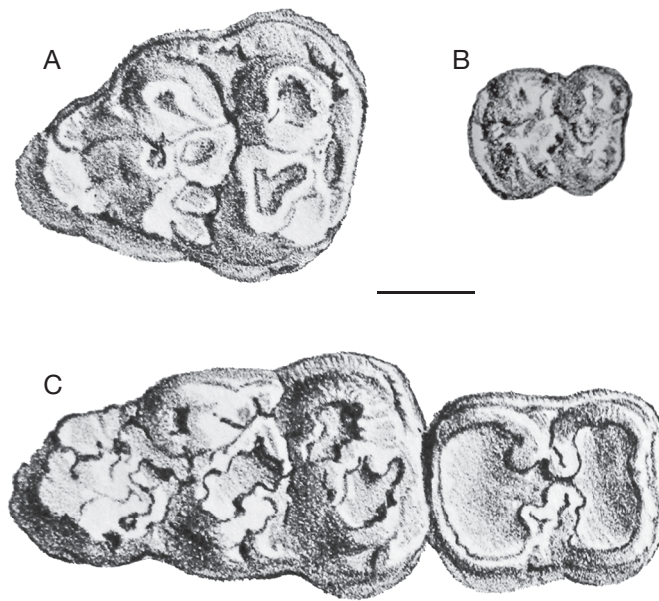


FIG. 1. — Blainville's (1847) hypodigm of *Sus provincialis* Blainville, 1847 from Montpellier: **A**, corresponds to UM SM 460, right M3/ which is here designated as the lectotype of the species; **B**, corresponds to UM SM 394, left D4/ (illustrated in reverse); **C**, corresponds to a specimen (right m/2-m/3 illustrated in reverse) housed in the MNHN which may be the specimen attributed to *Sus strozzii* Meneghini, 1862 by Fejfar (1964).

1822) from Africa and Madagascar). He did not, however, mention the fact that Blainville (1847: G. *Sus*, pl. 9) had labelled the illustrations of the specimens as *S. provincialis*, which, when combined with the description in the *Ostéographie* of Blainville (1847: 208) is to be regarded as a valid erection of the species. Gervais (1850) then published brief descriptions and illustrated several specimens (Fig. 2). Rüttimeyer (1857) evidently thought the name was created by Gervais as he refers to the species *S. provincialis* and pointed out several features of the dentition that allied it to the *Sus larvatus* and *S. penicillatus* group (i.e. *Potamochoerus* Gray, 1854) rather than to the *Sus scrofa* group. He did not mention Blainville's (1847) work.

For more than a century and a half, some of the original specimens in Gervais' (1850, 1859) hypodigm have been presumed to have been lost, although casts of two mandibles and an isolated molar are preserved in the Muséum national d'Histoire naturelle (MNHN), Paris (Fig. 3)

and some of the original material is preserved at the University of Montpellier II. Although most authors have considered Blainville's (1847) and Gervais' (1850) hypodigms to be taxonomically homogeneous, it is likely that it comprises a mixture of specimens belonging to two taxa, "*Sus*" *provincialis* and *Dasychoerus strozzii* (Meneghini, 1862) (teeth of two other species of suid, *Dasychoerus arvernensis* (Croizet & Jobert, 1828) and *Dasychoerus* sp. from Kvabebi, were found in the Sables marins subsequent to Gervais' publications). Fejfar (1964) for example, attributed an m/3 from Montpellier to *Sus strozzii* Meneghini, 1862. Extreme care therefore needs to be taken before nominating a lectotype. Much of the debate concerning the generic attribution of the suids from the Sables de Montpellier is due to the mixed nature of the hypodigms.

Two fossil suid teeth (Figs 4, 5) were discovered by the author in June 2011, among the recent suid collections in the office next to the Salle Gaudry in the MNHN that was housing the

TABLE 1. — Gervais' (1850) hypodigm of *Sus provincialis* Blainville, 1847 with measurements estimated from the figures labelled "grandeur naturelle". The specimen in bold is here attributed to *Dasychoerus strozii* (Meneghini, 1862).

Specimen	Gervais (1850)	Measurements (in mm) from the figures
m/2-m/3 in a fragment of mandible	pl. 3, fig. 3	m/2 – 25.3 × 20.4, m/3 – 42.0 × 23.3
M3/ (lectotype)	pl. 3, fig. 1	M3/ – 35.3 × 25.9
M2/	pl. 3, fig. 2	M2/ – 21.9 × 19.4
p/3	pl. 3, fig. 6, 6'	p/3 – 17.2 × 11.8
m/2	pl. 3, fig. 5	m/2 – 24.6 × 18.0
m/3	pl. 3, fig. 4	m/3 – 35.6 × 19.6
D4/	pl. 8, fig. 9	D4/ – 17.0 × 14.4
p/3-m/2 in mandible (buccal view only)	pl. 22, fig. 8	p/3 – 18.8, p/4 – 18.4, m/1 – 19.2, m/2 – 22.7

TABLE 2. — Measurements (in mm) of the m/2-m/3 from Montpellier MNHN.F.MON13 attributed to *Dasychoerus strozii* (Meneghini, 1862) for comparison with measurements in Table 1.

Tooth	Length	Breadth	Locality	Source
m/2 left	25	20.2	Montpellier	Own, 2011
m/3 left	43.3	24.1	Montpellier	Own, 2011

North Africa collection of Camille Arambourg. The two teeth agree in all pertinent details with a specimen figured by Blainville (1847) and by Gervais (1850; 1859: pl. 3, fig. 3) except that they are from the left side and not the right, and the fragment of mandible in which they occurred, as illustrated by Gervais (1850, 1859) is no longer preserved. The interstitial facets between the teeth provide conclusive evidence that they represent a single individual. One of the casts in the Montpellier collection at the MNHN is of the mandible fragment containing these teeth. Other undescribed original fossil suid specimens from the Sables marins de Montpellier housed in the MNHN (Figs 7-15), the Faculty of Science, Lyon and the University of Montpellier II, yield precious information concerning the affinities of "*Sus*" *provincialis* and they reveal that the m/2-m/3 probably belong to a species larger than the rest of the material from Montpellier as intimated by Fejfar (1964) and here attributed to *Dasychoerus strozii*.

The specimens comprising Gervais' (1850, 1859) hypodigm of *Sus provincialis*, of which the m/2-m/3 is one which was illustrated by

Blainville (1847) are listed in Table 1 (see also Table 2).

MATERIAL AND METHODS

Original fossils and casts of suids from the Sables marins de Montpellier were examined at the Muséum national d'Histoire naturelle, Paris, the Faculty of Science, University of Lyon and the University of Montpellier. Measurements were taken with sliding calipers to the nearest tenth of a mm. Images were taken with a Sony Cybershot 8 megapixel camera and cleaned and enhanced using Photoshop elements 3.

ABBREVIATIONS

Institutional abbreviations

IGF	Institute of Geology (Museum), Florence University;
FSL	Faculty of Science, University of Lyon;
MNHN	Muséum national d'Histoire naturelle, Paris;
UM SM	University of Montpellier II, Sables marins.

Dental abbreviations

Upper teeth in upper case letters with the meristic position above the slash (occlusal plane) e.g. M2/ – upper second molar; lower teeth in lower case with the meristic position beneath the slash (occlusal plane) e.g. m/ – lower second molar; P4/ – upper fourth premolar; p/ – lower fourth premolar.

Remark

Dental terminology and terms such as Fürchen and Innenhügel are defined in Hünemann (1968) and Pickford (1988).

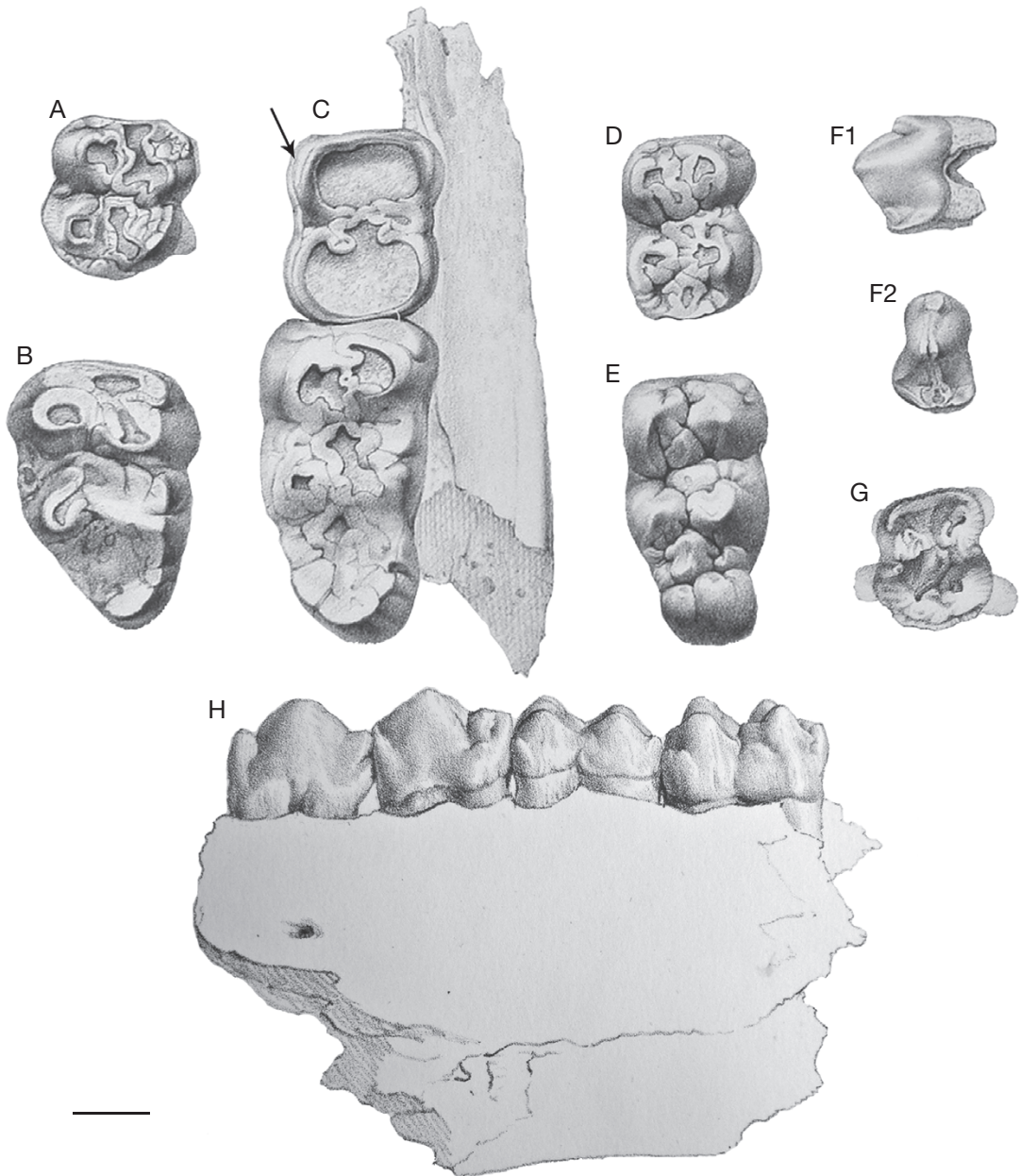


FIG. 2. — Gervais' (1850, 1859) hypodigm of *Sus provincialis* Blainville, 1847 with his plate and figure numbers: **A**, SM 461, right M2/ (correct orientation), pl. 3, fig. 2; **B**, SM 460, lectotype right M3/ (correct orientation), pl. 3, fig. 1; **C**, MNHN.F.MON13, left m/2-m/3 (reversed) pl. 3, fig. 3 here attributed to *Dasychoerus strozzii* (Meneghini, 1862); arrow points to the hypoplastic groove on the lingual side of the m/2; **D**, SM 462, left m/2 (reversed), pl. 3, fig. 5; **E**, left m/3, pl. 3, fig. 4, (reversed, specimen lost? Cast in MNHN); **F**, p/3 pl. 3, fig. 6 (specimen lost?) in lingual (**F1**) and occlusal (**F2**) views; **G**, D4/ pl. 8, fig. 9 (specimen lost?); **H**, SM 392, lateral view of right mandible containing p/3-m/2 (reversed), pl. 22, fig. 8. Scale bar: 10 mm.

LIST OF SUID SPECIMENS FROM THE SABLES MARINS DE MONTPELLIER

FSL 40 070, right m/2-m/3; 40 071, right mandible p/3-m/2; 40 072, right mandible i/2, p/1-m/3, left mandible m/2-m/3; 40 073, snout with cheek teeth; 40 144, right i/1; 40 145, left m/1; 40 151, right mandible m/1-m/3; 40 152, right M3/; 40 154, right m/3; 40 155, left m/3; 40 156, right M1/; 40 159, left I1/; 40 160, right i/2; 40 161, left mandible m/1-m/3; 40 881, left mandible p/4-m/3; 40 882, upper canine; 40 884, left mandible p/2-m/3; WO 417, right I1/.

UM SM 392, right mandible p/3-m/2; 393, right m/3; 394, left D4/; 395, left mandible p/2-p/4; 460, right M3/; 461, right M2/; 462, left m/2.

MNHN.F.MON13, left m/2-m/3; MON14, left M3/; MON15, left mandible m/2-m/3; MON16, left mandible p/1, p/4-m/2; MON17, left p/4.

CASTS OF GERVAIS' (1850) HYPODIGM OF *SUS PROVINCIALIS* HOUSED AT THE MNHN

Even though casts are inexact copies of original fossils, they can be important archives, particularly when original fossils have been misplaced or lost. Such is the case with some specimens of Gervais' (1850) hypodigm of *Sus provincialis* (Fig. 3). For example, the cast of the left m/3 illustrated in Gervais (1850: fig. 3c) appears to be missing from the collections in the MNHN, the FSL and at the University of Montpellier II.

SYSTEMATIC DESCRIPTIONS

Family SUIDAE Gray, 1821

Genus *Dasychoerus* Gray, 1873

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

Dasychoerus strozzi (Meneghini, 1862)

Sus strozzi Meneghini, 1862: 17-33. — Azzaroli 1975: pl. 4, fig. 8, 8a. — Faure 2004: 189, 190, fig. 1.

Sus provincialis Blainville, 1847: pl. 9, G *Sus*, *S. provincialis* Montpellier (only the m/2-m/3) *partim*. — Gervais 1850: 100, pl. 3 fig. 3 *partim*; 1859: 177, pl. 3, fig. 3 *partim*.

For an exhaustive synonymy list, see Azzaroli (1954).

LECTOTYPE. — IGF 424, adult male skull, mandible and partial skeleton from Upper Val d'Arno, Italy.

REMARK

Differential diagnosis *Dasychoerus strozzi* differs from *Dasychoerus arvernensis* by its much larger dimensions. It is also larger than "*Sus*" *provincialis*.

DESCRIPTIONS

The MNHN lower molars

Particularly convincing evidence that the m/2-m/3 in the MNHN.F.MON13 are the teeth that Blainville (1847) and Gervais (1850, 1859) illustrated, comprises the occlusal wear pattern which is a mirror image of the teeth in the illustration, and the m/2 which shows a hypoplastic groove running the length of its lingual side due to an irregularity in the growth of the tooth (Figs 3, 4). Hypoplasia represent a growth variable due to the particular health and developmental history of the individual concerned, and it would be highly unlikely that two different individuals would possess hypoplastic grooves in identical places, and also have identical occlusal wear patterns. It was quite common at the time of Blainville's and Gervais' studies for specimens to be illustrated in mirror image as a result of the method of the artwork and printing processes involved. The casts preserved at the Muséum national d'Histoire naturelle include three of the specimens illustrated by Gervais (1849) and all were illustrated in mirror image (Fig. 2).

The m/2 is heavily worn, showing two vast dentine lakes separated from each other by enamel in the base of the median transverse valley. Infolding of enamel on the distal side of the anterior dentine lake represent the bases of Fürchen 3 on the metaconid and 6 on the protoconid, whereas infoldings on the mesial side of the distal dentine lake correspond to the grooves that separate the median accessory cusplet from the entoconid and hypoconid behind (Pickford 1988). At the buccal end of the median transverse valley there

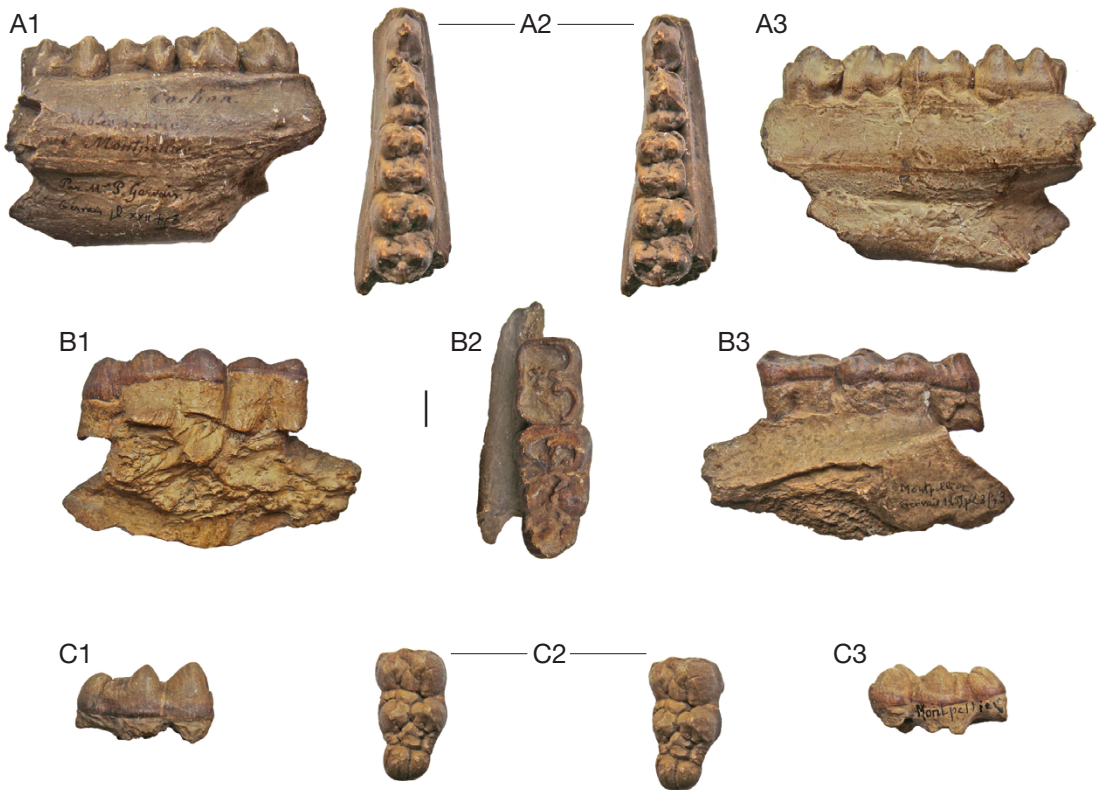


FIG. 3. — Casts of some of the specimens attributed to *Sus provincialis* Blainville, 1847 by Gervais (1850) housed at the MNHN: **A**, corresponds to his plate 22, fig. 8 in buccal (**A1**), stereo occlusal (**A2**) and lingual (**A3**) views; **B**, corresponds to his plate 3, fig. 3 in lingual (**B1**), occlusal (**B2**) and buccal (**B3**) views; **C**, corresponds to his plate 3, fig. 6 in lingual (**C1**), stereo occlusal (**C2**) and buccal (**C3**) views. B is here attributed to *Dasychoerus strozzi* (Meneghini, 1862). Scale bar: 10 mm.

is a shallow fovea bordered buccally by a short, low cingular ridge. The enamel descends further rootwards on the lingual side of the crown than it does on the buccal side.

The m/2 has four C-shaped roots, the two anterior ones being substantially smaller than the two distal ones (Fig. 4C). There is a broad depression between the buccal and lingual roots, which are slightly splayed out from the vertical.

The third lower molar is in medium wear with small dentine lakes at the apices of the main cusps, the mesial and median accessory cusplet, the hypoconulid and a low cusplet adjacent to the hypoconulid on its buccal side. The dentine lake on the hypoconulid is contiguous with that on the median accessory cusplet. The mesial cingulum

extends right across the front of the crown, ending at two shallow vertical grooves at the mesio-buccal and mesio-lingual corners of the tooth. Towards the centre of the cingulum there is the mesial accessory cusplet, which is joined by wear to the protoconid.

Wear on the protoconid has all but obliterated the Fürchen, but the bases of Fürchen 1, 2 and 3 are visible on the metaconid. The protoconid and metaconid are subequal in dimensions, with the protoconid slightly more mesially positioned than the metaconid, and its apex is lower than that of the metaconid.

The median accessory cusp is about half the breadth of the crown and is bordered on both ends by low ridges or pustules of enamel.

The second lophid of the tooth (entoconid and hypoconid) is slightly narrower than the mesial lophid, and the hypoconid is somewhat smaller than the entoconid and is slightly more mesially positioned than it. The Fürchen on the hypoconid have been largely removed by wear but the bases of those on the entoconid (nos 7, 8 and 9) are clearly visible, as are remnants of the median longitudinal valley that separates these two cusps at their base.

The talonid is comprised of a large main cusp slightly to the buccal side of the centre-line of the tooth, accompanied by two lingual cusplets and one buccal one, disposed either side of the hypoconulid (distal accessory cusplet in old literature). Its root is slightly inclined buccally as is the talonid as a whole. In lingual view there is an abrupt offset in the cervix level (Fig. 4D) by a distance of about 4.5 mm. The offset on the lingual side is smaller, only 2.5 mm.

Taking into account the degree of wear, it is clear that these teeth were relatively brachyodont, bunodont, but the rootwards offset of the cervix of the talonid suggests the possibility of the onset of selection for hypsodonty like that which typifies hypsodont suids such as *Kolpochoerus falconeri* (Lydekker, 1884). In distal view, the walls of the talonid show several shallow vertical grooves or undulations that hint at the potential for subdivision of the talonid into pillars (Fig. 5). Of interest in this respect is the presence of three pillars in front of the main talonid cuspid either side of the hypoconulid. However, the tooth is by no means hypsodont nor is it yet polycuspidate. It merely suggests that the population from which it came may have possessed the underlying morphology that could culminate in hypsodont, polycuspidate teeth like those of kolpochoeres and phacochoeres.

There are five roots in the m/3, C-shaped ones beneath the lingual and buccal margins of the four main cuspids (the two mesial roots somewhat smaller than the two distal ones the buccal and lingual roots being separated by a broad valley), and a large V-shaped root supporting the talonid. The latter root leans slightly disto-buccally such that its apex is almost in line with the buccal roots in front of it (Fig. 4C).

THE LYON SNOOT

In ventral view, the snout FSL 40 073 is preserved from the premaxillae to the posterior nares and contains the left upper canine, the right P3/-M3/ and left P2/-M3/ in moderate to heavy wear (Fig. 7). Dorsally the snout is complete from the apices of the nasals as far distally as the grooves that lead anteriorly from the supra-orbital foramina, although the foramina themselves are not preserved. In lateral view the fossae for the snout disc musculature is preserved, even though they are somewhat distorted due to crushing. The dorsal profile of the skull is straight. The snout is almost rectangular in section and the supra-canine flange, which is preserved on the left side extends distally from above the canine alveolus.

Stehlin (1899-1900: 59, pl. II, fig. 22; 62, pl. VI, fig. 1) described and illustrated the premolars and the last two molars of this snout.

Parts of the alveoli of the upper central and second incisors are preserved on the right premaxilla, but the incisors themselves are missing. The left upper canine shows three enamel bands, the ventral one of which is heavily wrinkled into coarse ridges and grooves. Immediately behind the canine there is an alveolus for the P1/ which is itself followed closely by the P2/.

The P2/ has a prominent main cusp with low anterior and posterior styles, and a prominent disto-lingual cusplet which is separated from the main cusp by a capacious fovea. It has two roots. The P3/ is larger than the P2/ and is relatively broader than it, but the two teeth are constructed along the same basic lines. The P4/ in contrast, possesses two buccal cusps which are joined closely together, separated from a large lingual cusp by a deep sagittal valley. The buccal styles are weak but clear, as are the mesial and distal cingula.

The M1/ and M2/ are deeply worn, and the M3/s are moderately worn, allowing some details of morphology to be accessed. The lingual and buccal notches are mesio-distally broad, the main cusps in each cusp pair are somewhat oblique, the lingual cusps lying behind the level of the buccal ones. The talon is simple, and is located in the midline of the crown. It was these features that prompted Stehlin (1899-1900) to suggest



FIG. 4. — *Dasychoerus strozzi* (Meneghini, 1862), left m/2-m/3, from the Sables marins de Montpellier, MNHN.F.MON13: **A**, stereo occlusal view; **B**, buccal view; **C**, radicular view; **D**, lingual view. Note the hypoplastic groove on the lingual aspect of the m/2 (arrow) which provides strong evidence that this is the specimen figured by Gervais (1850, 1859) in reverse (see Fig. 1C, 3C above in which the hypoplastic groove is visible on the lingual side of the occlusal view (i.e. the left side in the image). Scale bar: 10 mm.

that the snout belonged to *Potamochoerus* (with a question mark).

The posterior nares open up behind the distal edges of the upper third molars.

THE MNHN ISOLATED UPPER THIRD MOLAR

The isolated left M3/ housed in Paris, MNHN.F.MON14 (Fig. 9C) attributed to *Dasychoerus strozii* is almost unworn and has a relatively rectilinear lingual edge and a convex buccal edge. There are five main cusps; four subequal cusps forming two slightly oblique lophs, behind which is a lower and smaller talon. The minor structures of the crown, comprising the mesial cingulum, the anterior, median and posterior accessory cusplets, the low cusplets in the buccal and lingual ends of the median transverse valley, and the posterior cingulum are all heavily beaded. The main cusps possess the classic Fürchenplan of suid upper molars, but they do not invade deeply into the contour of the cusps. This suggests that the enamel is relatively thick.

Dasychoerus arvernensis (Croizet & Jobert, 1828)

Aper arvernensis Croizet & Jobert, 1828: 157, pl. 13, figs 3-5.

Sus palaeochoerus Gervais, 1853: 162, pl. 4, figs 7-9. — Lydekker 1885: 273 (specimens from the Red Crag). — Newton 1891: 36, pl. 3, figs 13, 14.

Sus arvernensis — Depéret 1885: 182-186, pl. 3 fig. 2, pl. V, fig. 1.

Sus provincialis race *minor* Depéret, 1890: 84, pl. 5, figs 12-14.

Potamochoerus provincialis var *minor* — Stehlin 1899-1900: 17, 18, 161, 257, pl. 1, fig. 29, pl. 7, figs 7, 8.

Sus minor — Dal Piaz 1930: 299. — Azzaroli 1954: 58-60, pl. 9, figs 1-6; 1975: 356, 366, pl. 1, fig. 2, pl. 2, fig. 2a, pl. 3, fig. 2b, pl. 5, fig. 2, 10, 11. — Hünemann 1971: 213-224, figs 1-9. — Golpe-Posse 1972: 150. — Mazo & Torres 1990: 214, 215, pl. 1, fig. 8. — Montoya et al. 2006: 144-149, fig. 4.

Propotamochoerus provincialis minor — Fejfar 1964: 68, 69, fig. 38.

Sus arvernensis arvernensis — Guérin & Faure 1985: 22.

Sus arvernensis minor — Guérin & Faure 1985: 22.

Korynochoerus palaeochoerus — Van der Made & Belin-chon 1991: 173-178.

Sus (Dasychoerus) minor — Berdondini 1992: 111-123, figs 1-6.

Sus arvernensis minor — Guérin et al. 1998: 443-447.

Kolpochoerus debeinzelini Brunet & White, 2001: 52-57, figs 1-2.

Dasychoerus arvernensis — Pickford 2012: 24, fig. 10.

See also synonymy list in Hünemann (1971).

HOLOTYPE. — MNHN, associated juvenile mandible and maxilla from Les Étouaires, Perrier, France.

REMARK

Differential diagnosis *Dasychoerus arvernensis* differs from *Dasychoerus strozii* by its much smaller dimensions, and from “*Sus*” *provincialis* by its smaller dimensions.

DESCRIPTION

In the Faculty of Science, Lyon, there is a right mandible fragment from Montpellier (FSL 40 151) (Fig. 14C) containing three molars, and an isolated right m/3 (FSL 40 154) (Fig. 15C) which are close in morphology and dimensions to specimens of *Dasychoerus arvernensis* from Les Etouaires (the type locality of the species) and Perpignan.

The isolated m/3 FSL 40 154 (Fig. 15C) is unworn and shows three pairs of cusps behind which is a talonid cusplet. The buccal and lingual notches are broad mesio-distally and extend well towards the cervix, showing sub-parallel sides for much of their depth. There are low subdivided basal pillars in the buccal ends of the transverse valleys. The mesial cingulum is beaded. The occlusal outline of the tooth is straight mesio-distally, unlike those of “*Sus*” *provincialis* which show a lateral bend of the talonid.

The overall morphology of this tooth — the addition of a third cusp pair behind the two anterior pairs, the breadth, depth and sub-parallel walls of the buccal and lingual notches, and the sub-divided basal pillars — resembles that of the genus *Kolpochoerus*, in particular *K. afarensis*.

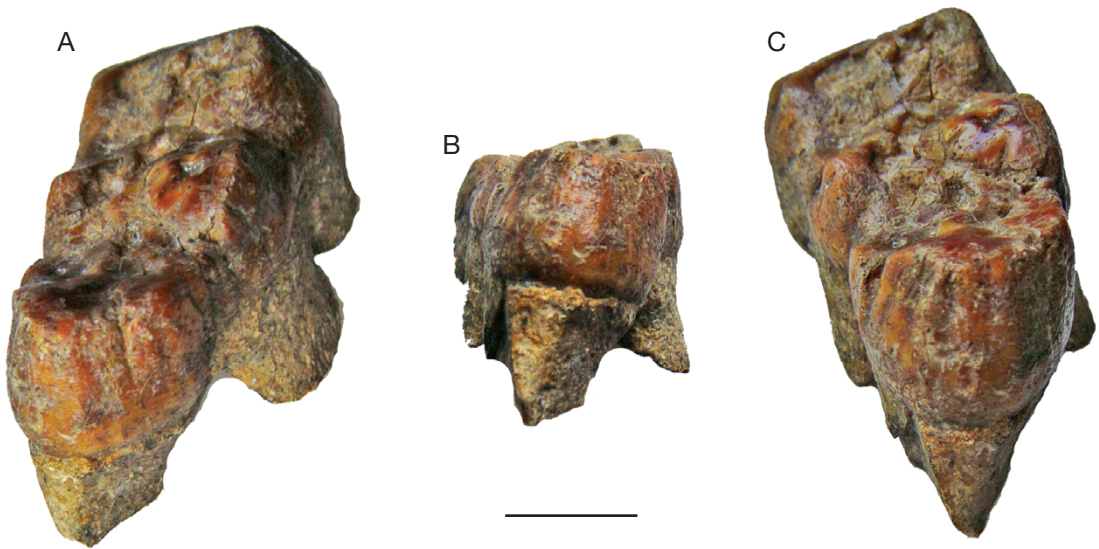


FIG. 5. — *Dasychoerus strozii* (Meneghini, 1862) from the Sables marins de Montpellier (MNHN.F.MON13), views of the distal end of the m/3 to show grooves and undulations in the walls of the talonid: **A**, oblique slightly lingual view; **B**, distal view showing buccally tilted distal root; **C**, oblique slightly buccal view. Scale bar: 10 mm.

The mandible, FSL 40 151, is juvenile, in which the m/3 is unerupted, although visible due to damage to the bone that used to surround it. This specimen is substantially smaller than other material from the Sables marins de Montpellier and is close in dimensions and morphology to *Dasychoerus arvernensis*.

The m/1 is heavily worn, despite the youthful age of the individual and little remains to describe and interpret. The m/2 shows mesio-distally broad buccal and lingual notches with sub-parallel margins. The hypoconid is large and the associated cingular structures are well developed. The m/3 is unworn, showing almost symmetrical arrangements of the cusps in each cusp pair. The hypoconulid (talonid complex) is in line with the rest of the crown, not showing the characteristic buccal bend that occurs in teeth of “*Sus*” *provincialis*.

Dasychoerus sp. from Kvabebi

Propotamochoerus provincialis race *minor* – Mottl 1939: 324, pl. 4, fig. 4, pl. 5, fig. 1.

MATERIAL. — FSL 40 152, right M3/ (Fig. 11A).

REMARK

Differential diagnosis. This un-named suid species is intermediate in dimensions between “*Sus*” *provincialis* and *Dasychoerus arvernensis*. Talon in upper third molar centrally positioned.

DESCRIPTION

An isolated upper third molar from Montpellier stands out from the rest of the specimens from the deposits by its dimensions and talon morphology, the tooth resembling specimens from Kvabebi, Georgia (Vekua 1972) (see Figs 5; 11A; 16). FSL 40 152, is lightly worn and has a symmetrical crown outline and a simple talon (Fig. 11A). The lingual cusps in each cusp pair are slightly behind the level of the buccal cusps. The mesial cingulum is mesio-distally broad the main cusps show marked lingual and buccal flare and the talon is slightly enlarged and centrally positioned directly behind the posterior accessory cusplet (hypoconule). The anterior, median and posterior accessory cusplets are mesio-distally compressed. The Fürchen are subdued indicating that the enamel is thick. There are basal pillars at the ends of the median and posterior transverse valleys.

TABLE 3. — Measurements (in mm) of teeth of “*Sus*” *provincialis* Blainville, 1847 (normal script) and *Dasychoerus strozii* (Meneghini, 1862) (italics) housed in the MNHN.

Specimen	Tooth	Mesio-distal length	Bucco-lingual breadth
Left mandible MNHN.FMON16	Right i/1	6.0 (root)	9.3
	Left i/1	5.5 (root)	9.3
	Left canine	14.8 (lingual side)	12.6 (distal side)
		13.6 (buccal side)	
	Diastema c/1-p/1	4.0	
	Left p/1	9.8	4.7
	Left p/1	11.5 (root)	6.0 (root)
	Diastema p/1-p/2	11.7	
	Left p/2	c. 17.5 (alveolus)	
	Left p/3	c. 17 (alveolus)	
	Left p/4	17.0	13.1
	Left m/1	18.9	15.6
	Left m/2	25.0	20.0
	Left m/2	25.0	18.6
Left mandible MNHN.FMON15	Left m/3	35.3	20.2
Isolated tooth MNHN.FMON17	Right p/4	16.8	12.2
Isolated tooth MNHN.FMON14	Left M3/	38.0	25.8

“*Sus*” *provincialis* Blainville, 1847

Sus provincialis Blainville, 1847: 208, pl. 9, G. *Sus*, *S. provincialis* (only the M3/ and D4/, not the m/2-m/3) *partim*. — Gervais 1850: 100, pl. 3 figs 1, 2, 4-6 *partim*; 1859: 177, pl. 3, figs 1, 2, 4-6 *partim*.

Potamochoerus (?) *provincialis* – Stehlin 1899-1900: pl. 1, fig. 29 (not the Lyon snout) *partim*.

Propotamochoerus provincialis – Morales 1984: 75-87, pl. 4, figs 1-18 (not the Lyon snout) *partim*.

cf. *Propotamochoerus provincialis* – Van der Made 2003: 313, 314, fig. 12a-12c.

LECTOTYPE. — UM SM 460, right M3/ from the Sables marins de Montpellier (here designated).

REMARKS

Differential diagnosis “*Sus*” *provincialis* differs from *Dasychoerus arvernensis* by its superior dimensions and from *Dasychoerus strozii* by its smaller dimensions (see Fig. 16).

NOTE ON THE GENERIC STATUS OF THE SPECIES “*Sus*” *PROVINCIALIS*

Over the years the Montpellier suids have been attributed to *Sus* Linneaus, 1758, *Potamochoerus*,

Propotamochoerus Pilgrim, 1925 and *Korynochoerus* Schmidt-Kittler, 1971. Employment of the latter three generic names was due in part to the fact that the hypodigm of the species contained remains of two taxa (here called “*Sus*” *provincialis* and *Dasychoerus strozii*) the “potamochoerine” aspect of the fossils usually being deduced from a snout which is here attributed to *Dasychoerus strozii*. The material attributed to “*Sus*” *provincialis* in this paper does not have enough diagnostic characters to settle its generic status. Pending the recovery of more complete material, or of access to undescribed material, the generic status is left open.

MNHN COLLECTION

In the MNHN there are four undescribed fossils from the “sables marins” of Montpellier which can be attributed with confidence to “*Sus*” *provincialis*. They are smaller than the specimen attributed to *Dasychoerus strozii* but are larger than *Dasychoerus arvernensis*. The most informative specimen is a left mandible with part of the symphysis (MNHN.FMON15), containing the roots of the left and right i/1, complete p/1, roots of the left p/2 and p/3, and the crowns of left p/4, m/1 and m/2/.

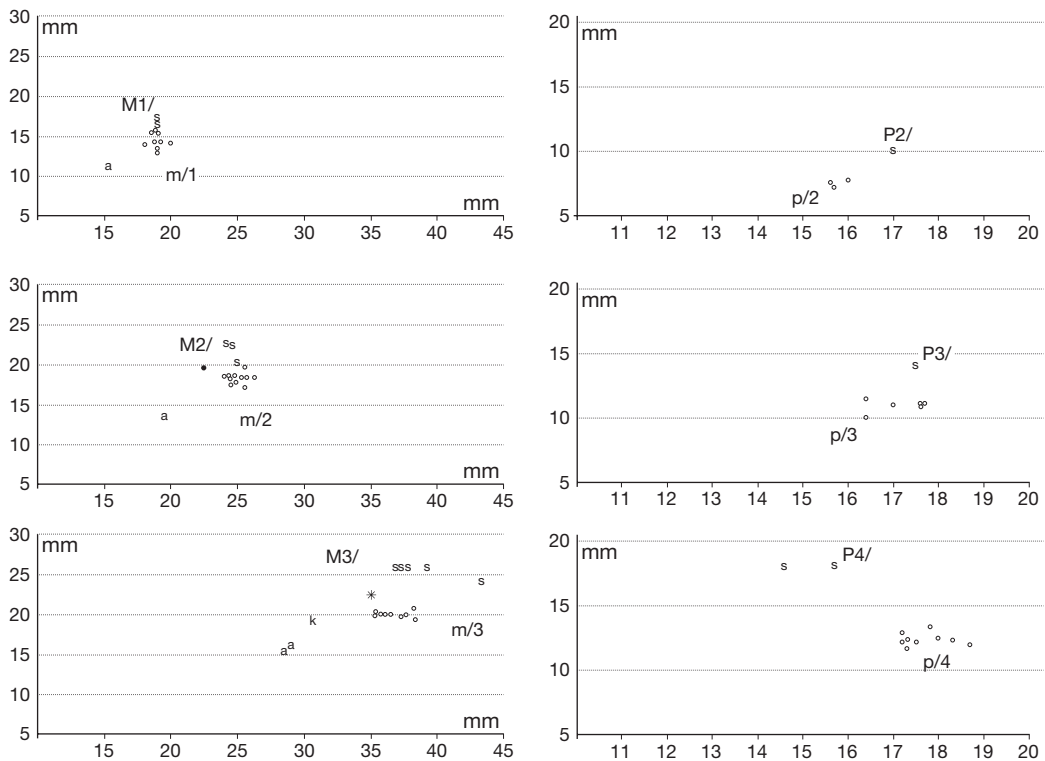


FIG. 6. — Bivariate plots of upper and lower cheek teeth of suids from the Sables marins de Montpellier, France. Abbreviations: **a**, *Dasychoerus arvernensis* (Croizet & Jobert, 1828); **k**, *Dasychoerus* sp. from Kvabebi; **s**, *Dasychoerus stozzii* (Meneghini, 1862); **o**, “*Sus*” *provincialis* Blainville, 1847, lower teeth; **●**, “*Sus*” *provincialis*, upper teeth; *****, lectotype right M3/ of “*Sus*” *provincialis*.

The canine alveolus is damaged, but its verrucosic section can be ascertained (Table 3).

The symphysis is not spatulate but resembles that of *Sus scrofa* Linnaeus, 1758 and it extends back as far as the midline of p/2. The depth of the jaw varies from 50.5 mm at p/2 to 55.4 mm beneath the front of m/3. It is not thickened laterally (24 mm beneath p/3; 34 mm beneath m/2). There are two prominent foramina, one each side of the genial fossa. On the buccal aspect of the mandible there are three small mental foramina in the upper half of the jaw arranged one behind the other.

The teeth in the mandible are moderately worn (Fig. 8). The p/1 is reduced. The crown is damaged, being comprised of a single cusplet posed on two coalescent roots that are substantially larger than the crown, as is often the case in *Sus scrofa* and *Dasychoerus verrucosus*. The p/4 has a bifid apex, a

tall mesial cusplet and mesial cingulum, and a tall and broad talonid cuspid. The m/1 is deeply worn and preserves little of the original morphology. The beaded mesio-buccal cingulum can be discerned, as can some wrinkled enamel in the buccal end of the median transverse valley. The buccal and lingual notches (the ends of the median transverse valley) are mesio-distally broad. The m/2 is deeply worn, but the Fürchen can be made out, as can the beaded mesio-buccal cingulum, mesio-lingual cingulum, a low enamel complex in the buccal end of the median transverse valley, and a distal cingulum that walls off two fovea, one each side of the posterior accessory cusplet. The buccal and lingual notches are broad mesio-distally.

The second mandible stored in the MNHN (Fig. 9B) has less worn teeth than the preceding specimen. The m/2 shows all the classic structures

of suid lower molars (Pickford 1988) with four main cusps at the four corners of the crown, accompanied by well developed anterior, median and posterior accessory cusplets, a beaded anterior cingulum and a posterior cingular complex either side of the posterior accessory cusplet closing off two posterior foveae. The Fürchenplan is clearly visible, comprising three grooves on each of the main cusps (Hünemann 1968), the anterior and posterior ones on each cusp being slit-like and mesio-distally oriented, and the central ones being less well defined and oriented more transversely. The m/3 is built along the same lines as the m/2 but has a large talonid cusp (the hypoconulid) posteriorly. This cuspid is offset slightly to the buccal side of the centre-line of the crown and the root which supports it is tilted slightly buccally. The cervix of the m/3 is almost straight, rising gently distally (best observed lingually).

The isolated right p/4 (Fig. 9A) has a bifid main cusp, a tall mesial cusplet and anterior cingulum, and a tall talonid and posterior cingulum. The preprotocristid is subdivided into three beads.

THE UNIVERSITY OF MONTPELLIER II COLLECTION (UM – OLD ABBREVIATION WAS USTL)

The University of Montpellier II possesses 24 suid specimens from the Sables marins de Montpellier, but they have not been accessible to researchers for more than 60 years, so little is known about them. Requests to examine the unpublished specimens were not successful.

SM 395 is a fragment of left mandible containing p/2–p/4 in light wear (Fig. 10F). The p/2 is a blade-like tooth, triangular in lateral view with a low anterior cusplet about one third the height of the crown, and a posterior cusplet about half the height of the tooth, bordered distally by a cingular structure. There are two stout, elongated roots (ca twice the height of the crown) that diverge gently from each other, both being slightly inclined anteriorly.

The p/3 is constructed along the same lines as the p/2 but all the structures are more developed. The anterior cusplet is about half the height of the crown, the distal one about two thirds the height of the tooth. The incisions separating the anterior

and posterior cusplets from the main one are better defined and deeper. The posterior cingulum broadens the distal extremity of the tooth, forming a low cusplet lingually and a beaded ridge buccally. There are two shallow depressions either side of, and just behind, the main cusp, which would soon disappear with wear. This represents a nascent Innenhügel (Hünemann 1968). The main cusp is slightly offset buccally when compared to the Innenhügel.

The p/4 is basically similar to the p/3 but all the elements are more robust and the grooves and valleys are deeper and wider. The anterior cusplet is taller than in the p/3, reaching two thirds the height of the crown and being bordered by descending buccal and lingual cingular ridges. The talonid cusplet is larger than in the p/3 and the incisions separating it from the main cusp are better defined. The posterior cingulum is beaded. The main cusp is bifurcate at the apex with a second cusp (the Innenhügel of Hünemann [1968]) behind and to the lingual side of the mesial cusp. The Innenhügel has a posterior groove descending into the valley that separates the Innenhügel from the posterior cusp. The preprotocristid is subdivided into three beads, not counting the mesial cusplet.

SM 392 is a right mandibular fragment containing p/3–m/2 figured in reverse by Gervais (1850: pl. 22, fig. 8). The premolars are less worn than they are in SM 395 but they are morphologically close to them, even down to fine details such as the presence of a small cusplet emanating from the lingual side of the distal cingulum of the p/3 and the presence of three beads on the preprotocristid of the p/4 (best appreciated in lingual view). The m/1 and m/2 are morphologically similar to each other, but it should be noted that the m/1 is appreciably smaller than the m/2. Both teeth are comprised of four main cusps arranged in two lophids, with small anterior accessory cusplets, but large median and posterior accessory cusplets. The buccal cusps are slightly lower than the lingual ones, as is the case in genera such as *Hippopotamodon* Lydekker, 1877 (Pickford 1988). The buccal ends of the median transverse valleys have low tubercles of wrinkled enamel, not quite forming basal pillars. The lingual ends of the median transverse valleys do not have cingula. The mesial cingulum is beaded in both the m/1 and the

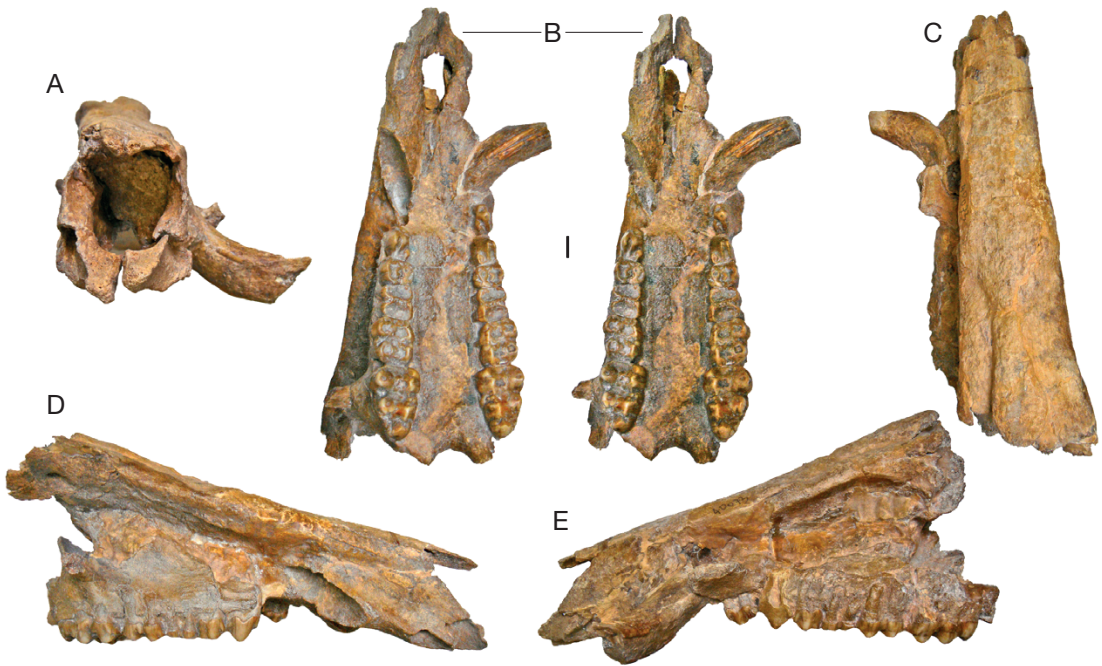


FIG. 7. — FSL 40 073, snout of *Dasychoerus strozzi* (Meneghini, 1862) from the Sables marins de Montpellier: **A**, anterior view; **B**, stereo occlusal view; **C**, dorsal view; **D**, right lateral view; **E**, left lateral view. Scale bar: 10 mm.

m/2, especially on the antero-buccal corners of the crowns. The distal cingulum is likewise beaded. The Fürchen of the main cusps are relatively subdued due to the thickness of the enamel, but are nevertheless clearly visible, especially in the lingual cusps.

A left m/2 in the Montpellier collection (SM 462, Fig. 10G) corresponds to a specimen illustrated in reverse by Gervais (1850: pl. 3, fig. 5). It is heavily worn, exposing dentine on all four main cusps, as well as on the median and posterior accessory cusplets and the postprotocristid (the 2/3 cusplet of Pickford [1988]). The anterior accessory cusplet is small and is incorporated into the premetacristid. In this specimen, the Fürchen are particularly clearly visible due to the wear stage of the tooth which exposes the bases of the Fürchen.

SM 393, is a right m/3 in light wear. The talonid is bent gently buccally and what remains of the root is inclined buccally. The talonid cusp is comprised of two subequal parts separated by an incision that descends about half the height of the crown. The notches either side of the posterior accessory cusplet

are closed by beaded cingula, as are the notches at either end of the median transverse valley. The anterior cingulum is beaded and does not reach the lingual aspect of the tooth. In lateral and medial views the cervix is seen to curve slightly occlusally.

SM 394 is a left D4/ in light wear. The enamel is thin and the occlusal outline slightly trapezoidal. The roots, although damaged, splay outwards and are quite thin. There are four main cusps and strong mesial and distal cingula which are finely beaded. At each end of the median transverse valley there is a low, rounded cusplet forming a basal pillar or style, one lingually, the other buccally. The median accessory cusplet is joined by a worn ridge to the hypocone.

A right M2/ curated at Montpellier II (SM 461, Fig. 10B) corresponds to the specimen figured in correct orientation by Gervais (1850: pl. 3, fig. 2). It is heavily worn, exposing dentine at the apices of the four main cusps as well as on the anterior and median accessory cusplets, but not on the posterior accessory cusplet. Indeed the dentine lakes of the

anterior and median accessory cusplets are coalescent with those of the protocone and hypocone respectively. There is a small cingular bead at the buccal end of the median transverse valley, and lingually there is a low cingulum. The mesial and distal cingula are robust, the distal one responsible for quite an overhanging distal margin of the crown.

Specimen SM 460 (old number 45) in the Montpellier II collection is the right M3/ (Fig. 10C) figured in correct orientation by Blainville (1847) and Gervais (1850: pl. 3, fig. 1). This specimen is hereby designated as the lectotype of *Sus provincialis*. The crown has a rectilinear lingual edge and a convex buccal one. The hypoconule (or talon) is positioned in line with the protocone and hypocone. The mesial cingulum is well developed and beaded where unworn. The median accessory cusplet is worn so much that dentine is exposed. The four main cusps, arranged in two pairs, all expose dentine at their apices. The buccal and lingual ends of the median transverse valley contain robust cingular structures resembling basal pillars or styles. The same applies to the posterior transverse valley located in front of the talon. The talon itself is small and consists of a single cusp. The median accessory cusplet is closely applied to the hypocone and exposes dentine at its apex. In lingual view, the cervix is seen to be almost horizontal, bending very slightly rootwards at the level of the talon. The root system in this specimen is interesting, as there are four main roots beneath the four main cusps, accompanied by small roots in the centre line of the tooth, one mesially beneath the anterior accessory cusplet, one beneath the posterior accessory cusplet and a third beneath the talon.

Pickford (2012) accepted Gervais' (1850) authorship of the species *Sus provincialis*, and indicated that a lower third molar in his hypodigm was to be the lectotype, but this is no longer tenable because Blainville's (1847) hypodigm does not contain such a tooth. Instead, the upper third molar figured by Blainville (1847) is here selected as the lectotype.

THE FACULTY OF SCIENCE, LYON, COLLECTION

The most comprehensive published sample of fossil suids from the Sables marins de Montpellier is housed at the Faculty of Science, Lyon.

The Lyon suid fossils from the Montpellier marine sands belong to four distinct taxa, *Dasychoerus arvernensis* (FSL 40 151, a mandible with three molars and FSL 40 154 a right m/3), *Dasychoerus* sp. from Kvabebi (FSL 40 152, an M3/), *D. stozzii* (FSL 40 073, a snout with a canine and most of the cheek teeth, previously attributed to "*Sus*" *provincialis*) and "*Sus*" *provincialis*, several mandibles and isolated teeth (see Table 4).

The previous identification of FSL 40 073 as "*Sus*" *provincialis* has coloured interpretations of European Pliocene suids ever since the specimen was first described by Stehlin (1899-1900) and, in retrospect, this determination has caused a great deal of confusion. For example, there has been doubt thrown on Vekua's (1972) identification of suids from Kvabebi, Georgia (Vekua 1972) as *Propotamochoerus provincialis* (Blainville, 1847) because they differ in morphology from the Lyon snout, prompting Azzaroli (1975) and Geraads *et al.* (2008) to doubt that it represented this species. Yet, when FSL 40 073 is removed from "*Sus*" *provincialis* and is instead classified as *Dasychoerus stozzii*, the cheek teeth in the Kvabebi fossils fall quite close to the range of morphometric variation of "*Sus*" *provincialis* (see Fig. 16).

FSL 40 152, a lightly worn right M3/ has a symmetrical crown outline and a simple talon (Fig. 11A). The lingual cusps in each cusp pair are slightly behind the level of the buccal cusps. The mesial cingulum is broad. The anterior, median and posterior accessory cusplets are mesio-distally compressed. The Fürchen are subdued indicating that the enamel is thick. There are basal pillars at the ends of the median and posterior transverse valleys.

The teeth in the five mandibles curated at the Faculty of Science, Lyon (FSL 40 061, Fig. 14B; FSL 40 07, Fig. 13A; FSL 40 072, Figs 13B, 14A; 40 881, Fig. 12A; FSL 40 884, Fig. 12B) are similar to those in the specimen at the MNHN, Paris. It is not necessary to describe each specimen in detail, but some comments on the m/3s is called for.

The p/4 in FSL 40 881 is unworn. The Innenhügel is slightly behind and to the lingual side

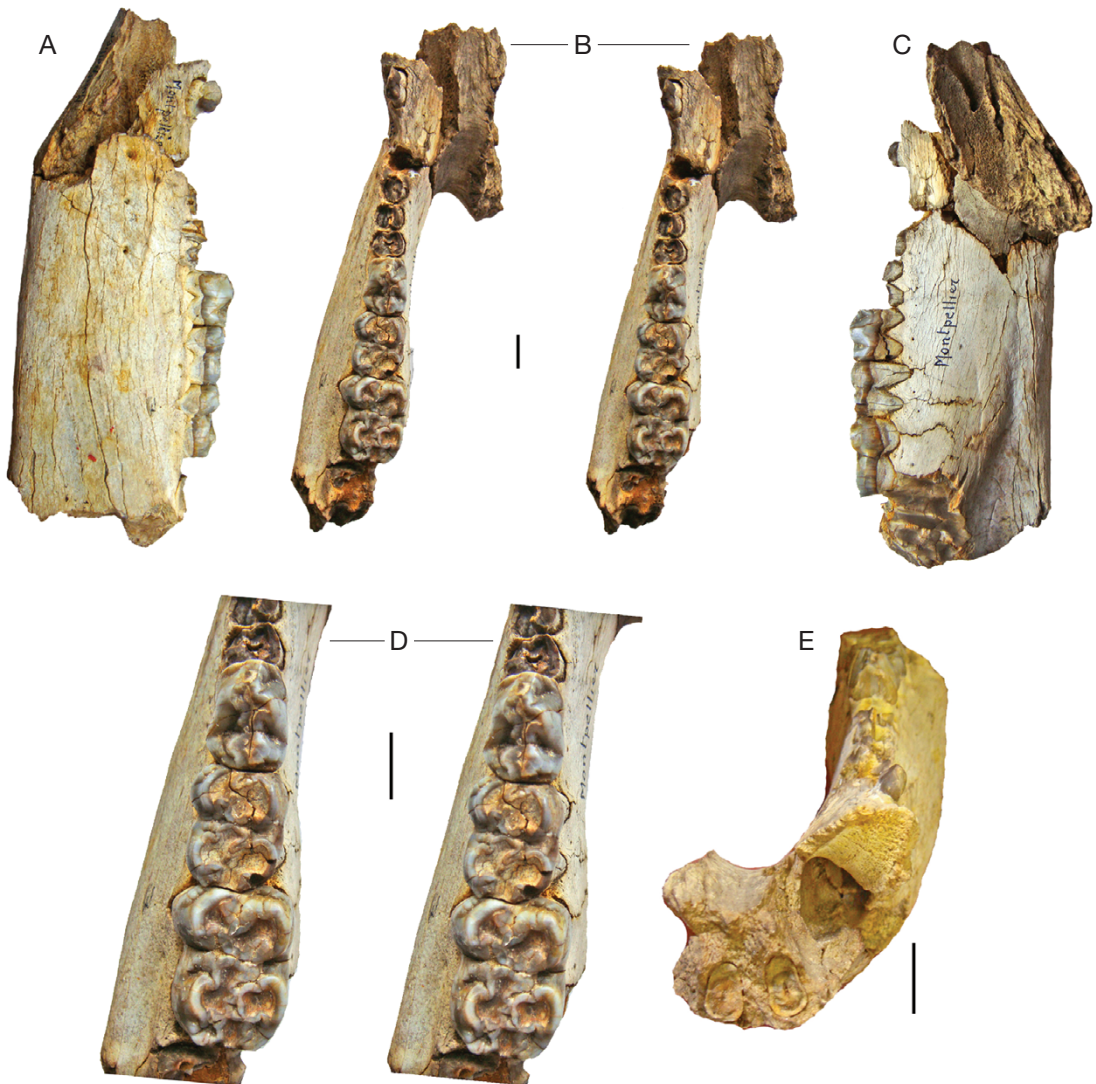


FIG. 8. — Left mandible of “*Sus*” *provincialis* Blainville, 1847 from the Sables marins de Montpellier, MNHN.F.MON16: **A**, buccal view; **B**, stereo occlusal view; **C**, lingual view; **D**, enlarged stereo occlusal view of the cheek teeth; **E**, oblique anterior view to show verrucosic section of canine alveolus. Scale bars: 10 mm.

of the main cusp but the incisions separating it from the main cusp are shallow. The mesial cusplet is low and the distal one is about $\frac{2}{3}$ of the height of the main cusp. The m/3 is unerupted, the Furchen are shallowly incised. The lingual and buccal notches are mesio-distally broad, and there are small basal pillars at the ends of the buccal notches. The talonid is subdivided into

two unequal moieties, the larger part slightly bent buccally.

FSL 40 884 has p/2-m/3. The p/2 is a single cusped tooth with low mesial and distal cusplets. The crown is bucco-lingually compressed, almost blade-like. The p/3 is broader, with bigger mesial and distal cusplets. The p/4 shows a distinct in-nenhügel and a large distal accessory cusp. The

TABLE 4. — Measurements (in mm) of the teeth of suids from the Sables marins de Montpellier housed in the Faculty of Science, Lyon (FSL), the Muséum national d'Histoire naturelle, Paris (MNHN), and the University of Montpellier II (UM). Abbreviations: *D.*, *Dasychœrus*; *S.*, *Sus*.

Catalogue	Tooth	Length	Breadth	Taxon	Reference
FSL 40 151	m/1 rt	15.3	11.3	<i>D. arvernensis</i>	Own 2011; Guérin, unpub. data 15 × 11.5
FSL 40 151	m/2 rt	19.6	13.4	<i>D. arvernensis</i>	Own 2011; Guérin, unpub. data 21 × 15
FSL 40 151	m/3 rt	29.0	16.2	<i>D. arvernensis</i>	Own 2011; Guérin, unpub. data 31 × 15.5
FSL 40 154	m/3 rt	28.7	15.7	<i>D. arvernensis</i>	Own 2011; extra pair of cusps length adjusted
MNHN.F.MON13	m/2 lt	25.0	20.2	<i>D. strozzi</i>	Own 2011
MNHN.F.MON13	m/3 lt	43.3	24.1	<i>D. strozzi</i>	Own 2011; Fejfar 1964 as 44 × 22.5
FSL 40 073	P2/ lt	17.0	9.9	<i>D. strozzi</i>	Own 2011; Morales 1984 as 17.5 × 10.5
FSL 40 073	P3/ rt	17.5	14.0	<i>D. strozzi</i>	Own 2011; Morales 1984 as 17 × 13.2
FSL 40 073	P4/ lt	14.6	18.0	<i>D. strozzi</i>	Own 2011; Morales 1984 as 15.5 × 17.5
FSL 40 073	P4/ rt	15.7	18.1	<i>D. strozzi</i>	Own 2011; Morales 1984 as 16.2 × 17.8
FSL 40 073	M1/ lt	19.0	16.7	<i>D. strozzi</i>	Own 2011; Morales 1984 as 18 × 17.2
FSL 40 073	M1/ rt	19.0	17.2	<i>D. strozzi</i>	Own 2011; Morales 1984 as 17.8 × 17.3; Mazo & Torres 1990
FSL 40 073	M2/ lt	24.5	22.4	<i>D. strozzi</i>	Own 2011; Morales 1984 as 24 × 22.8; Mazo & Torres 1990
FSL 40 073	M2/ rt	24.2	22.8	<i>D. strozzi</i>	Own 2011; Morales 1984 as 24.5 × 22.3; Mazo & Torres 1990
FSL 40 073	M3/ lt	37.0	26.0	<i>D. strozzi</i>	Own 2011; Morales 1984 as 37 × 26; Mazo & Torres 1990
FSL 40 073	M3/ rt	37.3	26.0	<i>D. strozzi</i>	Own 2011; Morales 1984 as 35.2 × 25.2; Mazo & Torres 1990
FSL 40 159	M3/ rt	39.3	25.8	<i>D. strozzi</i>	Morales 1984 as 39.3 × 25.8; Mazo & Torres 1990
FSL 40 152	M3/ rt	33.0	19.6	<i>D. cf. Kvabebi</i>	Own 2011
FSL 40 144	i/1 rt	7.3	11.6	<i>S. provincialis</i>	Own 2011
FSL 40 072	i/2 rt	7.3	13.0	<i>S. provincialis</i>	Own 2011
FSL 40 160	i/2 rt	7.0	12.6	<i>S. provincialis</i>	Own 2011
MNHN.F.MON16	p/1 lt	9.6	4.8	<i>S. provincialis</i>	Own 2011
FSL 40 072	p/1 rt	10.2	5.1	<i>S. provincialis</i>	Own 2011; Morales 1984 as 10 × 5
FSL 40 884	p/2 lt	16.0	7.8	<i>S. provincialis</i>	Own 2011; Morales 1984 as 18 × 8.8
UM SM 395	p/2 lt	15.7	7.2	<i>S. provincialis</i>	Own 2011
FSL 40 072	p/2 rt	15.6	7.6	<i>S. provincialis</i>	Own 2011; Morales 1984 as 15.8 × 7.6
FSL 40 884	p/3 lt	17.0	11.0	<i>S. provincialis</i>	Own 2011; Morales 1984 as 17.5 × 11.2
UM SM 395	p/3 lt	17.6	10.9	<i>S. provincialis</i>	Own 2011
FSL 40 071	p/3 rt	16.4	10.0	<i>S. provincialis</i>	Own 2011; Morales 1984 as 16 × 10
FSL 40 072	p/3 rt	16.4	11.4	<i>S. provincialis</i>	Own 2011; Morales 1984 as 16.6 × 11
FSL 40 884	p/3 rt	18.0	—	<i>S. provincialis</i>	Morales 1984
MNHN Cast	p/3 rt	17.7	11.1	<i>S. provincialis</i>	Own 2011
UM SM 392	p/3 rt	17.6	11.1	<i>S. provincialis</i>	Own 2011
FSL 40 881	p/4 lt	18.7	12.0	<i>S. provincialis</i>	Own 2011; Morales 1984 as 19 × 12
FSL 40 884	p/4 lt	17.5	12.2	<i>S. provincialis</i>	Own 2011; Morales 1984 as 17.5 × 13
MNHN.F.MON16	p/4 lt	17.2	12.9	<i>S. provincialis</i>	Own 2011
UM SM 395	p/4 lt	18.0	12.5	<i>S. provincialis</i>	Own 2011
FSL 40 071	p/4 rt	17.3	11.7	<i>S. provincialis</i>	Own 2011; Morales 1984 as 17 × 12
FSL 40 072	p/4 rt	17.8	13.4	<i>S. provincialis</i>	Own 2011; Morales 1984 as 17.2 × 0
FSL 40 884	p/4 rt	17.0	12.5	<i>S. provincialis</i>	Morales 1984
MNHN Cast	p/4 rt	17.3	12.4	<i>S. provincialis</i>	Own 2011
MNHN.F.MON16	p/4 rt	17.2	12.2	<i>S. provincialis</i>	Own 2011
UM SM 392	p/4 rt	18.3	12.3	<i>S. provincialis</i>	Own 2011
FSL 40 145	m/1 lt	18.8	14.3	<i>S. provincialis</i>	Own 2011
FSL 40 161	m/1 lt	19.0	13.0	<i>S. provincialis</i>	Own 2011; Morales 1984 as 17.2 × 13.8
FSL 40 881	m/1 lt	20.0	14.3	<i>S. provincialis</i>	Own 2011; Morales 1984 as 20 × 14.3

TABLE 4. — Continuation.

Catalogue	Tooth	Length	Breadth	Taxon	Reference
FSL 40 884	m/1 lt	18.0	14.0	" <i>S. provincialis</i>	Own 2011; Morales 1984 as 17.2 × 14
MNHN.F.MON16	m/1 lt	18.8	15.6	" <i>S. provincialis</i>	Own 2011
FSL 40 071	m/1 rt	19.0	13.6	" <i>S. provincialis</i>	Own 2011; Morales 1984 as 19 × 13.8
FSL 40 072	m/1 rt	19.0	15.5	" <i>S. provincialis</i>	Own 2011; Morales 1984 as 18 × 15
FSL 40 884	m/1 rt	18.5	15.5	" <i>S. provincialis</i>	Morales 1984
UM SM 392	m/1 rt	19.2	14.4	" <i>S. provincialis</i>	Own 2011; cast in MNHN 19 × 14.8
FSL 40 072	m/2 lt	24.4	18.5	" <i>S. provincialis</i>	Own 2011
FSL 40 161	m/2 lt	24.5	17.4	" <i>S. provincialis</i>	Own 2011; Morales 1984 as 24.9 × 17
FSL 40 881	m/2 lt	26.3	18.4	" <i>S. provincialis</i>	Own 2011; Morales 1984 as 25.3 × 18.2
FSL 40 884	m/2 lt	24.5	18.2	" <i>S. provincialis</i>	Own 2011; Morales 1984 as 25 × 18
MNHN.F.MON16	m/2 lt	24.8	18.5	" <i>S. provincialis</i>	Own 2011
MNHN.F.MON15	m/2 lt	25.5	19.8	" <i>S. provincialis</i>	Own 2011
UM SM 462	m/2 lt	24.9	18.0	" <i>S. provincialis</i>	Own 2011
FSL 40 070	m/2 rt	25.7	18.4	" <i>S. provincialis</i>	Own 2011
FSL 40 071	m/2 rt	25.5	17.2	" <i>S. provincialis</i>	Own 2011; Morales 1984 as 23.2 × 17.5
FSL 40 072	m/2 rt	24.1	18.5	" <i>S. provincialis</i>	Own 2011; Morales 1984 as 24 × 18.2
FSL 40 884	m/2 rt	25.3	18.3	" <i>S. provincialis</i>	Morales 1984
UM SM 392	m/2 rt	25.0	18.2	" <i>S. provincialis</i>	Own 2011; cast in MNHN 25.3 × 19.1
FSL 40 884	m/3 lt	—	20.5	" <i>S. provincialis</i>	Own 2011
FSL 40 161	m/3 lt	35.3	20.0	" <i>S. provincialis</i>	Own 2011; Morales 1984 as 33 × 19.5
MNHN.F.MON15	m/3 lt	35.4	20.3	" <i>S. provincialis</i>	Own 2011; Fejfar 1964 as 35 × 18.6
FSL 40 072	m/3 lt	35.7	20.0	" <i>S. provincialis</i>	Own 2011
FSL 40 155	m/3 lt	36.7	19.9	" <i>S. provincialis</i>	Own 2011
FSL 40 881	m/3 lt	38.3	19.6	" <i>S. provincialis</i>	Own 2011; Morales 1984 as 37 × 19.5
FSL 40 070	m/3 rt	36.5	20.0	" <i>S. provincialis</i>	Own 2011
FSL 40 072	m/3 rt	37.6	20.1	" <i>S. provincialis</i>	Own 2011; Morales 1984 as 35 × 20
UM SM 393	m/3 rt	38.2	20.9	" <i>S. provincialis</i>	Own 2011
FSL 40 159	I1/ lt	9.2	15.5	" <i>S. provincialis</i>	Own 2011
FSL WO 417	I1/ rt	8.5	13.6	" <i>S. provincialis</i>	Own 2011
UM SM 394	D4/ lt	16.3	13.7	" <i>S. provincialis</i>	Own 2011
FSL 40 156	M1/ rt	19	17.1	" <i>S. provincialis</i>	Own 2011
UM SM 461	M2/ rt	22.5	19.7	" <i>S. provincialis</i>	Own 2011
FSL 40 157	M3/ lt	35.0	22.6	" <i>S. provincialis</i>	Own 2011; Morales 1984 as 40159, 35 × 23; Mazo & Torres 1990
MNHN.F.MON14 (Vidal 34)	M3/ lt	37.7	25.9	" <i>S. provincialis</i>	Own 2011
UM SM 460 (old no. 45)	M3/ rt	35.1	26.4	" <i>S. provincialis</i>	Own 2011

three molars are deeply worn, but the m/3 lacks its talonid.

The right mandible, FSL 40 071, lacks its m/3. There are roots of the p/1 and p/2 close behind the canine alveolus, with a short diastema between the two premolars. The mental foramen is beneath this diastema.

FSL 40 072 the talonids of the left and right m/3s are subdivided into two parts (Figs 13B; 14A), a larger part bent somewhat buccally, and a smaller part lingually. The p/1 has a sin-

gle main cusp reposed on two roots which are fused throughout their height. The p/1 and p/2 are separated by a short diastema, beneath which there is a mental foramen at about half the height of the jaw. Smaller mental foramina are present beneath the front of the p/3 and p/4. The p/2 and p/4 are damaged apically but the preserved parts resemble their counterparts in other specimens. The talonid in the m/3 is subdivided, with a large buccal part and a small lingual part.

SUMMARY OF THE LITERATURE ON “*SUS*” *PROVINCIALIS*

Most authors have given the date of creation of the species *Sus provincialis* as Gervais 1859 (Vekua 1972; Azzaroli 1975; Morales 1984; Gallai & Rook 2011). However, the first mention of the name in print was by Blainville (1847) the next was by Gervais (1850) in *Zoologie et Paléontologie françaises* which was published from 1848-1852, followed by Rüttimeyer (1857). Gervais (1849) attributed to *Sus provincialis* a tooth from Cucuron, Vaucluse, that he later named *Sus major* (Gervais, 1850) of which it is the type specimen. The 1859 publication by Gervais, although usually cited as validating the species name *provincialis*, is in fact nine years later than the use of the name accompanied by illustrations by Gervais (1850) and 12 years later than Blainville's (1847) publication of the name.

Lydekker (1884) briefly discussed *Sus provincialis* while making comparisons with the Siwalik suids that he was examining. He reiterated the opinion of Blainville (1847) that the M3/ (i.e. SM 460) was morphologically like that of *Sus africanus* (i.e. *Potamochoerus*) and was larger than that of *Sus scrofa*, whereas its canines were small and it possessed four premolars (I am not aware of the source of his information concerning the canines and four premolar. Gervais' [1850] descriptions do not mention anterior premolars or canines).

Depéret (1890) created a new “race” *Sus provincialis minor* for one of the Early Pliocene suids from the Perpignan area (Roussillon) on account of their diminutive dimensions, the other he attributed to *Sus provincialis* because of its superior dimensions and morphological similarity to material from Montpellier. Later authors have tended to attribute the small material to *Sus arvernensis*, *Sus minor* or *Dasychoerus minor* (Azzaroli 1954, 1975; Guérin & Faure 1985; Berdondini 1992) and to classify the specimens from Montpellier in *Propotamochoerus provincialis*.

Stehlin (1899-1900) transferred the species *Sus provincialis* to *Potamochoerus* (but with a question mark) and illustrated additional specimens (P2/-P4/, pl. 2, fig. 22; M2/-M3/, pl. 6, fig. 1)

but he did not mention a type specimen. The upper premolars and molars that Stehlin studied are preserved in a snout housed at the Faculty of Science, Lyon, but my own examination of the fossil (FSL 40 073) indicates that it represents *Dasychoerus strozzi*. Stehlin (1899-1900) thus added to the mixture of fossils attributed to “*Sus*” *provincialis* started by Blainville (1847) and continued by Gervais (1850) and this has been a constant source of confusion to subsequent authors (Azzaroli 1975) who have tended to base their concept of the species on Stehlin's monumental work without realising that it was a chimera of two species.

In 1926, Pilgrim erected the genus *Propotamochoerus*, and in his phylogeny included the taxa from Montpellier and Roussillon in the genus as the new combinations *Propotamochoerus provincialis major* and *Propotamochoerus provincialis minor*, but without any discussion. Subsequent authors have tended to attribute the Montpellier species to this genus (Vekua 1972) despite the erroneous attribution of the subspecies *major* to it (Azzaroli 1975). The latter species is today attributed to the genus *Hippopotamodon*. Pilgrim (1926) appears to have been confused by the fact that Gervais (1849) attributed to *Sus provincialis* a tooth from Cucuron, (Léberon or Luberon) Vaucluse, which Gervais (1850) later called *Sus major*. The Cucuron tooth is the type specimen of *Hippopotamodon major* (Gervais, 1850) (Gervais 1850: 1859: pl. 12, fig. 2).

Simionescu (1930) described *Propotamochoerus* cf. *provincialis* from Malusteni, Eastern Romania (Radulescu *et al.* 2003).

Azzaroli (1954) designated the specimen depicted in Depéret's publication (1890: pl. 5, fig. 13), a juvenile left mandible containing unerupted p/2-p/4, and functional m/1-m/2 as the lectotype of *Sus minor*. This is specimen CCECL Pp 195. He considered *Sus provincialis* to be a doubtful taxon (a point he reiterated in his 1975 paper).

Fejfar (1964) attributed small suid teeth from Hajnacka, Slovakia, to *Propotamochoerus provincialis minor* and, seemingly unaware of Azzaroli's (1954) prior designation, nominated a lectotype for the subspecies (the incomplete lower left jaw

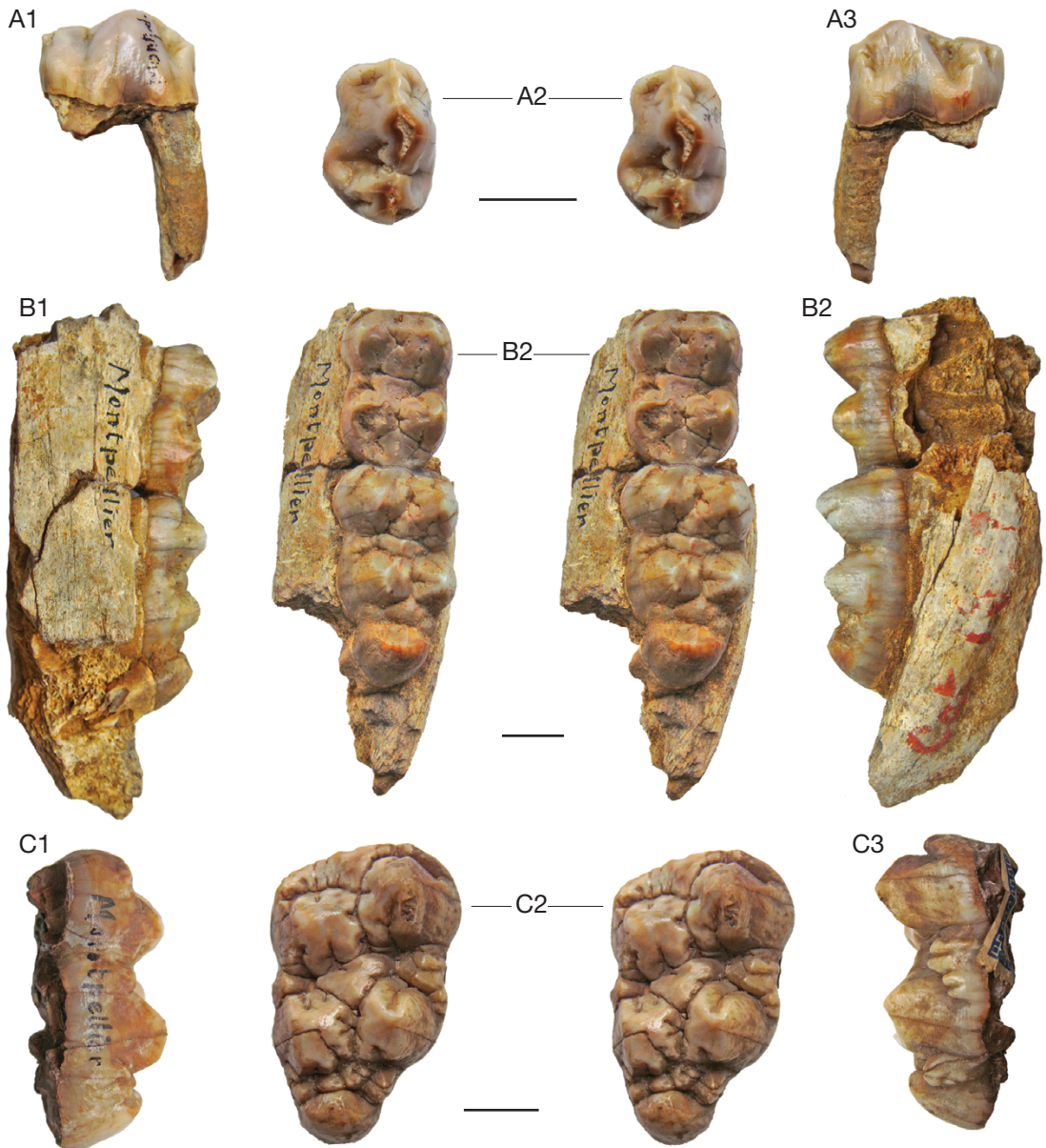


FIG. 9. — Suids from the Sables marins de Montpellier: **A**, **B**, “*Sus*” *provincialis* Blainville, 1847; **A**, MNHN.F.MON17, right p4 in buccal (**A1**), stereo occlusal (**A2**) and lingual (**A3**) views; **B**, MNHN.F.MON15, left mandible containing m/2-m/3, in buccal (**B1**), stereo occlusal (**B2**) and lingual (**B3**) views; **C**, *Dasychoerus strozzi* (Meneghini, 1862), MNHN.F.MON14, left M3/ in lingual (**C1**), stereo occlusal (**C2**) and buccal (**C3**) views. Scale bar: 10 mm.

with m/2 and m/3 in situ, described and figured in Depéret [1890: 85, 86, pl. V, fig. 12]). However, the said mandible is in fact depicted as figure 14

and not as figure 12 of Depéret’s 1890 publication, the latter being of an upper third molar. Azzaroli’s (1954) designation of a lectotype predates that of

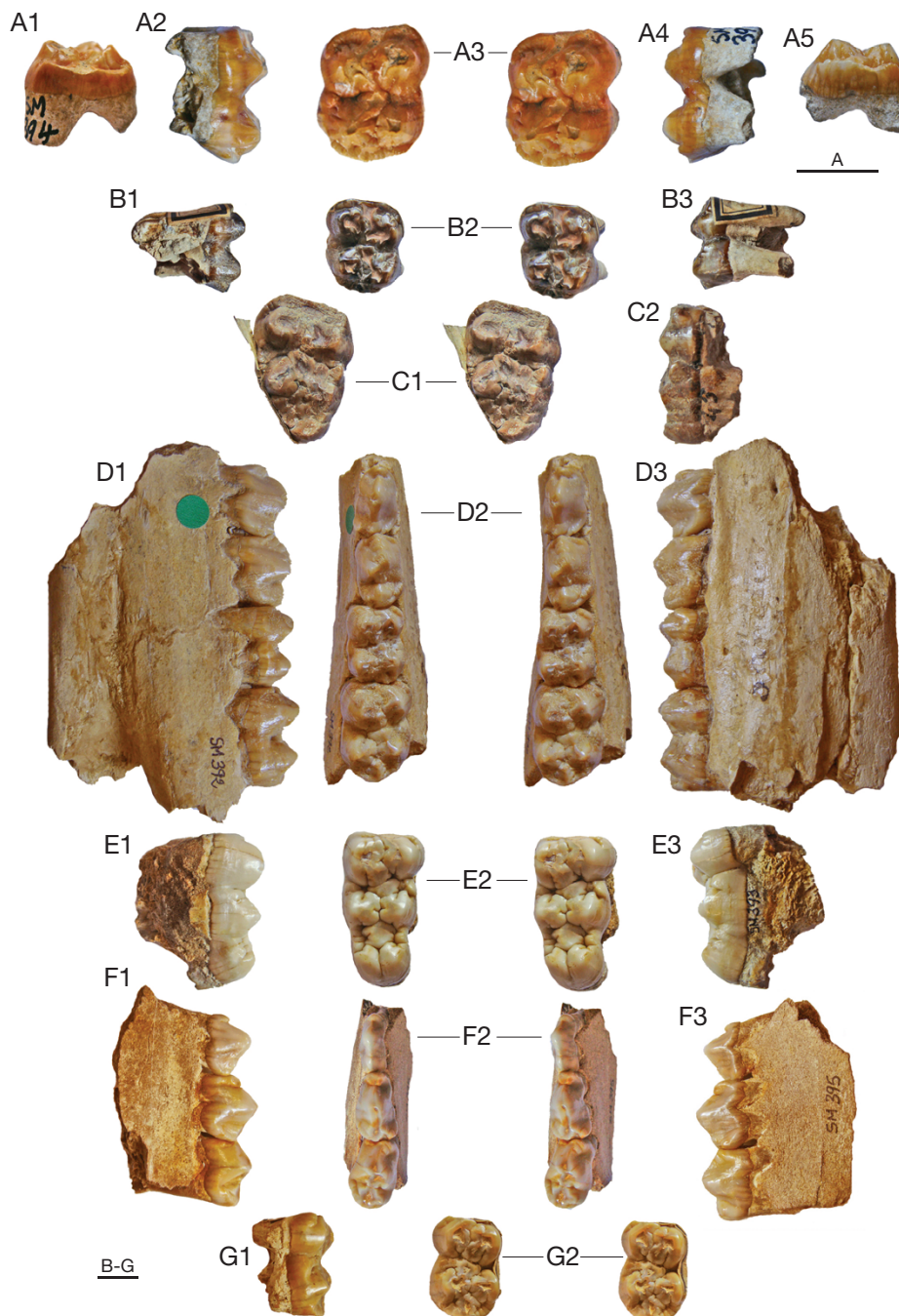


FIG. 10. — “*Sus*” *provincialis* Blainville, 1847 from the Sables marins of Montpellier housed at the University of Montpellier II: **A**, SM 394, left D4 in mesial (**A1**), buccal (**A2**), stereo occlusal (**A3**), lingual (**A4**) and distal (**A5**) views; **B**, SM 461, right M2/ in lingual (**B1**), stereo occlusal (**B2**) and buccal (**B3**) views; **C**, lectotype SM 460, right M3/ in stereo occlusal (**C1**) and lingual (**C2**) views; **D**, SM 392, right mandible with p/3-m/2 in lingual (**D1**), stereo occlusal (**D2**) and buccal (**D3**) views; **E**, SM 393, right m/3 in buccal (**E1**), stereo occlusal (**E2**) and lingual (**E3**) views; **F**, SM 395, left mandible with p/2-p/4 in buccal (**F1**), stereo occlusal (**F2**) and buccal (**F3**) views; **G**, SM 462, left m/2 in buccal (**G1**) and stereo occlusal (**G2**) views. Scale bars: 10 mm, A is double the dimensions of the others.

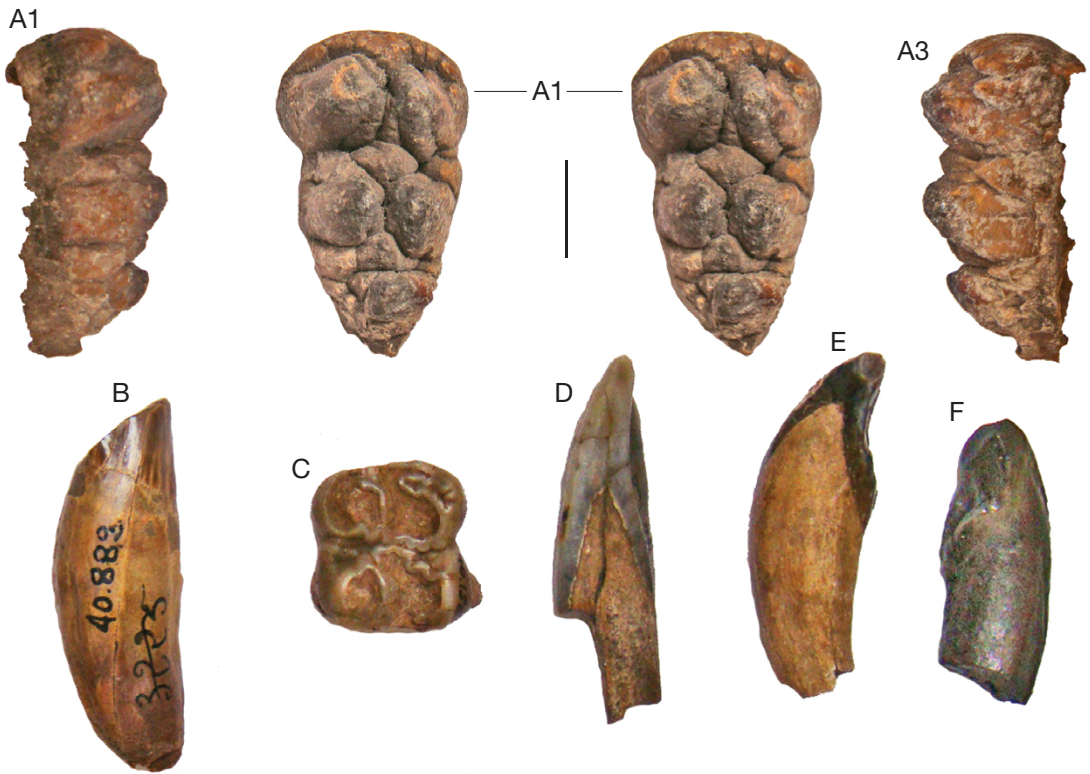


FIG. 11. — Isolated teeth of *Dasychoerus* sp. from Kvabebi (A) and “*Sus*” *provincialis* Blainville, 1847 (B–F) from the Sables marins de Montpellier: A, FSL 40 152, right M3/ in buccal (A1), stereo occlusal (A2) and lingual (A3) views; B, FSL 40 882, female upper canine, buccal view; C, FSL 40 156, right M1/, occlusal view; D, FSL 40 160, right I1/2, mesial view; E, FSL 40 159, left I1/, mesial view; F, FSL WO 417, right I1/, labial view. Scale bar: 10 mm.

Fejfar, and thus the valid lectotype is CCECL Pp 195. Fejfar (1964) did not mention a type specimen for the species *Propotamochoerus provincialis*. He did however, list the presence of *Sus strozzii* at Montpellier, giving measurements of 44×22.5 mm (l \times b) for an m/3 which corresponds to the large specimen, MNHN.F.MON13, illustrated by Blainville (1847) and Gervais (1850).

Vekua (1972) reported that no holotype had been specified for the species *Propotamochoerus provincialis* (Holotype: Ne vydelen – transliteration from the Russian). At his disposal he had some excellent but slightly crushed cranial and mandibular material from Kvabebi, Georgia. The third molars in the Georgian fossils are intermediate in dimensions between the Montpellier ones and material attributed to *Dasychoerus arvernensis*, as

shown in Table 4 and 5, and Figure 16. Azzaroli (1975) and Geraads *et al.* (2008) considered that the Kvabebi suid differed from the Montpellier sample at the species (or even the generic) level. The perception of a species difference is enhanced by the fact that the snout from Montpellier preserved in the Faculty of Science, Lyon, upon which the comparisons were partly based, belongs to the larger suid *Dasychoerus strozzii* rather than to “*Sus*” *provincialis*. Further research is required to resolve the issue.

The Kvabebi suid differs from species of *Propotamochoerus* by a number of features including an obvious cranial distinction – the presence of a sagittal crest in the neurocranium (Vekua 1972: pl. 27, fig. 1). Other species of *Propotamochoerus* possess a broader occiput (Pickford 1988) and

TABLE 5. — Dental measurements (in mm) of the Kvabebi fossils attributed to *Propotamochoerus provincialis* (Blainville, 1847) by Vekua (1972). Measurements labelled "Own, 1997" were taken by the author in 1997.

Catalogue	Tooth	Length	Breadth	Source
K 38	p/1	7.5	5.0	Vekua 1972
K 31	p/1	9.5	5.5	Vekua 1972
K 38	p/2	11.0	6.0	Vekua 1972
K 31	p/2	11.0	6.5	Vekua 1972
Kvabebi mandible	p/2	14.0	8.0	Vekua 1972
K 38	p/3	15.0	9.0	Vekua 1972
K 31	p/3	14.5	9.0	Vekua 1972
Kvabebi mandible	p/3	14.0	8.0	Vekua 1972
K 38	p/4	18.0	11.5	Vekua 1972
K 31	p/4	16.0	11.5	Vekua 1972
Kvabebi mandible	p/4	15.5	11.5	Vekua 1972
K 38	m/1	18.2	14.0	Own 1997; Vekua 1972 as 18 × 13
K 31	m/1	14.0	14.0	Vekua 1972
Kvabebi mandible	m/1	16.0	14.0	Vekua 1972
K 38	m/2	23.7	18.1	Own 1997; Vekua 1972 as 24 × 17.5
Kvabebi mandible	m/2	21.0	17.0	Vekua 1972
K 31	m/2	—	20.0	Vekua 1972 as 19.5 × 20
K 31	m/3	32.0	19.5	Vekua 1972
K 38	m/3	33.0	20.0	Vekua 1972
Kvabebi mandible	m/3	33.0	19.5	Vekua 1972; Own, 1997 as 36.1 × 20.6
K 975	P1/	10.0	5.0	Vekua 1972
K 975	P2/	13.0	8.0	Vekua 1972
Kvabebi skull	P2/	13.5	9.0	Vekua 1972
Kvabebi skull	P2/	13.5	8.0	Vekua 1972
K 975	P3/	14.5	12.0	Vekua 1972
Kvabebi skull	P3/	14.0	12.0	Vekua 1972
Kvabebi skull	P3/	15.0	12.5	Vekua 1972
K 975	P4/	13.5	17.0	Vekua 1972
Kvabebi skull	P4/	13.0	17.0	Vekua 1972
Kvabebi skull	P4/	13.5	16.5	Vekua 1972
Kvabebi skull	M1/	18.0	17.0	Vekua 1972
K 30	M1/	—	17.5	Vekua 1972
K 975	M1/	16.0	18.0	Vekua 1972
Kvabebi skull	M1/	24.5	21.0	Vekua 1972
Kvabebi skull	M2/	22.0	21.0	Vekua 1972
Kvabebi skull	M2/	23.0	21.0	Vekua 1972
K 975	M2/	24.0	21.0	Vekua 1972
K 30	M2/	22.0	22.0	Vekua 1972
Kvabebi	M3/	30.4	22.2	Own 1997; Vekua 1972 as 31 × 20
Kvabebi skull	M3/	32.0	21.5	Own 1997; Vekua 1972 as 31 × 22
K 30	M3/	30.6	21.8	Own 1997; Vekua 1972 as 31 × 22
K 975	M3/	30.0	22.0	Vekua 1972

have no sagittal crest, due to pneumatization of the cranial table, even though the distal part of the cranial table in *Propotamochoerus* tends to be narrower than it is in *Hippopotamodon*, *Kolpochoerus*, *Potamochoerus*, *Hylochoerus* Thomas, 1904, *Phacochoerus* Cuvier, 1826, *Dasychoerus* and *Sus*. The only extant suid which sports such a narrow cranial table distally is *Babyrusa* Perry, 1811. The extinct genus *Hippohyus* Falconer & Cautley

in Owen, 1840-1845 which was almost the size of a wild boar possessed a sagittal crest (Pilgrim 1926). In the tiny extant suid *Porcula salvania* Hodgson, 1847, the cranial table is broad. The development of the sagittal crest is thus not a reflection of allometry in small suids but is the retention of a primitive feature (lack of cranial table pneumatization) its presence is the rule in Early and Middle Miocene suids (Pickford 1988).

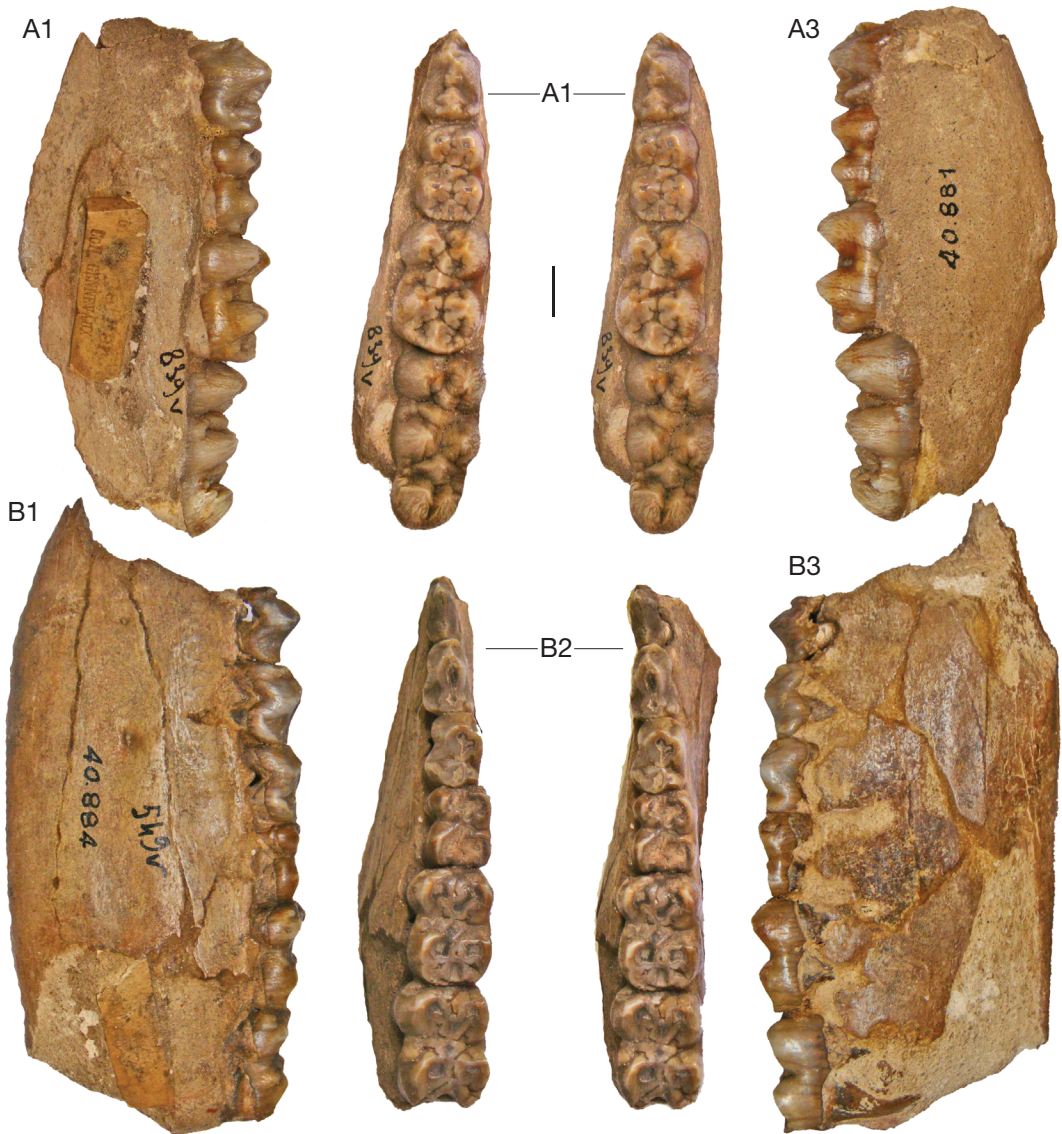


FIG. 12. — Mandibles of “*Sus*” *provincialis* Blainville, 1847 from the Sables marins de Montpellier: **A**, FSL 40 881, left mandible containing p/4-m/3 in buccal (**A1**), stereo occlusal (**A2**) and lingual (**A3**) views; **B**, FSL 40 884, left mandible containing p/2-m/3 in buccal (**B1**), stereo occlusal (**B2**) and lingual (**B3**) views. Scale bar: 10 mm.

Azzaroli (1975) considered that *Sus minor* and *Sus strozzi* were more closely related to each other than either was to *Sus scrofa* and that both shared close affinities with *Sus verrucosus* from the Far East. He also concluded that *Sus arvernensis* was a *nomen dubium* which is the main reason why he

did not declare *Sus minor* to be a junior synonym of *Sus arvernensis* despite his observation that the two taxa “may be practically indistinguishable on dental features alone”. He thought that the type specimen of *Sus arvernensis* was not sufficient to define the species, yet the material described by



FIG. 13. — Mandibles of “*Sus*” *provincialis* Blainville, 1847 from the Sables marins de Montpellier: **A**, FSL 40 171, right mandible containing p/3-m/2 in lingual (**A1**), stereo occlusal (**A2**) and buccal (**A3**) views; **B**, FSL 40 072, right mandible containing p/1-p/4, m/1-m/3 in lingual (**B1**), stereo occlusal (**B2**) and buccal (**B3**) views. Scale bar: 10 mm.

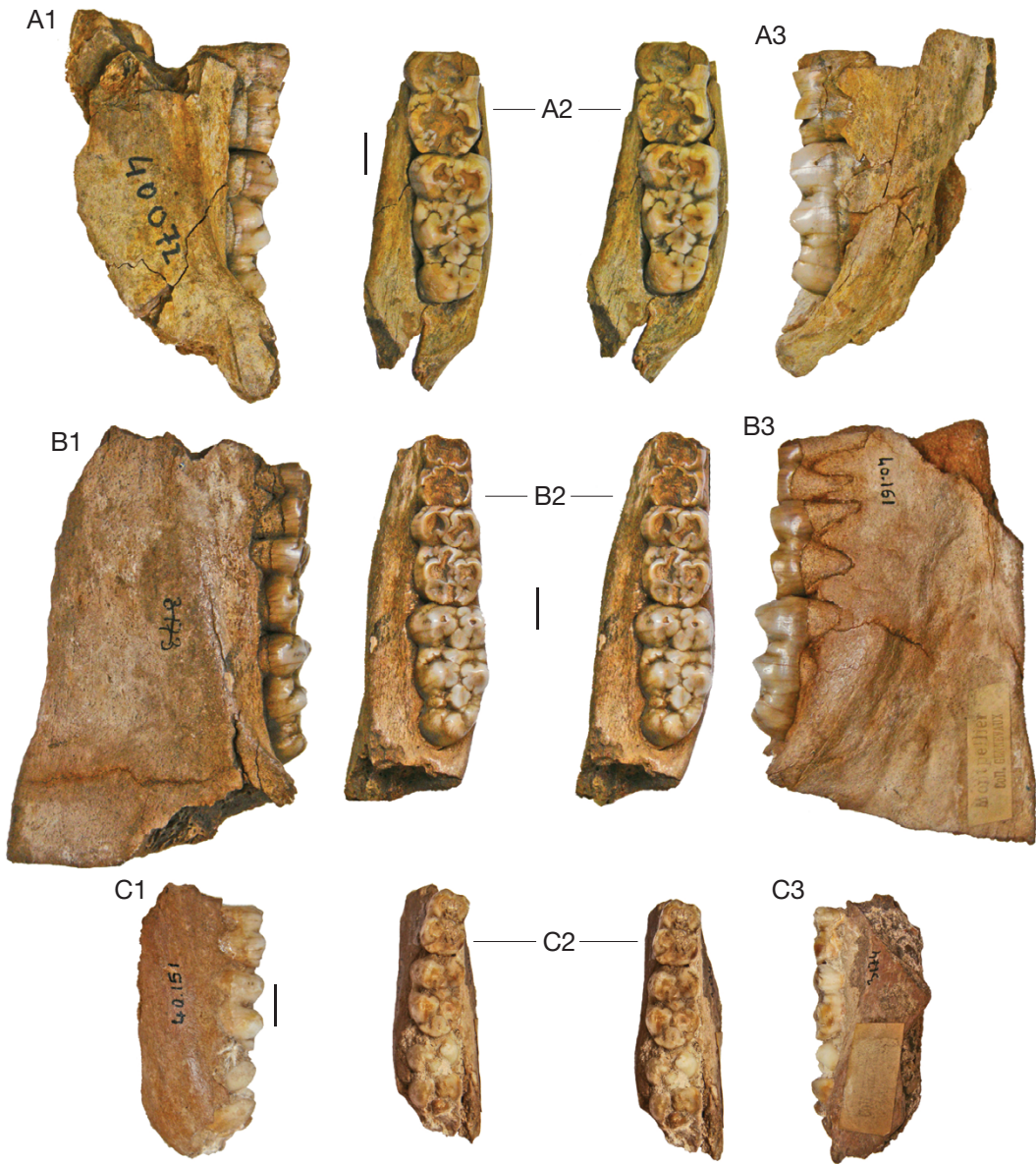


FIG. 14. — Mandibles of “*Sus*” *provincialis* Blainville, 1847 (**A**, **B**) and *Dasychoerus arvernensis* (Croizet & Jobert, 1828) (**C**) from the Sables marins de Montpellier: **A**, FSL 40 072, left mandible fragment containing m/2-m/3 in buccal (**A1**), stereo occlusal (**A2**) and lingual (**A3**) views; **B**, FSL 40 061, left mandible fragment containing m/1-m/3 in buccal (**B1**), stereo occlusal (**B2**) and lingual (**B3**) views; **C**, FSL 40 151, right mandible fragment containing m/1-m/3 in lingual (**C1**), stereo occlusal (**C2**) and buccal (**C3**) views. Scale bar: 10 mm.

Croizet & Jobert (1828) consists of an associated maxilla and mandible containing both deciduous and permanent teeth, and as such it is one of the

most informative known type specimens of species of fossil suids (Pickford 2012; Fig. 10). In the same paper, Azzaroli (1975) considered that

Sus provincialis was a doubtful taxon (*nomen dubium*) due to the scanty material available. He wrote that it was markedly larger than *Sus minor*, citing the lengths of the third lower molars (44 mm for *Sus provincialis* and 33 mm for *Sus minor*) but he was unaware that the Montpellier m/3 (MNHN.F.MON13) represents *Dasychoerus strozii* rather than *Sus provincialis*.

Ginsburg (1980) thought that “*Sus*” *provincialis* might be a descendent of *Korynochoerus palaeochoerus* (Kaup, 1833), to the extent that he transferred the species to *Korynochoerus* Schmidt-Kittler, 1971. The cranial morphology present in the Kvabebi fossils (if it represents the same species) indicates that this suggestion is unlikely to be correct. In terms of dental dimensions, the Kvabebi fossils cluster with suid specimens from Maramena (Hellmund 1995) Kalnitsa, and Vozarci (Geraads *et al.* 2008; see Fig. 16) usually classified as *Propotamochoerus palaeochoerus* (Kaup, 1833).

Morales (1984) described a sample of suids from Venta del Moro, MN 13, Spain, and compared it with *Propotamochoerus provincialis* from Montpellier, concluding that the two samples are morphometrically similar, despite minor differences due to individual and sexual variation. He found that the Venta del Moro specimens plotted out between *Korynochoerus palaeochoerus* which is smaller and *Microstonyx major* (Gervais, 1850) which is larger, which is a pretty fair summary of the data (Fig. 16). In bivariate plots the Venta del Moro sample (Fig. 16 [V]) groups with the Montpellier specimens (Fig. 16 [M]) attributed to *Sus provincialis* (and far from the large specimens from Montpellier classified as *Dasychoerus strozii*).

In their cladogram, Van der Made & Moya Solà (1989) attributed the species “*Propotamochoerus*” *provincialis* to *Korynochoerus*. In a later paper, Van der Made (1990) gave the stratigraphic range of the species from MN 13 to MN 15. Fortelius *et al.* (1996) attributed the species *provincialis* to the genus *Propotamochoerus* and reported that it ranged from MN 13 to MN 15.

Van der Made (2003) described two deciduous teeth from Çobanpınar, Turkey, which he attributed to cf. *Propotamochoerus provincialis*. The D4/AS.93.1124 is about the right dimensions (15.9 ×

13.2 mm) to accord with this identification even though Gervais’ (1850, 1859) specimen from Montpellier is slightly larger (see Table 1).

Gallai & Rook (2006) described casts of the long lost suids from Gravittelli, Italy (Seguenza 1902, 1907) but because of the scanty nature of the sample, the authors could not decide whether they represented *Propotamochoerus hysudricus* (Falconer & Cautley, 1847) or *Propotamochoerus provincialis*. The lack of third molars in the material makes it difficult to decide on the status of this material.

Geraads *et al.* (2008) described suid remains from the Balkans which they concluded were related to *Propotamochoerus palaeochoerus* and *Propotamochoerus provincialis* but which could not be attributed to either taxon. They wrote that it was likely that the material represents an undescribed species. Figure 16 shows that the fossils from the Balkans cluster with the Kvabebi material, and are smaller than the Montpellier specimens attributed to “*Sus*” *provincialis* although one tooth from Montpellier (FSL 40 152, right M3/) is similar in dimensions to this un-named taxon (see Fig. 16). The Balkan material is larger than *Dasychoerus arvernensis*. The authors discussed the systematic position of the Kvabebi suid (Vekua 1972) and concluded that it did not belong to *Propotamochoerus provincialis*, echoing the findings of Azzaroli (1975). Finally, Geraads *et al.* (2008) doubted that *Propotamochoerus provincialis* could be the ancestor of *Kolpochoerus* because its premolars were too thick, the protocone in the P4/ was mesially shifted and the talonid of m/3 is more complex than those of early species of *Kolpochoerus*. However, the only suid upper premolars known from the Sables de Montpellier occur in a snout housed at the Faculty of Science, Lyon, which is here attributed to *Dasychoerus strozii*, thereby modifying the basis of the argument.

Gallai & Rook (2011) recorded *Propotamochoerus provincialis* from Brisighella, Italy (MN 13), but the upper third molar from the site is large, falling into the range of variation of *Dasychoerus strozii* (Fig. 16) and close in dimensions to the third molars in the Montpellier suid snout curated at the Faculty of Science, Lyon.

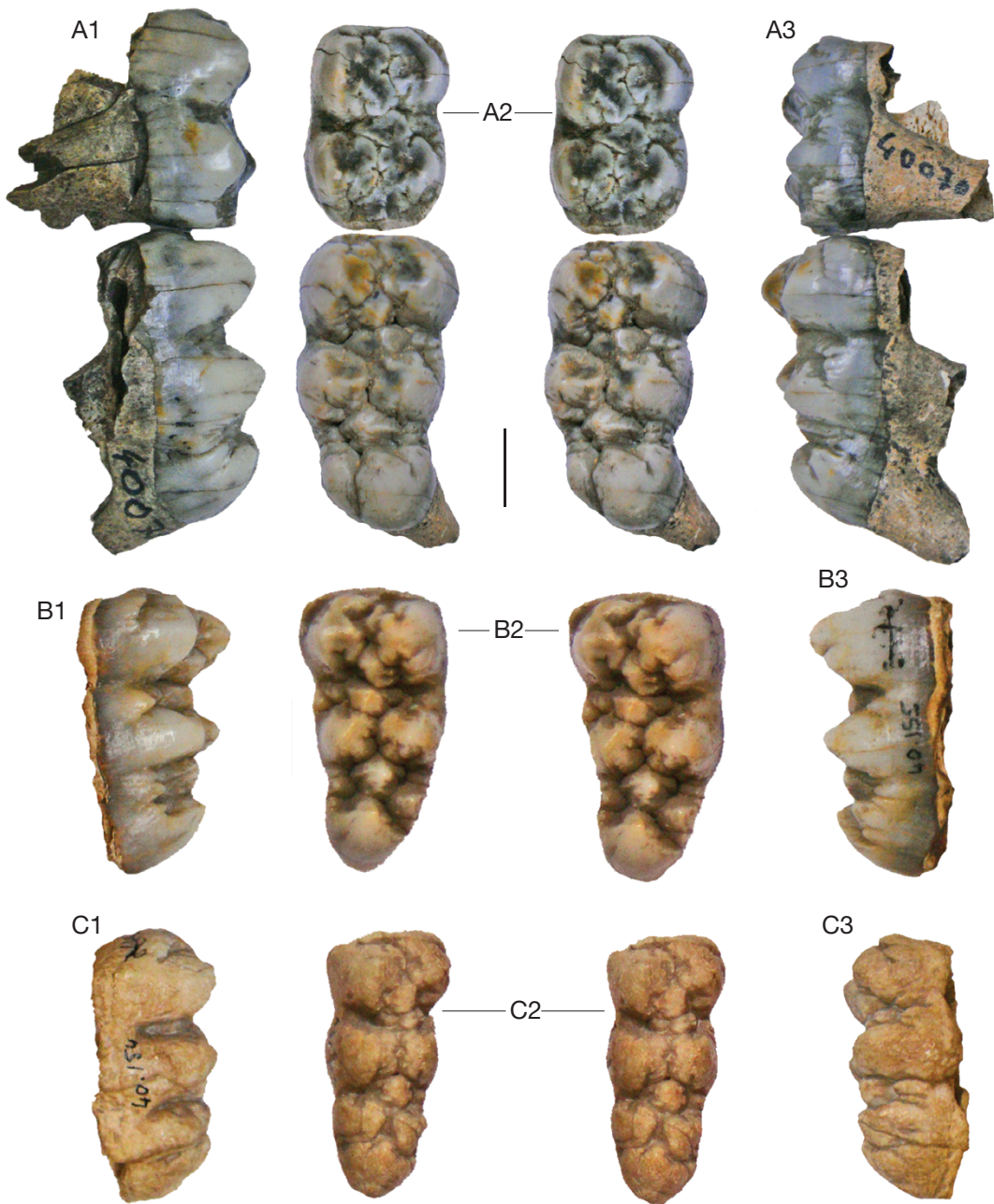


FIG. 15. — Lower molars of “*Sus*” *provincialis* Blainville, 1847 (**A**, **B**) and *Dasychoerus arvernensis* (Croizet & Jobert, 1828) (**C**) from the Sables marins de Montpellier: **A**, FSL 40 070, right m/2-m/3 in lingual (**A1**), stereo occlusal (**A2**) and buccal (**A3**) views; **B**, FSL 40 155, left m/3 in buccal (**B1**), stereo occlusal (**B2**) and lingual (**B3**) views; **C**, FSL 40 154, right m/3 in lingual (**C1**), stereo occlusal (**C2**) and buccal (**C3**) views. Scale bar: 10 mm.

BIOCHRONOLOGY

The fossils labelled “Sables marins de Montpellier” came from several different quarries in the neighbourhood of Montpellier, and the colour of the specimens varies from dark brown to pale yellowish grey, suggesting different depositional parameters and divergent taphonomic histories, but not necessarily diachronic deposition.

However, the presence of four taxa of suids in the Sables marins de Montpellier calls for comment. Van der Made (1990) reported that the stratigraphic range of *Korynochoerus provincialis* extended from MN 13 to MN 15, that *Sus arvernensis* ranged from MN 14 to MN 17a, and *Sus strozii* spanned zones MN 17a to MmQ1. Fossils intermediate in dimensions between *Dasychoerus arvernensis* and “*Sus*” *provincialis* have been reported from various localities (Gödöllő [Mottl 1939], Kalnitsa [Geraads *et al.* 2008], Kvabebi [Vekua 1972], Maramena [Hellmund 1995], Vozarci [Geraads *et al.* 2008] and unpublished specimens are known from Montpellier, Nikolskoe and the Red Crag) ranging in age from MN 13 to MN 16–17. Baccinello V3 (MN 13) has yielded similar material reported by Gallai (2007) to represent an undescribed species of *Propotamochoerus*.

There are three possibilities about the Montpellier deposits: 1) the Sables marins de Montpellier yield fossils of diverse ages; 2) the stratigraphic ranges of some of the suid taxa needs reassessment; or 3) some of the taxonomic determinations may be incorrect.

Further research is required on the biochronology of the Sables marins de Montpellier taking into account all the fossil mammals from the deposits. The suid dental metric data indicate that the sediments span a substantial period of time (Fig. 16). For example, study of the type material of the hyracoid *Pliohyrax occidentalis* (Viret & Thenius, 1952) from the Montpellier sands preserved in the FSL reveals that it is close in dimensions and morphology to *Kvabebihyrax kacheticus* Gabunia & Vekua, 1966 from Kvabebi, Georgia (the two species are probably synonymous). The presence of *Kvabebihyrax* Gabunia &

Vekua, 1966 in the Sables marins de Montpellier suggests that some of the deposits are close to, or equivalent in age to, Kvabebi, Georgia (MN 16 or MN 17).

BIOGEOGRAPHY

Suines dispersed from Europe to Africa during the basal Pliocene (Pickford 2012) and gave rise to two lineages, kolpochoeres and metridiochoeres, which have been important for understanding the biochronology of the Plio-Pleistocene faunas of the continent (Pickford 2012). The species *Kolpochoerus deheinzellini*, from Africa, is equivalent to *Dasychoerus arvernensis* from Europe. Recently, Haile-Selassie & Simpson (2012) created a new species of *Kolpochoerus*, *K. millensis* Haile-Selassie & Simpson, 2012 on the basis of fossils from the Woranso-Mille area, Ethiopia. The material attributed to this species is comparable in morphology and dimensions to large specimens of *Dasychoerus arvernensis*, such as the material from Roussillon that used to be classified as *Dasychoerus minor* (Depéret, 1890) and to fossils from Kvabebi, Gödöllő, Vozarci, and other sites in Europe (see Fig. 16) including Montpellier, here to attributed to *Dasychoerus* sp. from Kvabebi. Detailed comparisons of all these European and African Pliocene suid fossils is called for, but is beyond the scope of the present paper.

CONCLUSIONS

The aim of this paper is to report the rediscovery of some historically important fossil suid teeth representing part of the original hypodigm of *Sus provincialis* and to nominate a lectotype for the species. As was frequently the case in the 19th Century, authors did not nominate holotypes. In cases in which a single specimen was described, as for instance *Sus major*, it is automatically the type specimen, but in cases where several specimens were included in the species, subsequent authors have had to nominate a name-bearing type, known as a lectotype. Some historically im-

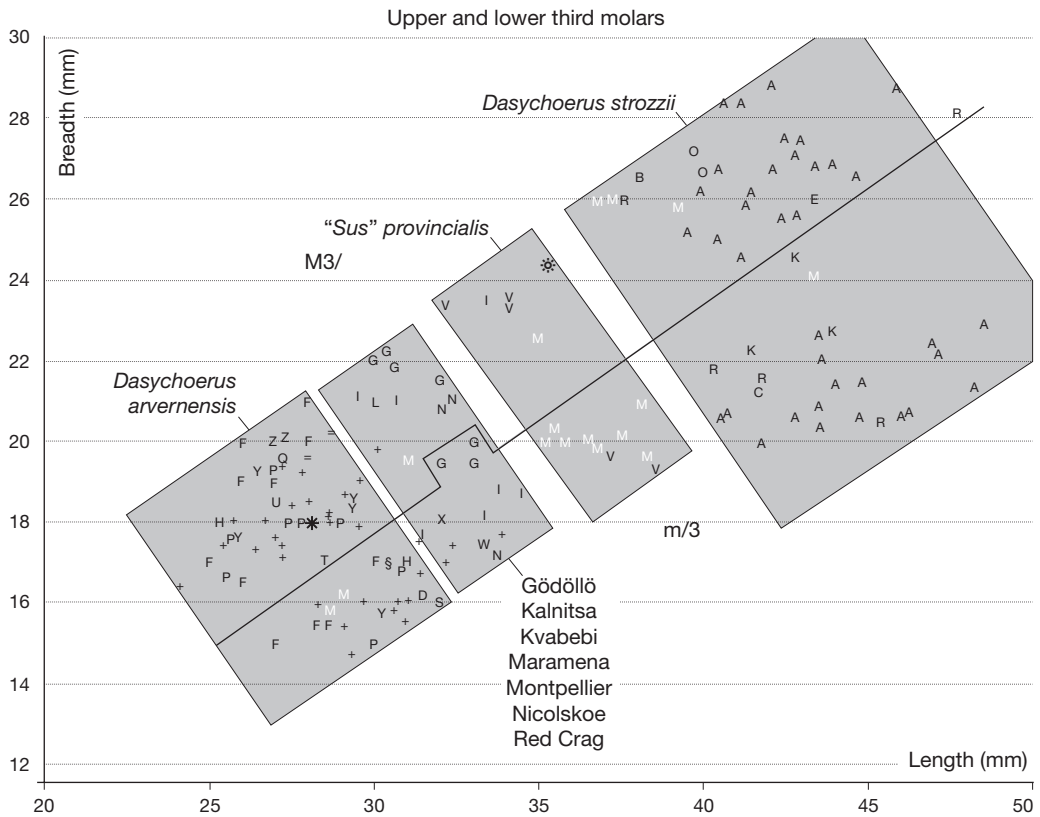


FIG. 16. — Bivariate plot of upper and lower third molars of suids from Montpellier (**white M**) and other Late Miocene and Plio-Pleistocene localities in Europe. The sloping black line separates the upper molars from the lower ones. There are four size groups of suids at Montpellier corresponding in dimensions to *Dasychoerus arvernensis* for the smallest group, *Dasychoerus* sp. from Kvabebi for an intermediate sized group, "*Sus*" *provincialis* for a slightly larger medium sized group, and *Dasychoerus strozii* for the largest one. Abbreviations: A, Val d'Arno; B, Brisighella; C, Corton; D, Dermenji; E, East Runton; F, Villafranca d'Asti; G, Kvabebi; H, Hajnacka; I, Vozarci; K, Khapry; L, Nikolskoe; M, Montpellier; N, Maramena; O, Olivola; P, Perpignan; Q, Bra; R, Red Crag (large specimens possibly belonging to *Hippopotamodon major*); S, Varghis; T, Çalta; U, Piedrabuena; V, Venta del Moro; W, Gödöllő; X, Kalnitsa; Y, Alcoy; Z, Musaitu; \$, Auvergne; +, Red Crag (small specimens); =, Trévoux; * – lectotype of *Dasychoerus arvernensis*; *, lectotype of "*Sus*" *provincialis*. Measurements are from Berdondini (1992), Depéret (1885), Gallai & Rook (2011), Geraads *et al.* (2008), Guérin (pers. comm.), Hellmund (1995), Hünemann (1971), Lydekker (1885), Mazo & Torres (1990), Morales (1984), Mottl (1939), Samson *et al.* (1971), Titov (2000), Vekua (1972). Measurements of the teeth of *Dasychoerus strozii* were kindly supplied by J. Van der Made.

portant specimens such as those that came under the gaze of Blainville (1847) and Gervais (1850, 1859) have been misplaced or lost, making the task more difficult than it is for those collections, like the type series of *Sus arvernensis* that still exist (MNHN, Paris). The rediscovery of such collections, even if incomplete, is an important event, as it enables a lectotype to be nominated usefully. In this case UM SM 460, the right upper third molar from the "sables marins" of Montpellier, illustrated by Blainville (1847) (see Fig. 1A) and

by Gervais (1850; 1859: pl. 3, fig. 4; see Fig. 2B) is selected as the lectotype of "*Sus*" *provincialis*.

It is important to keep in mind that some hypodigms of species erected during the 19th Century consist of specimens belonging to two or more taxa: this is the case with the species *Sus simorrensis* Lartet, 1851, the original hypodigm of which includes specimens of *Listriodon* Meyer, 1846 and *Conohyus* Pilgrim, 1925, and it is the case with *Sus provincialis* which contains specimens of *Dasychoerus strozii*, one of which was mentioned by Fejfar

(1964) and Azzaroli (1975). If the latter specimen were to be nominated as lectotype, it would cause confusion and instability as this would risk making *D. strozii* a junior synonym of *S. provincialis*, and would leave the remainder of the original hypodigm of Blainville (1847) without a name. For this reason, nomination of a lectotype should not be done without an in-depth analysis of the original hypodigm and subsequently discovered fossils from the same locality, linked to exhaustive comparisons with related material from other sites.

Study of the fossils and casts housed in the MNHN, the Faculty of Science of Lyon, and of the seven specimens that were made available to the author out of the 24 curated in the University of Montpellier II collections, reveals that the Sables marins de Montpellier have yielded four species of suids, small *Dasychoerus arvernensis* (one mandible and a lower third molar housed at the FSL), *Dasychoerus* sp similar to the Kvabebi suid (Vekua 1972), “*Sus*” *provincialis* (most of the fossils) and *Dasychoerus strozii* (MNHN.F.MON13, an m/2-m/3 and MNHN.F.MON14, an M3/, and FSL 40 073, a snout curated at the Faculty of Science, Lyon). Descriptions of the fossils are given, followed by a brief summary of the nomenclatorial history of the species *Sus provincialis*, which shows that it has successively been attributed to *Sus*, *Potamochoerus* (?), *Propotamochoerus* and *Korynochoerus*. In recent literature it has generally been attributed to *Propotamochoerus*, but some features of the canines (verrucosic), premolars and third molars, suggest that it does not fit comfortably within the genus, sharing as it does some features with *Dasychoerus*, to which warty (and verrucosic) species of extant suids belong.

The species “*Sus*” *provincialis* is widespread but rare in Europe, having been reported from Late Miocene and Basal Pliocene localities in Spain, France, Italy, Greece, Romania and other countries in “Western Europe”. Fossils from Kvabebi, Georgia (Vekua 1972) are interesting as the skull shows a sagittal crest in the neurocranium and dishing of the facial profile (i.e. the dorsal surface of the skull is slightly concave) features which indicate that it belongs to a genus distinct from *Propotamochoerus* but the affinities of the Kvabebi suid needs to be

settled before its relationship to “*Sus*” *provincialis* and species of *Dasychoerus* can be resolved. The teeth are smaller than those of “*Sus*” *provincialis* from Montpellier (Fig. 16) and they group with specimens from Maramena, Greece (Hellmund 1995) and the Balkans (Geraads *et al.* 2008). Similar cranial features occur in *Potamochoeroides hypsodon* Dale, 1948 from Makapansgat, South Africa (Pickford 2012) an observation that points the way to resolving the ancestry of this group of African suids, usually referred to as metridiochoeres (Cooke & Wilkinson 1978; Pickford 2012).

Detailed comparison between African and European Pliocene suines is urgently needed, not only to resolve taxonomic questions, but also to throw light on the possibility of proposing biochronological correlations between European localities that have yielded taxa such as *Dasychoerus arvernensis* and *Dasychoerus* sp. from Kvabebi and African localities that have yielded morphometrically similar taxa including *Kolpochoerus deheinzelini* (here considered to be a synonym of *D. arvernensis*) and *Kolpochoerus millensis* which is equivalent in dimensions and morphology to large specimens of *Dasychoerus arvernensis* and *Dasychoerus* sp. from Kvabebi. The European taxa span much the same time period as those from Africa, *Kolpochoerus deheinzelini* ranging from 5.5–4.5 Ma, and *Kolpochoerus millensis* from 3.8–3.5 Ma (Haile-Selassie & Simpson 2012).

Acknowledgements

I thank Christine Argot (MNHN) for help with the fossil collections at the Muséum national d’Histoire naturelle, Paris, Andy Currant, Jessica MacDonald and Roula Pappa of the Natural History Museum, London, Abel Prieur, Faculty of Science, Lyon, Didier Berthet, Centre de Conservation et d’Études des Collections, Musée des Confluences, Lyon, and Bernard Marandat and Suzanne Jicquel, University of Montpellier II. Thanks also to Claude Guérin, Lyon, for comments and measurements of fossils and to Didier Merle for editorial assistance. We also thank Maéva Orliac (CNRS), Annemarie Ohler (MNHN) and an anonymous reviewer for their valuable comments on an earlier version of the article.

REFERENCES

- AZZAROLI A. 1954. — Filogenesi e biologia di *Sus strozzi* e di *Sus minor*. *Palaeontographica italica* ns 18 : 41-76.
- AZZAROLI A. 1975. — Remarks on the Pliocene Suidae of Europe. *Zeitschrift für Säugetierkunde* 40: 355-367.
- BERDONDINI E. 1992. — Suids from the Early Villafranchian of Villafranca d'Asti and China. *Rendiconti Lincei Scienze Fisiche e Naturali* 9 (3) 2: 109-124.
- BLAINVILLE H. M. D. DE 1847. — *Ostéographie ou description iconographique comparée du squelette et du système dentaire des cinq classes d'animaux vertébrés récents et fossiles, pour servir de base à la Zoologie et à la Géologie*. Vol. 4, AA, *Sur les Hippopotames et les Cochons*. Atlas 4, Paris, Bertrand, 1-248, 93 pls.
- BRUNET M. & WHITE T. 2001. — Deux nouvelles espèces de Suini (Mammalia, Suidae) du continent Africain (Ethiopie, Tchad). *Comptes rendus de l'Académie des Sciences de Paris* 332: 51-57.
- COOKE H. B. S. & WILKINSON A. 1978. — Suidae and Tayassuidae, in MAGLIO V. J. & COOKE H. B. S. (eds), *Evolution of African Mammals*. Harvard University Press, Cambridge: 435-482.
- CROIZET J. B. & JOBERT A. 1828. — *Recherches sur les ossements fossiles du département du Puy-de-Dôme*. Adolphe Delahays, Paris, 226 p.
- DALE M. 1948. — New fossil Suidae from the Limeworks Quarry, Makapansgat, Potgietersrust. *South African Journal of Science* 2: 114-116.
- DAL PIAZ G. B. 1930. — Sopra gli avanzi di un suide scoperti nel Pliocene superiore di Bra in Piemonte. *Atti della Reale Accademia delle Scienze di Torino* 65: 299.
- DEPÉRET C. 1885. — Description géologique du bassin tertiaire du Roussillon. *Annales des Sciences Géologiques* 17: 1-272.
- DEPÉRET C. 1890. — Les animaux pliocènes de Roussillon. *Mémoires de la Société géologique de France* 3: 1-164.
- FAURE M. 2004. — Le *Sus strozzi* du Pliocène final de Saint-Vallier (Drôme). *Geobios* 37 : 189-190.
- FEJFAR O. 1964. — The Lower Villafranchian vertebrates from Hajnacka, near Filakovo in Southern Slovakia. *Rozprawy Ústředního ústavu Geologického* 30: 1-117.
- FORTELIUS M., VAN DER MADE J. & BERNOR R. 1996. — Middle and Late Miocene Suoidea of Central Europe and the Eastern Mediterranean: Evolution, Biogeography and Paleocology, in BERNOR R. L., FAHLBUSCH V. & MITTMANN H. W. (eds) *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York: 348-377.
- GABUNIA L. & VEKUA A. K. 1966. — A fossil hyrax in the Akchagylian of Eastern Georgia. *Trudy Instituta Paleobiologii Akademii Nauk Gruzinskoi SSR*: 93-100.
- GALLAI G. 2007. — Sistematica, Paleocologia, Paleogeografia dei Suidae fossili Italiani. *PaleoItalia* 17: 17-22.
- GALLAI G. & ROOK L. 2006. — *Propotamochoerus* sp. (Suidae, Mammalia) from the Late Miocene of Gravelli (Messina, Sicily, Italy) rediscovered. *Rivista Italiana di Paleontologia e Stratigrafia* 112: 317-321.
- GALLAI G. & ROOK L. 2011. — *Propotamochoerus provincialis* (Gervais, 1859) (Suidae, Mammalia) from the latest Miocene (Late Messinian; MN 13) of Monticino Quarry (Brisighella, Emilia-Romagna, Italy). *Bollettino della Società Paleontologica Italiana* 50 (1): 29-34.
- GERAADS D., SPASSOV N. & GAREVSKI R. 2008. — New specimens of *Propotamochoerus* (Suidae, Mammalia) from the Late Miocene of the Balkans. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 248: 103-113.
- GERVAIS P. 1849. — Sur la répartition des mammifères fossiles entre les différents âges tertiaires qui composent le sol de la France. *Comptes rendus de l'Académie des Sciences, Paris* 28: 546-552.
- GERVAIS P. 1850. — *Zoologie et Paléontologie françaises (animaux vertébrés) ou nouvelles recherches sur les animaux vivants et fossiles de la France*. Arthus Bertrand, Paris, 1-3, pp. viii + 271 (the volume is dated 1848-1852, but the part dealing with *Sus provincialis* dates from 1850).
- GERVAIS P. 1853. — Description des ossements fossiles de mammifères rapportés d'Espagne par MM. Verneuil, Collomb et Lorrière. *Bulletin de la Société géologique de France* 10: 147-168.
- GERVAIS P. 1859. — Nouvelles recherches sur les animaux vertébrés dont on trouve les ossements enfouis dans le sol de la France et sur leur comparaison avec les espèces propres aux autres régions du globe. *Zoologie et Paléontologie françaises*. Arthus Bertrand, Paris, 271 p.
- GINSBURG L. 1980. — *Xenohyus venitor*, suidé nouveau (Mammalia, Artiodactyla) du Miocène inférieur de France. *Geobios* 13: 861-877.
- GOLPE-POSSE J. M. 1972. — Suiformes del Terciario Español y sus yacimientos. *Paleontologia y Evolucion*, 2 : 1-197, annexes, 7 pls.
- GRAY J. E. 1821. — On the natural arrangement of vertebrate animals. *London Medical Repository* 15: 296-310.
- GRAY J. E. 1873. — *Handlist of the Edentate, Thick-skinned and Ruminant Mammals in the British Museum*. London, British Museum Trustees, 174 p., 41 pls.
- GUÉRIN C. & FAURE M. 1985. — Les Suidae (Mammalia, Artiodactyla) du Pliocène de la Formation de Perpignan (Roussillon) : hommage à Charles Depéret. *Paléontologie et Géologie néogènes en Roussillon* vol.: 22.
- GUÉRIN C., FAURE M. & SEN S. 1998. — Le gisement de vertébrés pliocènes de Çalta, Ankara, Turquie, 8. Suidae. *Geodiversitas* 20 (3): 441-453.
- HAILE-SELASSIE Y. & SIMPSON S. 2012. — A new species of *Kolpochoerus* (Mammalia: Suidae) from the Pliocene of Central Afar, Ethiopia: its taxonomy and phylogenetic relationships. *Journal of Mammal Evolution*: 1-13. <http://dx.doi.org/10.1007/s10914-012-9207-0>
- HELLMUND M. 1995. — The vertebrate locality Mara-

- mena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene) 13. Suidae (Artiodactyla, Mammalia). *Münchener Geowissenschaftliche Abhandlungen A*, 28: 143-156.
- HODGSON B. H. 1847. — On a new form of the hog kind or Suidae. *Journal of the Asiatic Society of Bengal* 16: 423-428.
- HÜNERMANN K. A. 1968. — Die Suidae (Mammalia, Artiodactyla) aus den Dinotheriensanden (Unterpliozän = Pont) Rheinhessens (Südwestdeutschland). *Schweizerische Paläontologische Abhandlungen* 86: 1-96.
- HÜNERMANN K. A. 1971. — Die Plio-Pleistozänen Wirbeltierfaunen von Hajnacka und Ivanovce (Slowakei) CSR. VII: *Sus minor* (Depéret, 1890). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1971: 213-230.
- KAUP J. J. 1833. — *Description d'ossements fossiles de mammifères*. 2. J. G. Heyer, Darmstadt, 31 p.
- LARTET E. 1851. — *Notice sur la Colline de Sansan, suivi d'une récapitulation des diverse espèces d'animaux vertébrés fossiles, trouvés soit à Sansan, soit dans d'autres gisements du terrain Tertiaire Miocène dans le bassin sous-pyrénéen*. J. A. Portes, Auch, 45 p.
- LYDEKKER R. 1877. — Notices of new and rare mammals from the Siwaliks. *Records of the Geological Survey of India* 10: 76-83.
- LYDEKKER R. 1884. — Indian Tertiary and Post-Tertiary Vertebrata: Siwalik and Narbada Bunodont Suina. *Memoir of the Geological Survey of India, Palaeontologica indica* (10) 3 (2): 35-104.
- LYDEKKER R. 1885. — *Catalogue of the Fossil Mammalia in the British Museum (Natural History)*. Part 2. British Museum, London: 273.
- MAZO A.V. & TORRES T. 1990. — El Pozo de Piedrabuena, un nuevo yacimiento de Vertebrados pliocenos en el Campo de Calatrava (Ciudad Real). *Paleontologia i Evolució* 23: 213-222.
- MENEGHINI G. 1862. — Descrizione dei resti di due fiere trovati nelle ligniti mioceniche di Montebamboli. *Atti della Società Italiana di Scienze Naturali, Milano* 4: 17-33.
- MEYER H. VON 1846. — Mitteilungen an Prof. Bronn gerichtet. *Neues Jahrbuch für Mineralogie und Paläontologie* 1846: 462-476.
- MONTOYA P., GINSBURG L., ALBERDI M. T., VAN DER MADE J., MORALES J. & SORIA D. 2006. — Fossil large mammals from the Early Pliocene locality of Alcoy (Spain) and their importance in biostratigraphy. *Geodiversitas* 28 (1): 137-173.
- MORALES J. 1984. — *Venta del Moro: Su macrofauna de mamíferos y biostratigrafía continental del Mioceno terminal mediterráneo*. PhD Thesis, Universidad Complutense de Madrid, 327 p., 13 pls.
- MOTTL M. 1939. — Die Mittelplozäne Säugetierfauna von Gödöllő bei Budapest. *Mitteilungen aus dem Jahrbuch der königliche Ungarnischen Geologischen Anstalt* 32: 257-350.
- MÜLLER S. & SCHLEGEL H. 1845. — Over die wilde zwijnen van den Indische Archipel, in TEMMINCK C. J. (ed.), *Verhandelingen ove de natuurlijke geschiedenis der Nederlandsche Overzeesche Bezittingen, door de leden der Natuurkundige Commissie in Oost-Indië en andere schrijvers*. Luchtmans & Van den Hoek, Leiden: 169-182, pls 28-32.
- NEWTON E. T. 1891. — *The Vertebrata of the Pliocene Deposits of Britain*. Eyre & Spottiswoode, London, 120 p.
- OWEN R. 1840-1845. — *Odontography; or, A treatise on the comparative anatomy of the teeth: their physiological relations, mode of development, and microscopic structure, in the vertebrate animals*. H. Baillière, London, 655 p.
- PERRY G. 1811. — *Arcana, or, the Museum of Natural History: containing the most Recent Discovered Objects, Embellished with Coloured Plates and Corresponding Descriptions: with Extracts Relating to Animals and Remarks of Celebrated Travellers Combining a General Survey of Nature*. George Smeeton, London, 84 p.
- PICKFORD M. 1988. — Revision of the Miocene Suidae of the Indian Subcontinent. *Münchener Geowissenschaftliche Abhandlungen* 12: 1-91.
- PICKFORD M. 2012. — Ancestors for Broom's Pigs. *Transactions of the Royal Society of South Africa* 67: 17-35.
- PILGRIM G. E. 1925. — Presidential address to the Geological Section of the 12th Indian Science Congress. *Proceedings of the 12th Indian Scientific Congress*: 200-218.
- PILGRIM G. E. 1926. — The Fossil Suidae of India. *Memoir of the Geological Survey of India, Palaeontologica indica* 8 (4): 1-65.
- RADULESCU C., SAMSON P.-M., PETRULESCU A. & STIUČĂ E. 2003. — Pliocene large mammals from Romania. *Coloquios de Paleontologia, Volume Ext.* 1: 549-558.
- RÜTIMEYER K. L. 1857. — Über lebende und fossile Schweine. *Verhandlungen der naturforschenden Gesellschaft in Basel* 1: 517-554.
- SAMSON P. R., DULESCO C. & KISGYÖRGY Z. 1971. — Nouvelles données sur la faune de Mammifères du Villafranchien inférieur de Căpeni-Vîrghis (Dépression de Brasov, Roumanie). *Eiszeitalter und Gegenwart* 22: 64-88.
- SCHMIDT-KITTLER N. 1971. — Die Obermiozäne Fossilagerstätte Sandelzhausen 3. Suidae, Artiodactyla, Mammalia. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie* 11: 129-170.
- SEGUENZA L. 1902. — I vertebrati fossili della provincia di Messina. Parte II: mammiferi e geologia del piano Pontico. *Bolletino della Società Geologica Italiana* 21: 115-172. Roma.
- SEGUENZA L. 1907. — Nuovi resti di mammiferi fossili di Gravittelli presso Messina. *Bolletino della Società Geologica Italiana* 26: 7-119. Roma.

- SIMIONESCU I. 1930. — Vertebratele Pliocene dela Malusteni (Corvului). *Academia Romana-Publicatiunile Adamachi* 9: 83-148.
- STEHLIN H. G. 1899-1900. — Über die Geschichte des Suiden Gebisses. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft* 26/27: 1-527.
- TITOV V. V. 2000. — *Sus* (Suidae, Mammalia) from the Upper Pliocene of the Northeastern part of the Azov Region. *Paleontological Journal* 34: 203-210.
- VAN DER MADE J. 1990. — Iberian Suoidea. *Paleontologia I Evolució* 23: 83-97.
- VAN DER MADE J. 2003. — Suoidea, Artiodactyla. in FORTELIUS M., KAPPELMAN J., SEN S. & BERNOR R. (eds), *Geology and Paleontology of the Sinap Formation, Turkey*. Columbia University Press, New York: 308-327.
- VAN DER MADE J. & BELINCHON M. 1991. — *Korynochoerus palaeochoerus* from the Uppermost Miocene of Alcoy. *Revista Española de Paleontología*, Extra number: 173-180.
- VAN DER MADE J. & MOYA-SOLÀ S. 1989. — European Suinae (Artiodactyla) from the Late Miocene onwards. *Bolletino della Societa Palaeontologica Italiana* 28: 329-339.
- VEKUA A. K. 1972. — [*The Akchaglyian Vertebrate Fauna from Kvabebi*]. Nauka, Moscow, 351 p., 36 pls (in Russian).
- VIRET J. & THENIUS E. 1952. — Sur le présence d'une nouvelle espèce d'hyracoïde dans le Pliocène de Montpellier. *Comptes rendus de l'Académie des Sciences de Paris* 235 : 1678-1680.

*Submitted on 24 January 2012;
accepted on 22nd October 2012;
published on 27 September 2013.*