The Suoidea (Mammalia, Artiodactyla), exclusive of Listriodontinae, from the early Miocene of Béon 1 (Montréal-du-Gers, SW France, MN4)

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Orliac M. J., Antoine P.-O. & Duranthon F. 2006. — The Suoidea (Mammalia, Artiodactyla), exclusive of Listriodontinae, from the early Miocene of Béon 1 (Montréal-du-Gers, SW France, MN4). *Geodiversitas* 28 (4) : 685-718.

ABSTRACT
The French locality of Béon 1, located in the district of Montréal-du-Gers (Gers, France), has yielded a rich collection of suoids, including dental, cranial, and postcranial remains. The small suoids from Béon 1 (i.e. Listriodontinae excepted) are revised in this article. *Hyotherium lacaillei* n. sp. is named and *Chicochoerus* n. gen. is described for a very small species of Suidae previously known as "*Aureliachoerus*" *minus* (Golpe Posse, 1972) from the Spanish localities of Can Canals and El Canyet and from Austria (Styria); some specimens of a member of the Palaeochoeridae, *Taucanamo grandaevum* (Fraas, 1870), are also described. Based on the literature and on new observations, a phylogenetic analysis including 44 dental, cranial, and postcranial characters, proposes a sketch of the relationships of 23 early and middle Miocene European suoids. In the strict consensus of the 240 shortest trees, Suidae and Palaeochoeridae are sister groups. Palaeochoeridae are arranged as [European *Taucanamo*, Palaeochoeriinae] and Suidae as [*Eurolistriodon* [*Albanohyus*, Hyotheriinae]] where Hyotheriinae group is as [*Chicochoerus* n. gen. [*Hyotherium*, *Aureliachoerus aurelianensis*, *Xenohyus*]].

KEY WORDS
Mammalia,
Artiodactyla,
Suoidea,
Orleanian,
early Miocene,
MN4,
Aquitaine Basin,
systematics,
phylogeny,
new genus,
new species.

RÉSUMÉ
Les Suoidea (Mammalia, Artiodactyla), Listriodontinae exceptés, du Miocène inférieur de Béon 1 (Montréal-du-Gers, SO France, MN4).
La localité française de Béon 1, située sur la commune de Montréal-du-Gers (Gers, France), a livré une importante collection de suoïdes, comprenant des restes dentaires, crâniens et postcrâniens. Les petits suoïdes (i.e. à l'exception des Listriodontinae) sont révisés dans cet article. L'espèce *Hyotherium lacaillei* n. sp. est décrite pour le matériel rapporté à *Hyotherium*, caractérisée par l'absence de diastème et par la forme globuleuse des première et seconde prémolaires supérieures. Un nouveau genre, *Chicochoerus* n. gen., est décrit pour une très petite espèce de Suidae, connue précédemment sous le nom d'« *Aureliachoerus* » *minus* (Golpe Posse, 1972) et signalée dans les localités de Can Canals et d'El Canyet (Espagne) et de la région de Styrie (Autriche). *Chicochoerus* n. gen. est indubitablement un suidé, mais diffère d'*Hyotherium* et d'*Aureliachoerus* par une p2 asymétrique, une postcristide tranchante au niveau des prémolaires inférieures, et des molaires inférieures à l'endométacristide étroite, sans endométaconulide naissant. Quelques spécimens d'un représentant des Palaeochoeridae, *Taucanamo grandaevum* (Fraas, 1870), sont également décrits. Une analyse phylogénétique, fondée sur la littérature et sur de nouvelles observations, inclut 44 caractères dentaires, crâniens et postcrâniens, contrôlés chez 23 suoïdes du Miocène inférieur et moyen. Dans l'arbre de consensus strict des 240 arbres équiparcimonieux, les Suidae sont groupe frère des Palaeochoeridae, tous deux monophylétiques. Les Palaeochoeridae sont de la forme [*Taucanamo* d'Europe, Palaeochoeriinae] et les Suidae [*Eurolistriodon* [*Albanohyus*, Hyotheriinae]] où les Hyotheriinae regroupent [*Chicochoerus* n. gen. [*Hyotherium*, *Aureliachoerus aurelianensis*, *Xenohyus*]].

MOTS CLÉS
Mammalia,
Artiodactyla,
Suoidea,
Orléanien,
Miocène inférieur,
MN4,
Bassin aquitain,
systématique,
phylogénie
nouveau genre,
nouvelle espèce.

INTRODUCTION

The Aquitaine Basin, in southwestern France, is a key area for Oligocene and Miocene continental biostratigraphy and mammal biochronology (Richard 1948; Bruijn *et al.* 1992). The Béon 1 locality, initially referred to as "Montréal-du-Gers" (Crouzel *et al.* 1988; Bruijn *et al.* 1992), has yielded among the richest and most diverse Miocene vertebrate faunas in France with *c*. 90 listed vertebrate taxa; it is referred to the middle part of zone MN4 (Bruijn *et al.* 1992; Duranthon *et al.* 1995; Antoine *et al.* 1997, 2000a, b; Rage & Bailon 2005). Large mammals such as ruminants (Duranthon *et al.* 1995) and rhinocerotids (Antoine *et al.* 2000b) are well represented. Suoid remains are also numerous and remarkably preserved. Preliminary faunal lists for Montréal-du-Gers (Crouzel *et al.* 1988; Antoine & Duranthon 1997; Antoine *et al.* 1997) mention the co-occurrence of the hyotheriine suids *Hyotherium soemmeringi* (Meyer, 1829) (Meyer 1841) and *Aureliachoerus minus* (Golpe Posse, 1972), the listriodontine suid *Bunolistriodon lockharti* (Pomel, 1848) and the palaeochoerid *Taucanamo sansaniense* (Lartet, 1851). A recent revision of the listriodontine material (Orliac in press) reveals that it represents a new species, closely related to the Spanish taxon *Eurolistriodon adelli* Pickford & Moyá Solá, 1995.

The small suoids, less well represented in comparison to the Listriodontinae, are described here. A new species is created for the hyotheriine mate-

rial and a new genus is erected for the smaller suid, previously allocated to *Aureliachoerus* Ginsburg, 1974. Dental and postcranial remains of *Taucanamo grandaevum* (Fraas, 1870) are also described from this locality. The description of this new material provides new morphological observations, exploited in a phylogenetic analysis including 44 cranio-dental characters coded for 23 taxa, including characters from the literature as well as new characters. The systematics of the Suoidea of Béon 1 is discussed in the present article, based on the results of the phylogenetic analysis.

MATERIAL AND METHODS

The studied material is curated in the MHNT and was collected by Duranthon and colleagues between 1987 and 2003. Dental nomenclature mainly follows Van der Made (1996b); the nomenclature for the lower second and third molars of *Hyotherium soemmeringi* is given in Figure 1 as an example. The names of secondary structures, such as crests, are constructed as follows: the name of the structure (cristid/crista, fossid/fossa) is combined with the name of the cusp that bears it, and a prefix indicates the position of the secondary structure. The groove between two cristids is named after the crest in front of it. Capital letters are used for upper teeth (I, C, P, M), and lower-case for lower teeth (i, c, p, m).

Suprageneric systematics

The suprageneric systematics of Suoidea has experienced several changes in past decades, especially concerning the small Miocene suoids and more precisely the "Old World peccaries". The so-called "Old World peccaries" were first placed in the family Tayassuidae Palmer, 1897 (Pearson 1927; Simpson 1945; McKenna & Bell 1997). Van der Made (1996b, 1997a) separated this group from tayassuids and proposed to include them within a third family of Suoidea, the Palaeochoeridae Matthew, 1924. Recently, Liu (2003) proposed the first classification of the superfamily Suoidea based on a phylogenetic analysis including a large number of fossil taxa. She stated that the family Palaeochoeridae was not monophyletic and that "Old World peccaries" were part of the Suidae. The situation of some taxa such as *Hyotherium* and *Palaeochoerus* remained problematic and they were placed in "Suidae indet.". The subfamily Hyotherinae Cope, 1888 was not recognized, but only *Hyotherium* was included in the analysis. We recognise the importance of her results, as they ensue from a phylogenetic analysis and we agree that the position of those taxa is problematic. However, several taxa included in the present article (i.e. *Doliochoerus*, *Xenohyus*, *Albanohyus*) are lacking in Liu's paper; hence, the results of this paper are different from Liu's conclusion. The suprageneric classification

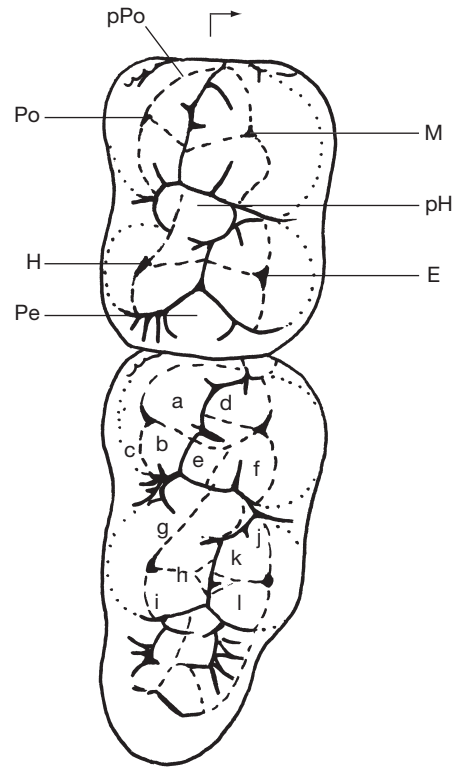

Fig. 1. — Nomenclature used for lower molars illustrated on the basis of left m2-m3 of *Hyotherium soemmeringi*. Abbreviations: **E**, entoconid; **H**, hypoconid; **M**, metaconid; **Pe**, pentaconid; **pH**, prehypoconulid; **Po**, protoconid; **pPo**, preprotoconulid; **a**, preprotocristid; **b**, endoprotocristid; **c**, postprotocristid; **d**, premetacristid; **e**, endometacristid; **f**, postmetacristid; **g**, ectohypocristid; **h**, prehypocristid; **i**, endohypocristid; **j**, ectoentocristid; **k**, preentocristid; **l**, endoentocristid. For upper molars, replace -id by -e (hypoconid and hypocone) or -a (preprotocristid and preprotocrista).

proposed by Van der Made (1997a, b) agrees better with the taxa mentioned in this paper and the results of the present analysis.

Postcranial skeleton

The homogeneity of suoid postcranial morphology partly explains why postcranial elements have received so little attention in the literature; however, thanks to this morphological homogeneity, the high-level taxonomic identification of suoid postcranial remains is quite easy. The specific attribution mainly relies on the size of the material (Table 2): the boar-sized material has been attributed to *Eurolistriodon* Pickford & Moyá Solá, 1995; the medium-sized material is referrable to *Hyotherium* and tiny postcranial elements to the small suoids. Further comparison of the small elements from Béon 1 with those of *Taucanamo sansaniense* from its type locality (Sansan, MN6) permitted us to differentiate the palaeochoerid from the small suid.

Abbreviations

BSPGM	Bayerische Staatssammlung für Paläontologie und historische Geologie, München;
ELMA	European Land Mammal Age;
IPS	Institut de Paleontologia Miguel Crusafont, Sabadell;
MHNL	Muséum d'Histoire naturelle, Lyon;
MHNT	Muséum d'Histoire naturelle, Toulouse;
MNHN	Muséum national d'Histoire naturelle, Paris;
NHM	Natural History Museum, London;
SMNS	Staatliches Museum für Naturkunde, Stuttgart.

SYSTEMATICS

Order ARTIODACTYLA Owen, 1848
Family Suidae Gray, 1821
Subfamily Hyotheriinae Cope, 1888
Genus *Hyotherium* H. von Meyer, 1834

Hyotherium lacaillei n. sp.
(Figs 2; 3; 5)

Hyotherium soemmeringi – Crouzel *et al.* 1988: 86. — Antoine & Duranthon 1997: 211. — Antoine *et al.* 1997: table 1. — Duranthon *et al.* 1999: 86.

Holotype. — MHNT Béon 2003 H5-4, left hemimandible with alveolus of canine and p1 and p2-m3, associated with a left premaxilla with I1 and a portion of maxilla with P1-P2 (MHNT Béon 91 G4 41), a fragment of P3, and associated maxilla fragment with P4-M1 (MHNT Béon 91 G4 111).

Etymology. — In memory of the late Michel Lacaille (1946-2005) who initiated the field work for teenagers at Béon 1, and took part in all the summer excavations.

Type locality. — Béon 1, Montréal-du-Gers, Gers, France.

Material examined. — I1 (l), MHNT Béon 92 G3 111; I2 (l), MHNT Béon AR SN 2; I3 (r), MHNT Béon AR SN 3; Cm (r), MHNT Béon AR SN 1; i1 (l), MHNT Béon 92 G3 1170; i2 (r), MHNT Béon 93 G4 468, MHNT Béon 99 G4 408; cm (r), MHNT Béon 92 G4 268; p1 (r, l), MHNT Béon G4 537; m2 (l), MHNT Béon AR SN 6 associated with m3, MHNT Béon AR SN 4; postcranial elements: humerus (l), MHNT Béon SN 4520; astragalus (l), MHNT Béon SN 181; astragalus (l), MHNT Béon 92 F3 738 (juvenile); calcaneum (l), MHNT Béon SN 4535; calcaneum (r), MHNT Béon SN 4533; navicular (l), MHNT Béon F3 810; cuboid (l), MHNT Béon 92 F3 739; Mt III (l), MHNT Béon F3 794, MHNT Béon G3 629.

Diagnosis. — *Hyotherium* with complete and continuous row of upper and lower cheek teeth; I1 with a distal cusplet; P1 located lingually to the canine alveolus; upper premolars globular in their anterior part; M1 without buccal cingulum.

Differential diagnosis. — *Hyotherium* with no first-second premolar diastema on both lower and upper dentition, in contrast to other species of the genus; upper premolars more globular in their anterior part than in *H. soemmeringi* and *H. shanwangense*, P1 located in an anterior position, lingually to the canine, as in *H. meisneri*; lower premolars more slender than those of *H. meisneri* and *H. major*, but more globular than those of *H. soemmeringi* and *H. shanwangense*; posterior part of the lower premolars weakly developed, less than in *H. soemmeringi* and *H. shanwangense*.

Comparative description

Upper dentition (Figs 2: 1; 3: 5-8)

A portion of premaxilla with the I1 and the I2-I3 alveoli, a portion of maxilla with P1-P2, a broken P3, and another portion of maxilla with P4-M1, are referred to the same individual and associated with the hemimandible MHNT Béon 2003 H5-4. The I1 exhibits a high bicuspid crown of typical

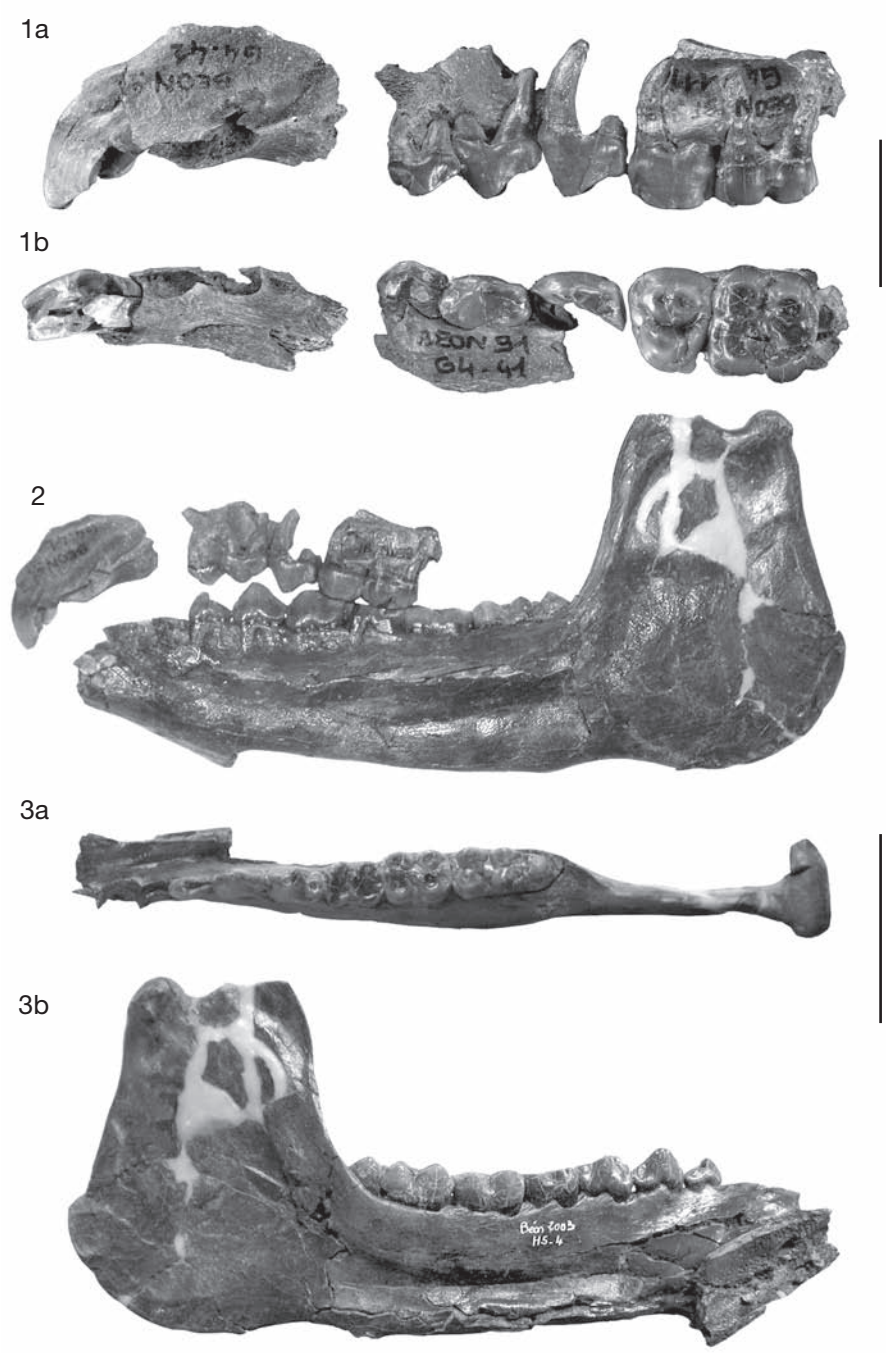

FIG. 2. — *Hyotherium lacaillei* n. sp. from Béon 1 (Montréal-du-Gers, Gers, France, MN4), holotype: **1**, upper dentition (MHNT Béon 91 G4 41, 91 G4 111); **1a**, lateral view; **1b**, occlusal view; **2**, complete holotype (upper dentition + associated mandible), lateral view; **3**, mandible (MHNT Béon 2003 H5-4); **3a**, occlusal view; **3b**, lingual view. Scale bars: 5 cm.

hyotheriine morphology. Another I1 (MHNT Béon 92 G3 111, Fig. 3: 5) is similarly robust with a large labio-lingual diameter. There is a major apical wear facet and a reduced posterior contact with I2. The curvature of the crown in lateral view follows the general curvature of the root, so that the tooth is strongly bent downwards. The overall morphology of I1 is similar to that of *H. soemmeringi* with two apical cusps, whereas the morphology of that of *H. major* (Pomel, 1847) (MNHN SG 3618) and *H. meisneri* (Meyer, 1829) (Van der Made 1994: figs 4, 5) is simpler with only one apical cusp. On MHNT Béon 91 G4 41, the upper incisor alveoli row is rectilinear and the two premaxillae form a sharp angle (*c*. 60°). The precanine diastema is reduced, which could be a sexually dimorphic difference. The anterior part of the snout is narrow, in agreement with the morphology of the associated mandibular symphysis.

Some isolated anterior teeth are preserved: I2 (MHNT Béon AR SN 2, Fig. 3: 6) is globular, and bears a clear separate posterior cusp. Its structure is simple, with a rounded lingual cingulum. I3 (MHNT Béon AR SN 3, Fig. 3: 7) also presents a simple asymmetrical and short crown, without any cingulum. A right upper canine (MHNT Béon AR SN 1, Fig. 3: 8) is known; it exhibits all typical hyotheriine characters: an anterior and a posterior crest of enamel and an anterior groove. The ventral enamel band is present but limited to a small inflection in the lingual anticline. The tooth is globular and of large size and most likely belongs to a male individual.

The upper premolars are present in the holotype (Fig. 2: 1); they are robust and globular: their anterior part is inflated and their transverse diameter is higher than in *H. soemmeringi* (see measurements in Table 1). The two first premolars are closely juxtaposed and there is no postcanine diastema, the canine emerging laterally to the P1. This morphology differs from that of *H. soemmeringi* from Sandelzhausen (MN5, Germany; Schmidt-Kittler 1971), which presents a clear postcanine diastema and in which P1 lies posterior to the canine alveoli. Lingually, the P2 bears a small enamel bud in front of the precrista; the posterior part of the tooth presents only a small incipient lingual basin. The lingual basin in *H. soemmeringi* is more developed. The P3 attributed to the same individual is too fragmentary to be described. The P4 bears two well separated buccal cusps. There is no lingual cingulum. The lingual roots of the P4 are coalescent, separated by a shallow groove; there are two buccal roots. The M1 is a square tooth with four well separated roots, without buccal cingulum.

Mandible (Fig. 2: 2, 3)

The anterior part of the mandible (MHNT Béon 2003 H5-4) is broken in front of the lower canine alveolus; the mandibular angle and the ascending ramus of the mandible are intact, except from the coronoid process, which is broken at its base. The symphysis appears to be narrow (*c*. 20 mm), but this dimension is certainly underestimated because of slight distortion. The diameter of the lower canine alveolus is wide (DMD = 14 mm; DLL = 8 mm), but its depth is reduced indicating that the tooth was not ever-growing and that the specimen was a female. The main mandibular foramen opens at the level of p2, while a smaller one lies below p4. The height of the horizontal ramus is similar to that of the female specimen of *H. major* housed in the MNHN. The ventral edge of the horizontal ramus is thick. The vascular incisura is present but reduced; its anterior edge bears a small tuberosity on the lingual side. The posterior edge of the angle of the mandible is thin and forms a small process extending beyond the posterior border of the ascending ramus. The masseteric fossa is deep. The lateral profile of the articular condyle is slender and sub-cylindrical; in dorsal view it is slender and slightly inclined medially.

Lower dentition (Fig. 3: 1-4)

One i1 and two i2s of *H. lacaillei* n. sp. are known; these lower incisors present a typically hyotheriine morphology with mesio-distally compressed roots but broad labio-lingually, endocristids and no lingual synclinid (Fig. 3: 2). The lower canine MHNT Béon 92 G4 268 has a scrofic section (i.e. the endofacet is much more developed than the postfacet). The ectofacet is slightly convex. Enamel bands are visible on the endo- and postfacet. A pair of p1s (MHNT Béon G4 537, Fig. 3: 1) displays a short and weakly

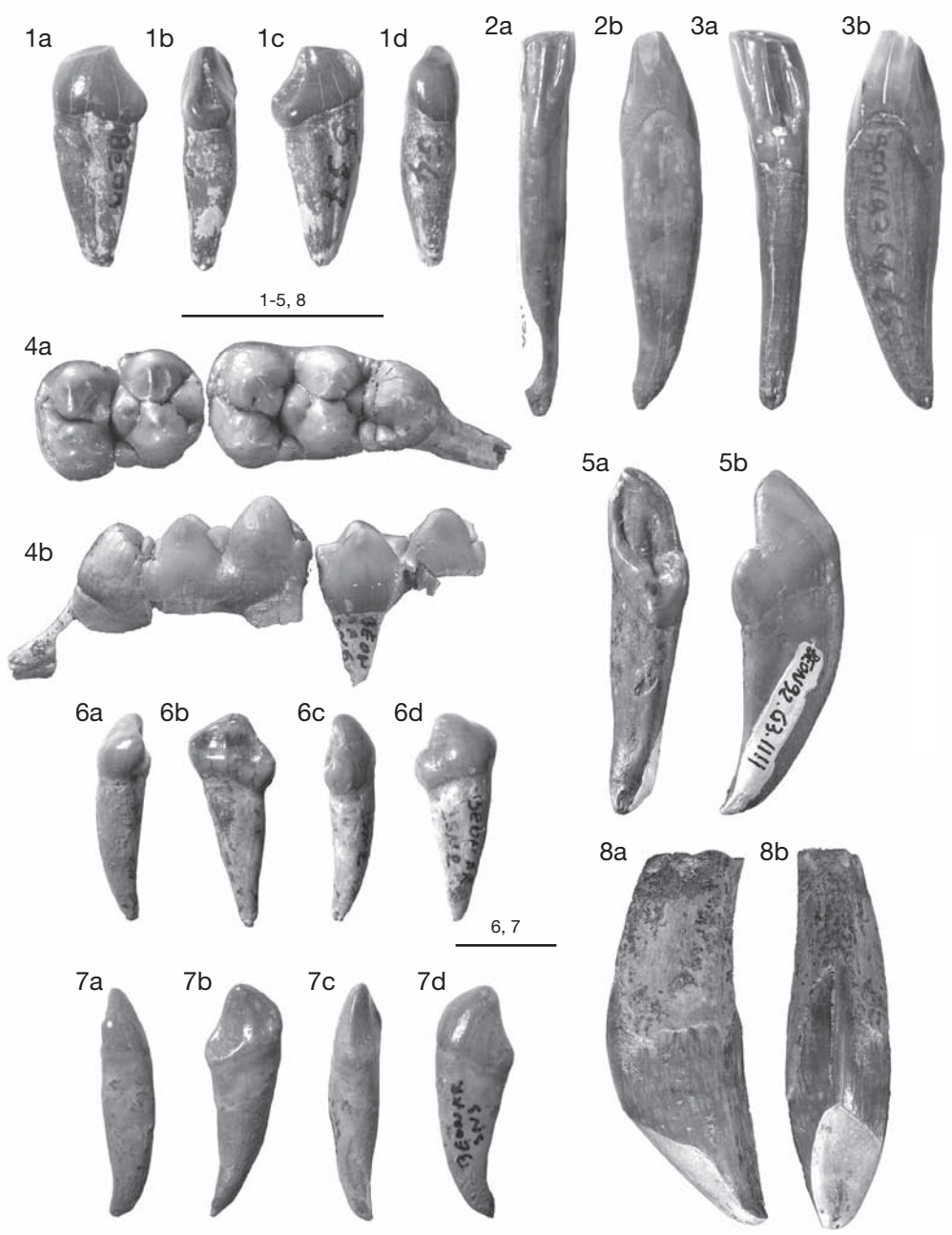

FIG. 3. — Isolated dental remains of *Hyotherium lacaillei* n. sp. from Béon 1 (Montréal-du-Gers, Gers, France, MN4): **1**, left p1, MHNT Béon G4 537 (**a**, buccal; **b**, posterior; **c**, lingual; **d**, anterior); **2**, left i1, MHNT Béon 92 G3 1170 (**a**, lingual; **b**, mesial); **3**, right i2, MHNT Béon 93 G4 468 (**a**, lingual; **b**, mesial); **4**, left m2-m3, MHNT Béon AR SN 6, MHNT Béon AR SN 4 (**a**, occlusal; **b**, lingual); **5**, left I1, MHNT Béon 92 G3 111 (**a**, lingual; **b**, distal); **6**, left I2, MHNT Béon AR SN 2 (**a**, mesial; **b**, lingual; **c**, distal; **d**, labial); **7**, right I3, MHNT Béon AR SN 3 (**a**, mesial; **b**, lingual; **c**, distal; **d**, labial); **8**, right Cm, MHNT Béon AR SN 1 (**a**, lingual; **b**, anterior). Scale bars: 1-5, 8, 2 cm; 6, 7, 1 cm.

TABLE 1. — Measurements in mm of suoid dental remains from Béon 1 (Montréal-du-Gers, Gers, France) (Listriodontinae excepted). Abbreviations: **B1**, maximum breadth of incisors and premolars, breadth of the anterior lobe of molars; **B2**, breadth of the posterior lobe; **B3**, breadth of the talon(id); **L**, length; **N**, quantity; **#**, missing data.

		***Taucanamo grandaevum* (Fraas, 1870)**			
Element	**N**	**L**	**B1**	**B2**	**B3**
p2	1	8.7	4.2		
p4	2	8.9-9.0	5.3		
m1	2	9.5-9.8	6.7-6.8	6.6-6.7	
m2	2	10.3-11.3	7.6-7.9	7.3-7.4	
m3	2	12.1-14.5	7.6-7.7	6.5-6.6	4.3-4.6
P4	1	8.6	9.0		
M2	1	10.4	9.4	9.0	
M3	1	11.0	9.1	7.5	
		***Chicochoerus minus* (Golpe Posse, 1972) n. comb.**			
m2	1	10.3	8.0	7.8	
m3	2	14.9-15.1	8.0	6.9-7.1	5.5
M1	1	9.2	9.4	9.3	
M2	2	9.9-10.4	10.0-#	9.5-10.3	
M3	1	11.0	9.1	7.5	4.0
		***Hyotherium lacaillei* n. sp.**			
i1	1	5.3	7.9		
i2	2	6.5-#	9.4-#		
p1	2	9.0-9.1	6.0-6.2		
p2	1	11.7	5.8		
p3	1	14.5	7.3		
p4	1	15.5	9.1	8.5	
m1	1	15.4	11.4	11.8	
m2	2	16.6-18.2	#-14.0	#-14.0	
m3	2	23.5-27.0	12.7-13.9		
I1	1	9.0	11.0		
I2	1	8.6	5.2		
I3	1	8.0	4.8		
P1	1	10.1	5.6		
P2	1	12.6	7.6		
P3	1	#	#		
P4	1	12.5	12.7		
M1	1	14.8	15.5	15.5	

developed posterior part, which confers a globular aspect to the tooth. In the mandible of *H. soemmeringi* from Sandelzhausen, the posterior part of p1 is more elongated (Schmidt-Kittler 1971).

The hemimandible MHNT Béon 2003 H5-4 displays a complete cheek tooth series (Fig. 2: 3a). All the teeth are preserved except p1; the corresponding alveolus indicates that p1 had two coalescent roots. There is no diastema, neither between c1 and p1 nor between p1 and p2. The size of the diastemata can vary individually and with sex and age (Hellmund 1991; Van der Made 1991), but members of *Hyotherium*, including *H. soemmeringi*, exhibit diastemata anterior and posterior to p1, even reduced ones. The lower cheek tooth enamel is thick and subtly wrinkled. The premolars are slender, which is characteristic of *H. soemmeringi*, but the teeth are still slightly inflated at the level of the central cusps (Fig. 4A) and not constricted as observed in *H. soemmeringi* from Germany (Sandelzhausen, MN5; Georgensmünd, MN6; Meyer 1834; Schmidt-Kittler 1971) or France (Baigneaux-en-Beauce, MN5). The antero-posterior lengths of the lower premolars increase from p1 to p4 and the size of the p2 is reduced with respect to p3-p4 (Fig. 4A, B). The central cusps of the premolars lie in a subcentral position so that the tooth appears subsymmetrical in lateral view. On p4, the metaconid

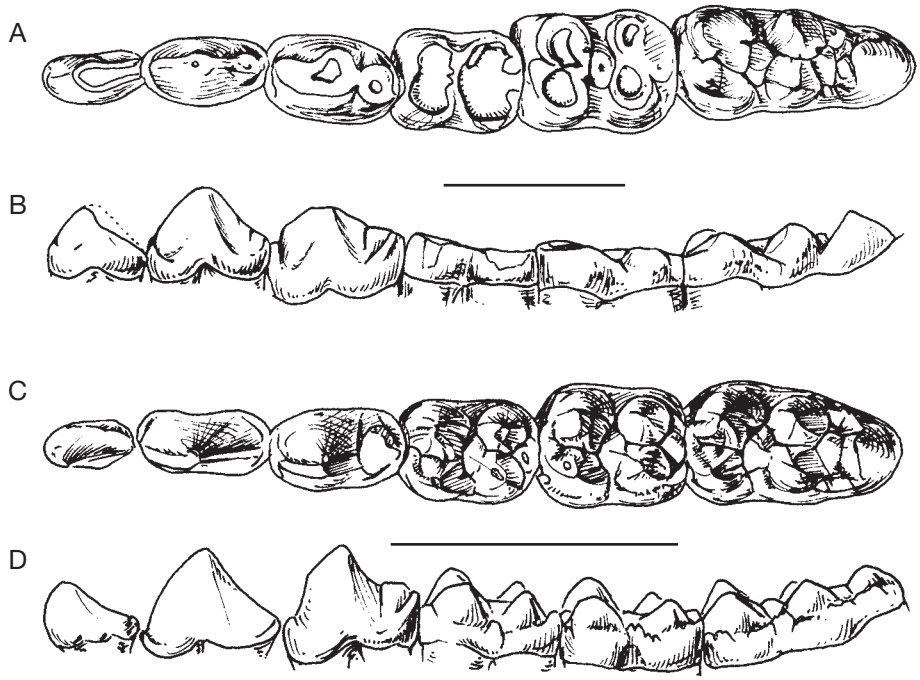

FIG. 4. — **A**, **B**, lower cheek tooth row of the type specimen of *Hyotherium lacaillei* n. sp. (MHNT Béon 2003 H5-4) from Béon 1 (Montréal-du-Gers, Gers, France, MN4); **A**, occlusal view; **B**, buccal view; **C**, **D**, lower cheek tooth row of *Chicochoerus minus* n. comb. (MHNT Pel. 1) from Pellecahus (Gers, France, MN4); **C**, occlusal view; **D**, buccal view. Scale bars: 2 cm.

is weak, whereas the posterior accessory cuspid is well developed. The metaconid differentiation occurs posteriorly to the protoconid. The premolars lack a lingual cingulum. As in all Hyotheriinae, m1 is only slightly smaller than m2; the transverse diameter of the anterior lobe of m3 is clearly greater than the second lobe, as in *H. soemmeringi.* The lower molars lack an endoentofossid, which is correlated with the convergence of the two posterior cusps. An isolated m2 (MHNT Béon AR SN 6) and one m3 (MHNT Béon AR SN 4) belong to the same individual (Fig. 3: 4a). The teeth present globular cusps with a reduced groove pattern and a well developed talonid, particularly on m3. This morphology is similar to that of *H. soemmeringi*.

Postcranial skeleton

Forelimb. Humerus (Fig. 5: 4): the adult left humerus MHNT Béon SN 4520 is much smaller than available specimens of *Eurolistriodon* sp. (Orliac in press), the distal width of MHNT Béon SN 4520 being *c*. 60% that of specimens of *Eurolistriodon* sp. The former is here attributed to *H. lacaillei* n. sp. The proximal end is missing. The diaphysis, preserved from the level of the deltoid tuberosity, is badly crushed medio-laterally; the distal end is intact. The morphology of this bone closely resembles that of recent *Sus scrofa* Linnaeus, 1758 being slenderer than in *Eurolistriodon*. The median groove is shallow and the distal trochlea is slender in distal view. The distal extension of the medial epicondyle is somewhat more developed than in *Sus scrofa*.

Hindlimb. Astragalus (Fig. 5: 1): two medium-sized suoid astragali (smaller than those of *Eurolistriodon* sp.) are attributed to *Hyotherium lacaillei* n. sp. Their inclined proximal trochlea and their convex sustentacular facet clearly indicate their suoid affinities. Even though their morphological features are identical, the astragalus MHNT Béon

FIG. 5. — Postcranial remains of *Hyotherium lacaillei* n. sp. from Béon 1 (Montréal-du-Gers, Gers, France): **1**, left astragalus, MHNT Béon 92 F3 738 (**a**, anterior; **b**, lateral; **c**, posterior; **d**, medial); **2**, left cuboid, MHNT Béon 92 F3 739 (**a**, anterior; **b**, lateral; **c**, posterior; **d**, medial; **e**, distal; **f**, proximal); **3**, left navicular, MHNT Béon F3 810 (**a**, anterior; **b**, lateral; **c**, posterior; **d**, medial; **e**, distal; **f**, proximal); **4**, left humerus, MHNT Béon SN 4520 (**a**, anterior; **b**, lateral; **c**, distal); **5**, right calcaneus, MHNT Béon SN 4533 (**a**, anterior; **b**, lateral; **c**, posterior; **d**, medial; **e**, proximal); **6**, left Mt III, MHNT Béon G3 629 (**a**, anterior; **b**, lateral; **c**, posterior; **d**, medial; **e**, distal). Scale bars: 1, 5, 6, 2 cm; 2, 3, 1 cm; 4, 5 cm.

SN 181 is much larger than MHNT Béon 92 F3 738 (Table 2); this could be due to individual age, the small one belonging probably to a juvenile or subadult individual. The bone is slender and high, more than in extant suids. However, the astragalus is more robust than in *Taucanamo sansaniense* from Sansan (specimens MNHN Sa 4632-38, 4640-44, 7802, 9319, 10749). The sustentacular facet presents a strong convexity; its maximum width occurs at the mid-level of the facet; the facet is slender at its distal end and the medial border bears a clear crest, as in all extant Suinae. The cuboid facet represents a small portion of the distal trochlea. The "P index" ([cuboid-facet length/total distal trochlea length] × 100) defined by Dehm (1934) equals 39.5 for the large specimen and 42.2 for the small one; these values are higher than in *Aureliachoerus aurelianensis* (33.0-36.5 range measured on the three specimens of *A. aurelianensis* from Artenay, France, MN4; MNHN Ar 2789, 2790, 2791) and close to that of *Sus scrofa* (P = 40; Leinders 1976). In lateral view, the articular surface corresponding to the coracoid process of the calcaneum is wide and concavo-convex, whereas it is slender and concave in *Palaeochoerus typus* Pomel, 1847 (specimens from Saint-Gérand-le-Puy; MNHN SG 133390, SG 9862).

Calcaneum (Fig. 5: 5): two calcanea are preserved (MHNT Béon SN 4594; MHNT Béon SN 4533). The global morphology is close to that of *Sus scrofa*: the sustentaculum tali is short with a posterior side sloping ventro-laterally. The posterior border of the sustentaculum tali is, however, slightly inflated, more than in *Aureliachoerus aurelianensis* (MNHN Ar 2792, 2794, and 2795; Artenay, France, MN4). The calcaneum presents a slight constriction anterior to the tuber calcanei. In dorsal view, the tuber calcanei is higher than wide and bears a deep sulcus.

Cuboid (Fig. 5: 2): the overall shape of the cuboid is close to that of Listriodontinae with a robust body, thicker than that of *A. aurelianensis* (specimen from Artenay, MNHN Ar 5655). The articular surface for the astragalus is more developed than in the latter taxon, this character being directly correlated to the medio-lateral width of the cuboid-facet of the astragalus described above. The scissure for the tendon of the *fibularis longus* muscle is short and rounded as in *A. aurelianensis*. On the medial surface of the bone, the contact for the ectocuneiform is short, triangular and anteriorly oriented as is the case in extant Suinae; in contrast the ectocuneiform facet is oriented medially in *A. aurelianensis*.

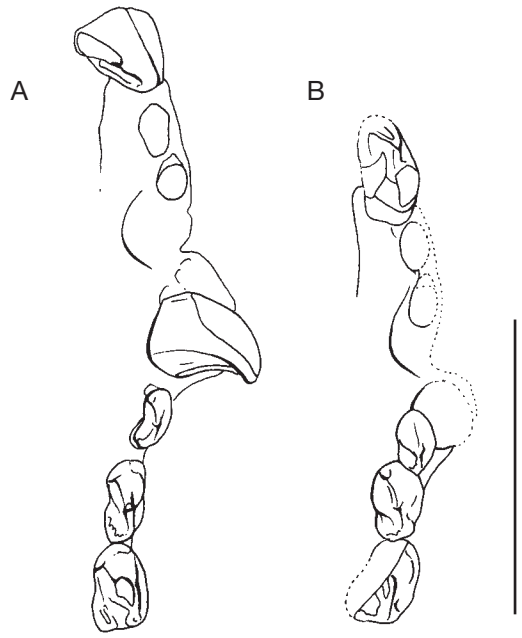

FIG. 6. — **A**, anterior part of the snout in occlusal view of *Hyotherium soemmeringi* from Sandelzhausen (1959 II 305); **B**, reconstruction of *Hyotherium lacaillei* n. sp. from Béon 1 (Montréal-du-Gers, Gers, France) (MHNT Béon 91 G4 41, G4 111). Scale bar: 5 cm.

Navicular (Fig. 5: 3): the navicular MHNT Béon 92 F3 810 is associated with the cuboid described above. The extension of the posterior process of *H. lacaillei* n. sp. is similar to that of *Eurolistriodon*; it is, however, more slender and its proximal development does not reach the level of the proximal surface of the bone contrary to what occurs in Listriodontinae. The lateral part of the posterior process bears a large sulcus, absent in *Aureliachoerus* and in *Eurolistriodon*. Like in Listriodontini Gervais, 1859, the contact for the mesocuneiform is reduced in comparison to extant suids (Van der Made 1996b; Orliac in press).

Mt III (Figs 5: 6): two fragmentary left Mt IIIs of *H. lacaillei* n. sp. are known from Béon 1; MHNT Béon G3 629 is almost complete, only lacking the posterior part of the proximal surface; MHNT

TABLE 2. — Measurements in mm of the postcranial elements of suoids from Béon 1 (Montréal-du-Gers, Gers, France) (Listriodontinae excepted). Abbreviations: **AP ct**, antero-posterior breadth of the corpus tali; **AP d**, antero-posterior breadth of the mid-diaphysis; **AP mx**, maximal antero-posterior breadth; **APD**, antero-posterior distal breadth; **APD m**, antero-posterior distal breadth medial side; **APD l**, antero-posterior distal breadth lateral side; **APP**, antero-posterior proximal breadth; **Fc**, cuboid facet breadth; **H mx**, global length (without posterior apophysis for metacarpal); **L lat**, lateral length; **L med**, medial length; **ML ct**, medio-Lateral breadth of the corpus tali; **ML d**, medio-lateral breadth of the mid-diaphysis; **MLD**, medio-lateral distal breadth; **MLD as**, medio-lateral distal breadth of the articular surface; **MLD mx**, maximum medio-lateral distal breadth; **MLP**, medio-lateral proximal breadth; **#**, missing data.

Humerus								
	No.	**APD m**	**APD l**	**MLD mx**	**MDL as**			
H. lacaillei n. sp.	SN 4520	300	207	328	240			
Mc III								
		H mx	**APP**	**MLP**	**APD**	**MLD**		
C. minus n. comb.	E3 103		92	95	82	76		
	SN 4509		#	#	82	76		
Astragalus								
	No.	**L lat**	**L med**	**MLP**	**APD**	**MLD**	**Fc**	
H. lacaillei n. sp.	92 F3 738	310	286	140	124	156	66	
H. lacaillei n. sp.	98 SN 181	354	323	155	155	176	61	
T. grandaevum	321	243	216	113	96	132	40	
C. minus n. comb.	4540	238	220	107	90	120	40	
C. minus n. comb.	4541	248	226	108	84	120	38	
Calcaneum								
	No.	**H mx**	**ML ct**	**AP ct**	**AP mx**	**MLD**	**APD**	
H. lacaillei n. sp.	SN 4534	620	80	155	#	140	148	
H. lacaillei n. sp.	SN 4535	#	84	155	#	145	160	
C. minus n. comb.	E3 48	425	60	107	160	90	94	
Navicular								
	No.	**H mx**	**APD**	**MLD**				
H. lacaillei n. sp.	F3 92 810	143	206	120				
Cuboid								
	No.	**H mx**	**APD**	**MLD mx**				
H. lacaillei n. sp.	92 F3 739	165	171	112				
Mt III								
	No.	**H mx**	**ML d**	**AP d**	**APP**	**MLP**	**APD**	**MLD**
H. lacaillei n. sp.	G3 629	711	100	90	#	130	150	126

Béon F3 794 consists only of a proximal extremity. The bone is slender and elongated (Table 2); its distal articular surface bears a well developed median crest. On the proximal surface, the mesocuneiform facet is small, as is the mesocuneiform facet of the navicular.

DISCUSSION

The larger hyotheriine specimens from Béon 1 were initially attributed to *H. soemmeringi* (Antoine & Duranthon 1997). Many dimensions and morphological features are indeed similar to those of *H. soemmeringi*: the lower premolars are slender with a p4 devoid of a clear metaconid; the I1 bears a well developed distal cusp and P4 is globular. However, other characters differ from those of *H. soemmeringi*: the lack of diastemata; the anterior position of the P1, located lingually to Cm; premolars more globular, especially in their anterior part; the lack of buccal cingulum in upper molars (while it occurs in all other European *Hyotherium* species). The plausible morphology of the anterior part of the

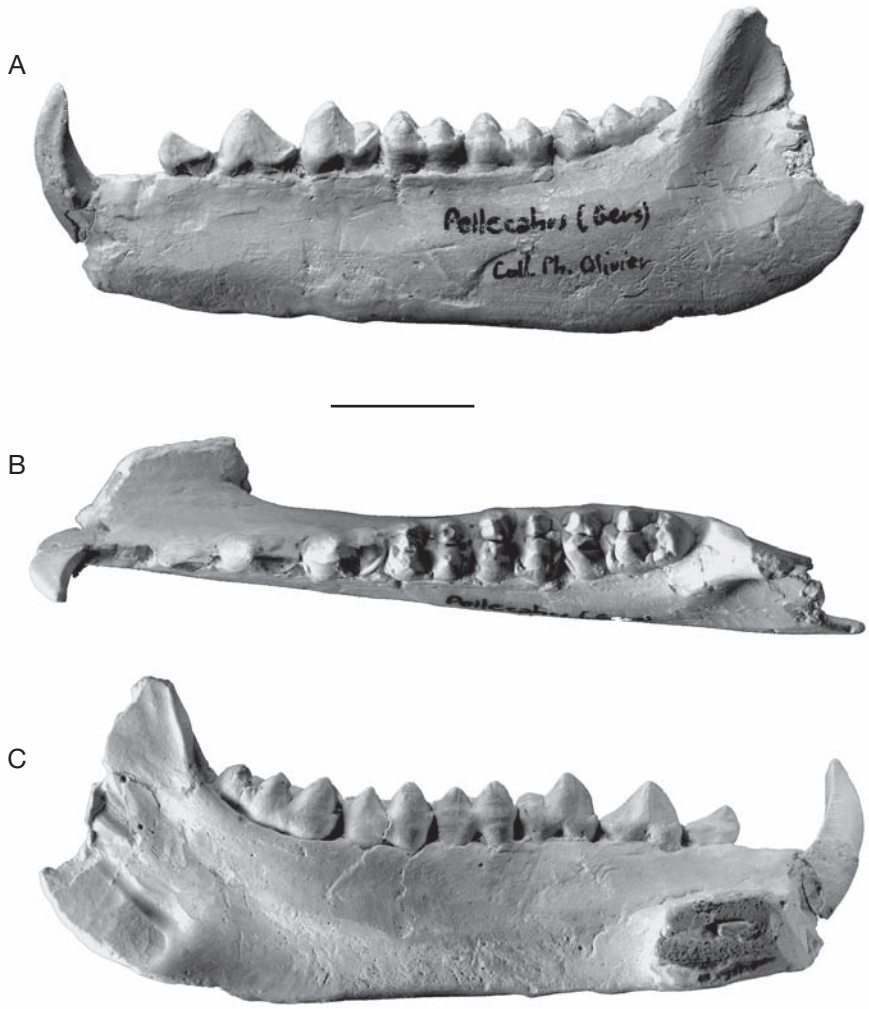

FIG. 7. — Mandible of *Chicochoerus minus* n. comb., MHNT Pel. 1 (cast) from Pellecahus (Gers, France, MN4): **A**, buccal view; **B**, occlusal view; **C**, lingual view. Scale bar: 2 cm.

snout of *H. lacaillei* n. sp. and a comparison with *H. soemmeringi* from Sandelzhausen are proposed in Figure 6. It is noteworthy that diastemata are also lacking in some specimens of *H. soemmeringi*: a specimen from Eibiswald (Styria, Austria; basal MN5, Steininger *et al.* 1990) and figured by Peters (1868); this specimen also presents inflated lower premolars and may document the new species. Another specimen from Buchenthal figured by Stehlin (1899-1900: table 1, fig. 3) also lacks diastema, but the anterior two premolars are incompletely erupted suggesting a juvenile individual, in which case a short diastema could develop with maturity.

Hyotherium from Béon 1 differs from *H. meisneri* and *H. major* by its elongated and slender lower premolars, by the lack of a clear metaconid on the p4, and the lack of diastema. The anterior position of the P1 of *H. lacaillei* n. sp., lingual to the CM, also occurs in *H. meisneri* (Orliac pers. obs. on unpublished material from Grépiac, France) and *H. major* (Hellmund 1991: pl. 2) but the latter two species lack of a clear distal cusp on the I1 and present a

stronger reduction of the two anterior premolars than *H. lacaillei* n. sp. from Béon 1.

Hyotherium shanwangense Liu, Fortelius & Pickford, 2002, from the late early Miocene of Shanwang (Shandong, China), is also closely related to *H. soemmeringi* and it presents a morphology close to the specimen from Béon 1 with reduced diastemata, reduced buccal cingula on the upper molars, and globular premolars (Liu *et al.* 2002). The size of the material from Shanwang is also congruent with that of *H. lacaillei* n. sp., but the p3 and p4 of *H. shanwangense* are wider, the latter being characterised by an inflated p4 bearing a posterobuccal bulge as in Tetraconodontinae (Liu *et al.* 2002). *H. lacaillei* n. sp. presents a very short premolar row with closely juxtaposed teeth, and the P1-P2 are much more inflated in their anterior part (see measurements in Table 1) than is the case in *H. shanwangense*.

Van der Made (1998) considers two subspecies of *H. soemmeringi*: *H. s. soemmeringi* and *H. s. wylensis* (Meyer, 1866), the latter subspecies being "morphologically similar, but smaller" than the former. *H. s. wylensis* includes material from Sandelzhausen and Baigneaux-en-Beauce; this material differs from the material from Béon 1 by more slender lower and upper premolars, with more developed posterior part of the teeth and by the morphology of the anterior part of the snout (Fig. 6).

Chicochoerus n. gen.

TYPE SPECIES. — *Palaeochoerus minus* Golpe Posse, 1972 by present designation.

ETYMOLOGY. — *Chico* means small in Spanish, this language was chosen because Spain is the first place from which material of the genus was reported, chico refers to the small size of the material.

DIAGNOSIS. — Same as for the type species.

Chicochoerus minus
(Golpe Posse, 1972) n. comb.
(Figs 7; 8: 1-4; 9: 2, 4, 5)

Palaeochoerus minus Golpe Posse, 1972: 117, pl. IV, fig. 4b, pl. V, fig. 5a.

Aureliachoerus minus – Van der Made 1998: 244, pl. 1. — Van der Made & Morales 1999: fig. 3.

HOLOTYPE. — Fragment of left maxilla with P4-M2 (IPS 1417) figured by Golpe Posse (1972: pl. V, fig. 5a) from El Canyet (Spain, Burdigalian; Golpe Posse 1972).

GEOGRAPHICAL RANGE. — Europe (Spain, France, Austria).

STRATIGRAPHICAL RANGE. — Middle part of the Orleanian European Land Mammal Age (MN4), late early Miocene.

LOCALITIES. — El Canyet (Spain), Can Canals (Spain), Oberdorf (Styria, Austria), Seegraben (Styria, Austria), Béon 1 (Montréal-du-Gers, Gers, France), Pellecahus (Gers, France), La Romieu (Gers, France). The material from Wintershof West has also been referred to this species by Van der Made (1989-1990b, 1998; Van der Made & Morales 1999) and might well belong to *C. minus*.

MATERIAL EXAMINED. — **Béon 1** (Montréal-du-Gers, MN4, SW France), dental remains: from the same individual: M1 (r), MHNT Béon AR SN 19; M2 (r), MHNT Béon E3 95; M3 (r), MHNT Béon AR SN 16; portion of mandible with m2-m3 (r), MHNT Béon E3 67; isolated remains: Cm (l), MHNT Béon E3 894; P4 (r), MHNT Béon AR SN 21; M2 (r), MHNT Béon AR SN 18; m3 (l), MHNT Béon E3 818; postcranial elements: astragalus (l), MHNT Béon F3 238; astragalus (r), MHNT Béon SN 4540; calcaneum (l), MHNT Béon E3 48; Mc III (r), MHNT Béon SN 4509; Mc III (r), MHNT Béon E3 103.
Pellecahus (MN4, Gers, SW France; Antoine *et al.* 2000b): left hemimandible with cm, p2-m3, MHNT Pel. 1 (Philippe Olivier collection, Toulouse; cast available at the MHNT).

DIAGNOSIS. — Small suid with simple lower premolars with sharp postcristids; p2 strongly asymmetrical with a convex precristid; size of p2 greatly reduced when compared to p3 and p4; p4 simple without a metaconid; lower molars with clear prefossids between the two anterior cusps, forming an internal basin; endocristids of both anterior cusps oriented posteriorly; endometacristid narrow without incipient endometaconulid; upper canine without incipient ventral enamel band, and slender compared to other Hyotheriinae.

DIFFERENTIAL DIAGNOSIS. — Small Hyotheriinae which differs from *Aureliachoerus*, *Hyotherium* and *Xenohyus* by its simpler lower molars with sharper postcristids; p2 strongly asymmetrical and without anterior enamel bud; p4 lacking a metaconid; lower molars with an internal basin in the anterior lophid and without an incipient endometaconulid; slender upper canine without incipient ventral enamel band.

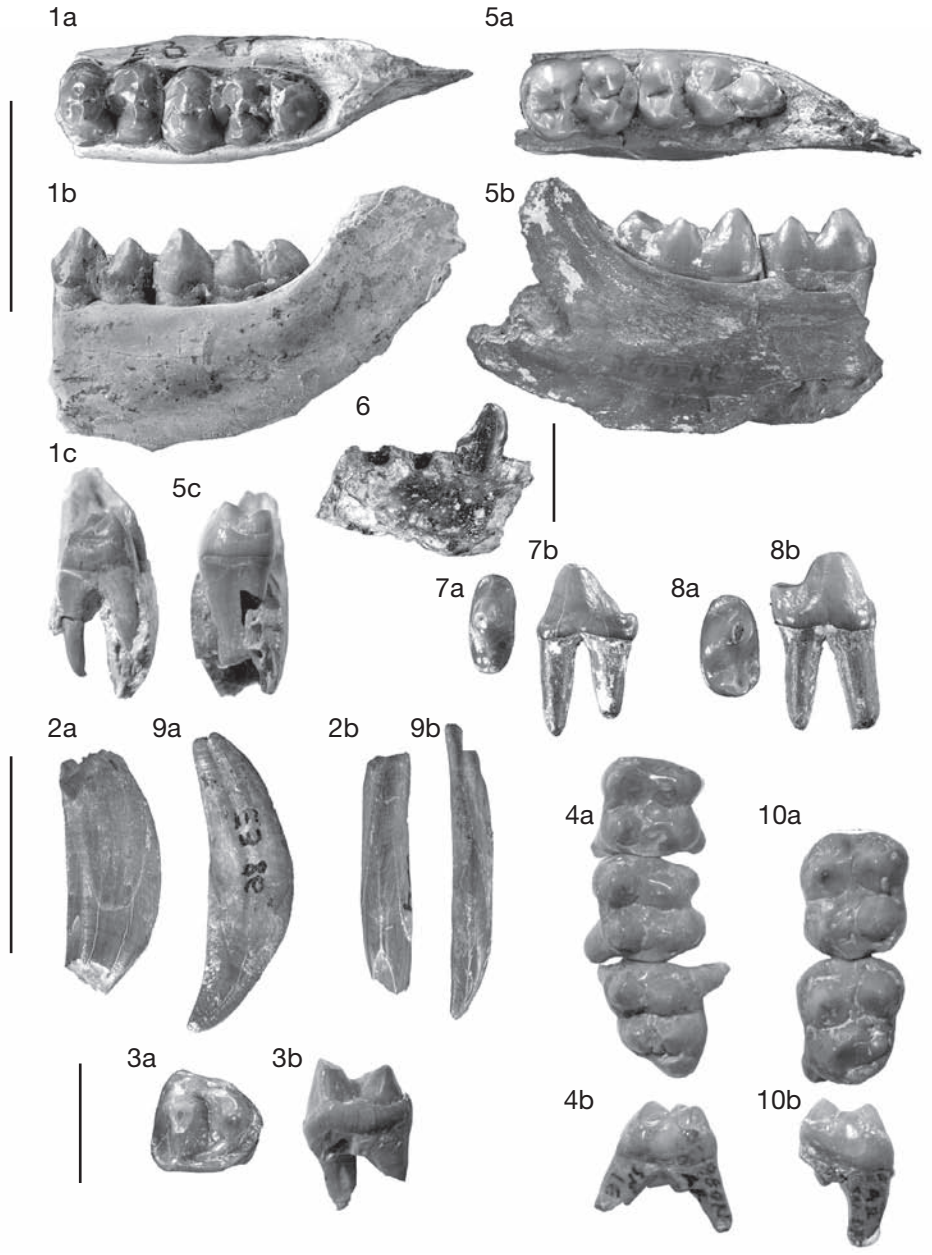

FIG. 8. — **1**-**4**, *Chicochoerus minus* n. comb. from Béon 1 (Montréal-du-Gers, Gers, France); **1**, portion of right mandible with m2-m3, MHNT Béon E3 67 (**a**, occlusal; **b**, lingual; **c**, anterior view of m2); **2**, left Cm, MHNT Béon E3 894 (**a**, lingual; **b**, anterior); **3**, right P4, MHNT Béon AR SN 21 (**a**, occlusal; **b**, posterior); **4**, upper right molar row from the same individual, MHNT Béon AR SN 19 (M1), MHNT Béon E3 95 (M2), MHNT Béon AR SN 16 (M3) (**a**, occlusal; **b**, anterior view of the M2); **5**-**10**, *Taucanamo grandaevum* from Béon 1 (Montréal-du-Gers, Gers, France); **5**, left mandibular fragment with m2-m3, MHNT Béon AR SN 7 (**a**, occlusal; **b**, lingual; **c**, anterior view of m2); **6**, right mandibular fragment with p1 in buccal view, MHNT Béon F2 627; **7**, right p2, MHNT Béon AR SN 10 (**a**, occlusal; **b**, lingual); **8**, left p4, MHNT Béon AR SN 9 (**a**, occlusal; **b**, lingual); **9**, right upper canine (mirror image to facilitate comparison with *Chicochoerus* n. gen.), MHNT Béon E3 86 (**a**, lingual; **b**, anterior); **10**, left associated M2-M3, MHNT Béon AR SN 15, AR SN 17 (**a**, occlusal; **b**, anterior view of the M2). Scale bars: 1, 2, 4, 5, 9, 10, 2 cm; 3, 6-8, 1 cm.

Comparative description

Upper dentition (Figs 8: 2)

The upper cheek teeth are represented by an upper canine, a P4, and a complete molar row from Béon 1. The upper canine (MHNT Béon E3 894, Fig. 8: 2) has a shallow antero-dorsal groove (illustrated in Appendix 5: 2e); it is straight and slightly inflated on the lingual side; it is, however, strikingly slender for a hyotheriine suid. In *Taucanamo* Simpson, 1945, there is no antero-dorsal groove, the upper canine is slightly twisted from the root to the apex, and the lingual side is flat. The P4 (MHNT Béon AR SN 21, Fig. 8: 3) was attributed to *C. minus* on the basis of the rectangular occlusal outline of the tooth, which is rounded in *Taucanamo* (*T. sansaniense* MNHN Sa 4662 and *T. grandaevum*; Chen 1984: pl. 3, figs 2, 3a). The tooth presents only one buccal cusp and the protocone lies in an anterior position, even anterior to the paracone. The P4 from El Canyet (IPS 1417) presents a well developed metacone, and the specimen (IPS 1416) from Can Canal has a more reduced one. A complete row of right upper molars is associated with a portion of right mandible bearing m2-m3. The quadratic occlusal outline of the teeth (Fig. 8: 4a) and the separated buccal roots indicate a suid condition. The separation of buccal roots is correlated with divergent anterior roots (Fig. 8: 4b, 10b); this character is interesting as a lot of specimens have lost their buccal roots so that it is impossible to say if they were fused or not. The anterior position of the preprotoconulid, which is fused to the anterior cingulum and is not included in the preprotocrista is also characteristic of suids (Van der Made 1996a, b). The M3 MHNT Béon AR SN 16 presents a well developed talon with its own root.

Mandible and lower dentition (Figs 7; 8: 1)

In the Béon 1 material, the lower dentition of *Chicochoerus minus* n. comb. is represented by an m2-m3 series (MHNT Béon E3 67, Fig. 8: 1) and an isolated m3 (MHNT Béon E3 818). A left hemimandible with cm and p2-m3 (Fig. 7) from Pellecahus (MN4 according to Antoine *et al.* 2000b) greatly improves our knowledge of this species. The horizontal ramus is broken in front of the lower canine and the ascending ramus is missing. The horizontal ramus is slender, but its height increases backwards. There is no trace of the vascular incisura; in *Taucanamo* and *Palaeochoerus* Pomel, 1847, the height of the horizontal ramus does not increase backwards and even decreases at the level of the vascular incisura. On the buccal side, there is a deep masseteric fossa, which is shallower in *Taucanamo* (*T. sansaniense* from Sansan MNHN Sa 4661; *T. primum* from Artenay, type specimen MNHN Ar 5). On the lingual side, the bone bulges under m3 (flat in *Taucanamo*) whereas the ventral part bears a deep concavity and the ventral edge is recurved lingually.

The large and robust lower canine (MHNT Béon E3 894) is typical of a male. It is compressed labiolingually, as in *Taucanamo*, but the posterior face is less developed. The p1 is lacking, but its alveolus is preserved and it further indicates that there was neither postcanine diastema nor p1-p2 diastema. The lower cheek tooth row is shown in Figure 4C, D. The p2 is small when compared to p3 and p4 for all its measurements; this recalls Tetraconodontinae, but the latter present only low crowned p1-p2, whereas the length of the tooth remains consistent with p3-p4. The p2 of *Chicochoerus minus* n. comb. is strongly asymmetric with a short convex precristid and a long concave postcristid (Fig. 4D). There is no anterior enamel bud. The morphology of p2 differs markedly from that of *A. aurelianensis* from Artenay (MNHN Ar 2662): in *A. aurelianensis*, p2 is more symmetrical, the precristid is straight and there is a small anterior enamel bud. The p4 presents hyotheriine morphology, with a high precristid and no paraconid; the posterior accessory cusp is well developed but the metaconid only consists of a small bulge on the lingual part of the protoconid; this structure would disappear with wear. In *A. aurelianensis*, the metaconid is more developed.

The lower molars present high angular cusps (Fig. 4C, D); the internal crests are not developed, but the global aspect of the teeth is more sublophodont than in *A. aurelianensis*, in which the cuspids are more rounded. The endometacristid is slender and does not bear an incipient endometaconulid (secondary cusp originating from an important development of the endometacristid), in contrast to other Hyotheriinae which present a large en-

FIG. 9. — **1**, *Taucanamo grandaevum* from Béon 1 (Montréal-du-Gers, Gers, France), left astragalus, MHNT Béon 321 (**a**, anterior; **b**, lateral; **c**, posterior; **d**, medial); **2**-**5**, *Chicochoerus minus* n. comb. from Béon 1 (Montréal-du-Gers, Gers, France) (**a**, anterior; **b**, lateral; **c**, posterior; **d**, medial); **2**, right astragalus, MHNT Béon SN 4540 (mirror image to allow comparison with *T. grandaevum*) (**a**, anterior; **b**, lateral; **c**, posterior; **d**, medial); **3**, left calcaneum, MHNT Béon E3 348 (**a**, anterior; **b**, lateral; **c**, posterior; **d**, medial); **4**, right Mc III, MHNT Béon SN 4509 (**a**, anterior; **b**, lateral; **c**, posterior; **d**, medial; **e**, proximal); **5**, right Mc III, MHNT Béon E3 103 (**a**, anterior; **b**, lateral; **c**, posterior; **d**, medial; **e**, distal). Scale bars: 2 cm.

dometacristid (see *H. lacaillei* n. sp., Fig. 3: 4a). The two cusps of each lobe are, however, close to each other, whereas in *Taucanamo* and *Doliochoerus* they are well separated. The endoprotocristid is inflated, which reduces the space between the two anterior cusps and separates the prefossids from the groove at the junction of the preprotoconulid. In *Taucanamo*, the endoprotocristid is not inflated and the space between the anterior cuspids is wider. The anterior cusps of the lower molars are closer to each other in *Chicochoerus minus* n. comb. than in *Taucanamo*; this determines a slight inflection in the buccal and lingual walls of the lower molars, separating the cusps from the base of the crown. In *Taucanamo* and *Palaeochoerus*, the lingual and buccal walls are straight. The prehypoconulid of *Chicochoerus minus* n. comb. is clearly separated from the hypoconid by a deep groove, still present with considerable wear; this groove is found in all other Hyotheriinae. The roots of the lower molars are clearly separated from cervix to apex (Fig. 8: 1c), as in hyotheriines in general (Ginsburg 1974; Hellmund 1992) and even suids (Van der Made 1996a). The enamel is slightly wrinkled horizontally, while it is vertically wrinkled in *Taucanamo* in unworn teeth or smooth when worn. The endoprotocristid and endometacristid of m2-m3 are low and well developed; they meet in the sagittal plane of the teeth. Anterior to the two endocristids, the two prefossids form a small internal basin. Such morphology of the anterior lophid differs from what is observed in Hyotheriinae (endometacristid much more developed than the endoprotocristid; no internal basin; this internal basin can also be weakly developed in some *Taucanamo sansaniense*). The representatives of *Taucanamo* also differ from the small suid from Béon 1 both by the absence of deep prefossids and the presence of high endocristids in the anterior lophid. The prehypoconulid is transversely stretched, and clearly separated from the hypoconid by a deep groove, still visible on worn teeth, whilst the prehypocristid is strong and fused to the prehypoconulid in *Taucanamo*. On the buccal side of the teeth, there is a clear demarcation between the cusps and the inflated base of the crown, which increases the tooth width. In *Taucanamo*, the lingual wall is straight and the tooth therefore appears slender.

Postcranial skeleton

Forelimb. Mc III (Fig. 9: 4, 5): two Mc III fragments are attributed to *Chicochoerus minus* n. comb. on the basis of their small size and of the presence of a well developed median crest on the anterior surface of the distal trochlea which is lacking in palaeochoerids (Van der Made 1996a, 1997a, 1998). The specimen MHNT Béon SN 4509 lacks the proximal end, but the shape of the diaphysis is congruent with that of a third metacarpal. The distal part of the diaphysis is not inflated as is the case in *T. sansaniense* (MNHN Sa 10895 from Sansan). MHNT Béon E3 103 corresponds to the proximal two thirds of the diaphysis of Mc III. The proximal surface slopes latero-posteriorly to a higher degree than in *T. sansaniense*. On the posterior side, the proximal facet and the postero-lateral facet are separated by a small tuberosity, which confers a rounded shape to the posterior extension of the proximal facet. In *T. sansaniense*, the proximal facet and the postero-lateral facet contact each other and the posterior extension of the proximal facet is sharp.

Hindlimb. Astragalus (Fig. 9: 2): three small suoid astragali are known from Béon 1. Two of them are attributed to *C. minus* (MHNT Béon F3 238, SN 4540) notably on the basis of: 1) the orientation of the crest lining the medial border of the sustentacular facet, which is straight as in *Hyotherium*; and 2) the large concavo-convex facet corresponding to the coracoid process of the calcaneum on the lateral side. In *Taucanamo sansaniense*, the medial crest is more oblique, restricting the distal surface of the facet and the contact with the coracoid process of the calcaneum is more simple (comparative sample of 15 astragali, specimens Sa 4632-38; 4640-44; 7802; 9319; 10749 from the type locality Sansan). The cuboid-facet represents a small portion of the distal trochlea: the P index (Dehm 1934) is superior to that of the specimen attributed to the small *Taucanamo grandaevum*, the value for both specimens of *C. minus* is P = 33.9. This value is within the 33.0-36.5 range measured on the three specimens of *A. aurelianensis* from Artenay (MNHN Ar 2789, 2790, 2791) and within the

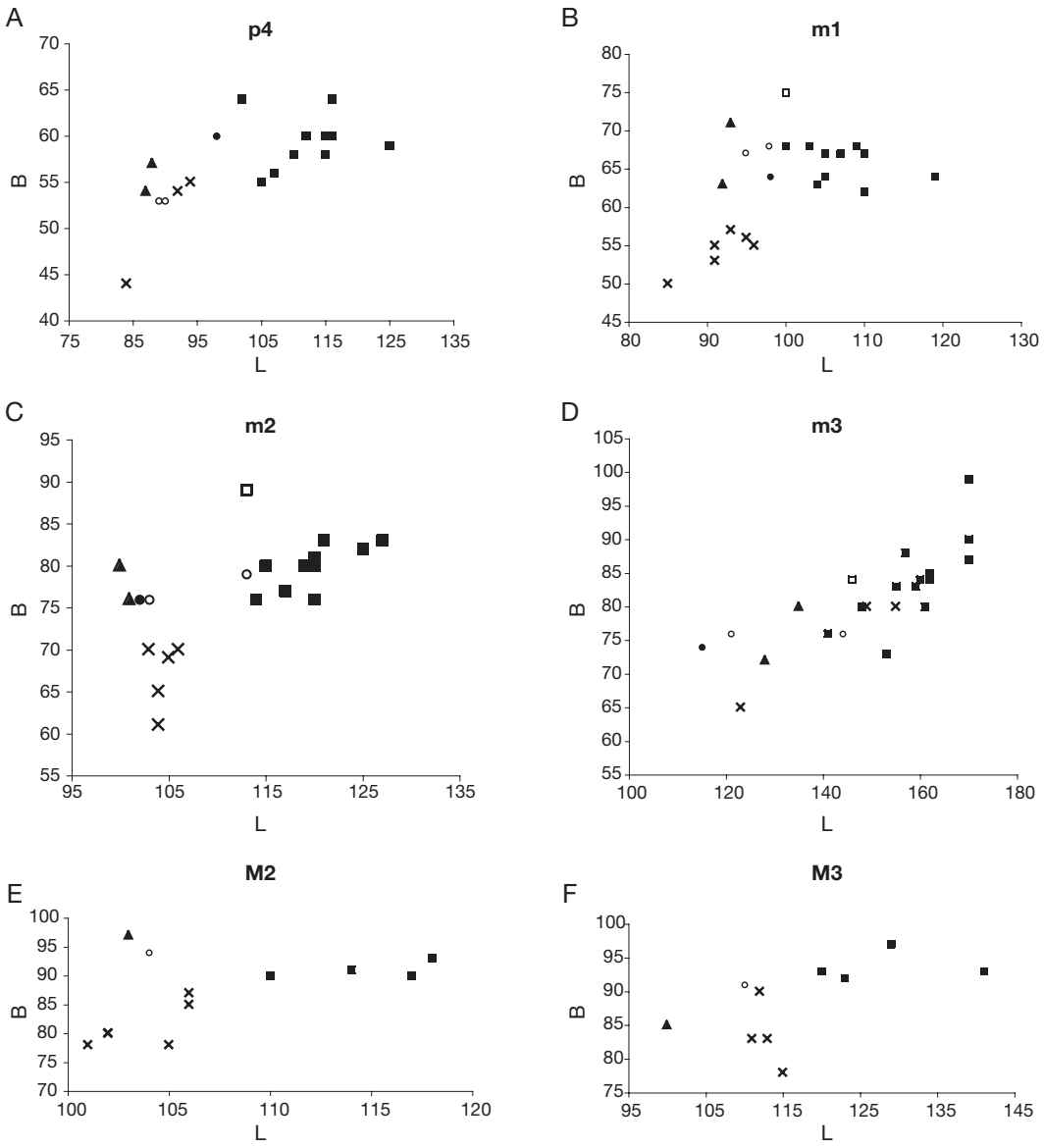

FIG. 10. — Scatter plots of the dental dimensions of *Taucanamo primum* from Artenay (type locality; ●), *T. grandaevum* from Steinheim (type locality; ×), Bézian (□), Els Casots (▲), and Béon 1 (○), and *Taucanamo sansaniense* from the type locality of Sansan (■). Abbreviations: **B**, maximum tooth breadth; **L**, tooth length.

32.7-36.5 range measured on a 15-specimen sample from Sansan.

Calcaneum (Fig. 9: 3): the shape of the sustentaculum tali posterior face of MNHN Béon E3 348, which slopes laterally, clearly indicates that it is a suoid and not a small ruminant. It is allocated to the genus *Chicochoerus* n. gen., on the basis of its small size and because of the complex concavo-convex contact with the astragalus on the coracoid process. This contact appears to be simpler in

Taucanamo (astragalus from Sansan) and *Palaeochoerus* (MNHN SG 133390, 9862). The lateral edge of the sustentaculum tali is thin; there is no thickening to guide the tendon of the *peroneus longus* muscle. The extension of the bone from the sustentacular facet to the distal end is reduced when compared to *A. aurelianensis* (MNHN Ar 2792, Artenay) and to *Sus scrofa*. The posterior extremity of the tuber calcanei is sub-circular in dorsal view, whereas in *H. lacaillei* n. sp. the antero-posterior breadth exceeds the medio-lateral breadth.

Discussion

At Béon 1, small-sized suoid specimens can clearly be assigned to two distinct taxa: one is related to the Palaeochoeridae and the other to the Suidae. If some features can clearly differentiate suids from palaeochoerids, such as the anterior development of the median crest on the distal part of the metapodials, it is, however, more difficult to assign isolated and fragmentary elements to a given group.

Until this study, two species were included in *Aureliachoerus*, *A. aurelianensis* and "*A.*" *minus*, the former being the type species. Here, "*A.*" *minus* is removed from *Aureliachoerus* and considered to be the type species of *Chicochoerus* n. gen. The smaller suid from Béon 1 presents the same lower cheek tooth morphology as that from Oberdorf, previously referred to "*Aureliachoerus*" *minus* (Van der Made 1998: pl. 1, figs 1-5). Tooth measurements are also congruent, even if the specimen from Pellecahus is somewhat larger. Comparison to the type material of "*Palaeochoerus minus*" from El Canyet (MN4, Spain) is more difficult because the type specimen is considerably worn. However, morphology of the material from the type locality and from Can Canals (IPS 1415) is also congruent. Van der Made (1989-1990b, 1998; Van der Made & Morales 1999) differentiated "*A.*" *minus* from *A. aurelianensis* on the basis of the smaller size of the former and of the absence of a posteriorly elongated talonid on m3. Golpe Posse (1972, 1981) referred the species to the genus *Palaeochoerus*. Later, the material from El Canyet and Can Canals was included in *Aureliachoerus aurelianensis* by Hellmund (1992: 23). Indeed, dental and postcranial characters indicate without doubt that this taxon is a suid. Yet the lower cheek tooth morphology is markedly different from that of the type species *Aureliachoerus aurelianensis* and resembles the palaeochoerid condition: the lower male canine is slender; the morphology of the lower premolars is simpler than in *A. aurelianensis*, with no metaconid in the p4, no posterior accessory cusps in the p3, and asymmetrical p2 without anterior enamel bud. The buccal and lingual cusps of lower molars are not as closely apposed as in *A. aurelianensis* and the endometacristid is more reduced, without incipient endometaconulid. However, the small size of the second premolar in respect to the third one is a hyotheriine character (see part "Results and systematic implications").

The smallest Miocene European suids are usually referred either to *Albanohyus* Ginsburg, 1974 or to *Aureliachoerus*. A third genus, *Barberahyus* Golpe Posse, 1977, is considered to be a junior synonym of *Albanohyus* by Van der Made (1996a). The small suid from Béon 1 differs from *Albanohyus* by the following characters: 1) the male upper canine of *C. minus* presents only two enamel bands and has no trace of the ventral one, whereas in *Albanohyus* the morphology is derived with a fully developed ventral enamel band (MHNL LGr 6003, La Grive-Saint-Alban, MN7-8; Van der Made 1996a: fig. 3E); 2) the lower canine of *C. minus* is slender whereas in *Al. castellensis* (Golpe Posse, 1977), it is wide; 3) p2 is much smaller than p3 and p4, in contrast to what occurs in *Al. castellensis*; 4) the p4 of *C. minus* lacks a metaconid whereas it is developed in *Al. castellensis*; and 5) in m2-3, the two prefossids of the first lobe form a basin which is lacking in both *Albanohyus pygmaeus* (Deperet, 1892) and *Al. castellensis*.

The material from Béon 1 is similar to the small suid found in Can Canals and El Canyet but it cannot be referred to *Aureliachoerus* neither to *Albanohyus*. This statement, together with the results of the phylogenetic analysis (see part "Results and systematic implications" of the phylogenetic analysis), lead to the creation of a new genus.

Family PALAEOCHOERIDAE Matthew, 1924
Subfamily SCHIZOCHOERINAE Golpe Posse, 1972
Genus *Taucanamo* Simpson, 1945

Taucanamo grandaevum (Fraas, 1870)
(Figs 8: 5-10; 9: 1)

MATERIAL EXAMINED. — From the same individual: p4 (l), MHNT Béon AR SN 9; p4 (r), MHNT Béon AR SN 8; mandibular fragment with m1 (r), MHNT Béon AR SN 12; m1(l), MHNT Béon AR SN 11, mandibular fragment with m2-m3 (l), MHNT Béon AR SN 7; isolated cranio-dental elements: mandibular fragment with p1 (r), MHNT Béon F2 627; p2 (r), MHNT Béon AR SN 10; mandibular fragment with p3 (r), MHNT Béon E3 37; Cm (r), MHNT Béon E3 86; M2 (l), MHNT Béon AR SN 15 associated with M3 (l), MHNT Béon AR SN 17; cm (r), MHNT Béon SN 201; m2 (l), MHNT Béon AR SN 14; m3, MHNT Béon AR SN 13 (l); postcranial elements: astragalus (l), MHNT Béon 321; Béon 1, Montréal-du-Gers (MN4, SW France).

STRATIGRAPHICAL AND GEOGRAPHICAL RANGE. — Late early to late middle Miocene (MN4 to MN7-8) of Western Europe (Germany, France). *T. grandaevum* is not documented during the MN5 and MN6 zones.

COMPARATIVE DESCRIPTION

Upper dentition (Fig. 8: 9, 10)

The upper canine (MHNT Béon E3 86, Fig. 8: 9) is highly compressed, with slight torsion from the root to the tip and it only presents two enamel bands (i.e. the ventral one is lacking). The anterior edge is sharp, and its dorsal part does not present the groove that is present in Hyotheriinae. The posterior edge bears a sharps crest of enamel.

The occlusal outline of M2 is rectangular whereas it is more quadrate in *Chicochoerus* n. gen. (Fig. 8: 10a); the lingual wall of the tooth is not sloping laterally but is straight as in other species of *Taucanamo*. The associated M3 displays a reduced third lobe and a very small metacone. The lingual roots being absent, it is impossible to determine whether they were fused or not. However, considering the vertical orientation of the lingual roots and the vertical lingual wall of the crown (Fig. 8: 10b), it is likely that the lingual roots where also vertical and fused (suid roots in contrast flare outward and are separated, Fig. 8: 4b). The upper molars are smaller than in *T. sansaniense* and the M2 is slightly wider than that of *T. grandaevum* from Steinheim (Fig. 10E, F).

Lower dentition (Fig. 8: 5-8)

A partial mandible, split into several fragments, contains p4-m3 (MHNT Béon AR SN 9, MHNT Béon AR SN 8, MHNT Béon AR SN 12, MHNT Béon AR SN 11, MHNT Béon AR SN 7). The tooth enamel is smooth. The p1 is uniradiculate and caniniform, high and narrow-crowned (Fig. 8: 6). The p2 is a very simple tooth with a high straight cuspid sloping lingually, a short precristid and a low simple postcristid without differentiated accessory cusps (Fig. 8: 7). The posterior cingulum forms a small bud. The p4 is also very simple, with one major cuspid and a reduced incipient metaconid, erased after slight wear (Fig. 8: 8). There is no paraconid, the postcristid is short and low, and the posterior accessory cuspid is reduced compared to that of *Taucanamo sansaniense*. Anterior, posterior, and buccal cingula are weakly developed. The lower molar dimensions overlap the size range of *T. sansaniense* from Sansan (Fig. 10B-D), while the premolars are smaller and correspond to the size of *T. grandaevum* from Steinheim (type locality, MN7; Fig. 4A; Chen 1984). The cuspids are pointed and present sharp angles (Fig. 8: 5). On each lobe, the cuspids are well separated, with wide intermediate grooves. The lingual and buccal roots of each lobe are fused (Fig. 8: 5b). Buccal and lingual walls are continuously convex and there is no demarcation at the cervix. The preprotocristid is reduced in comparison to *Aureliachoerus*.

Postcranial elements

Astragalus (Fig. 9: 1): the astragalus MHNT Béon 321 is here referred to *T. grandaevum* by comparison with specimens from Sansan referred to *T. sansaniense* (specimens Sa 4632-38; 4640-44; 7802; 9319, 10749). Even if MHNT Béon 321 is wider (transverse diameter) than MHNT SN 4541 and MHNT SN 4540 (here attributed to *Chicochoerus minus* n. comb.), which recalls *Hyotherium*, the crest lining the medial border of the sustentacular facet is oblique in contrast to *Hyotherium*, and the sustentacular facet is convex in its dorsal part. The cuboid facet represents a small portion

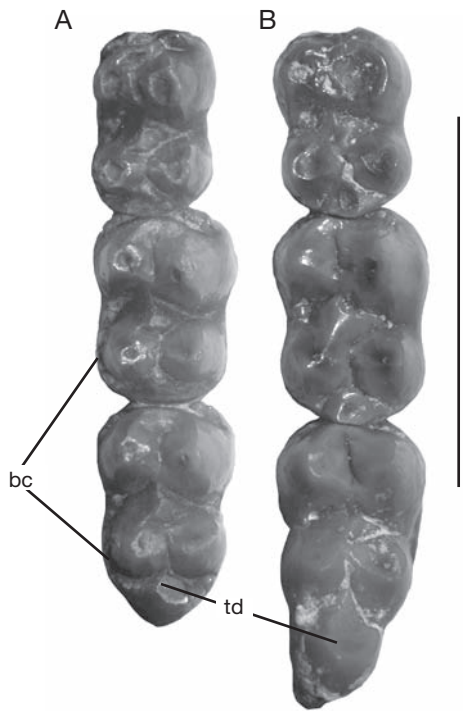

FIG. 11. — Comparison of the lower molars of: **A**, *Taucanamo primum* (holotype MNHN Ar 5); **B**, *Taucanamo grandaevum* from Béon 1 (Montréal-du-Gers, Gers, France) (MHNT Béon1 AR SN 7, SN 11). Abbreviations: **bc**, buccal cingulum; **td**, talonid. Scale bar: 2 cm.

of the distal trochlea. The P index (Dehm 1934) equals 30.6, i.e. less than in *Taucanamo sansaniense* from Béon 1 (P = 33.9) and from the type locality, Sansan (15 specimens, with values ranging from 32.7 to 36.5).

DISCUSSION

Colobus grandaevum from Steinheim (MN7, Germany) was named by Fraas (1870) and misidentified as a small primate. Subsequently, Stehlin (1899-1900) recognised that the specimens belong rather to Suidae and placed the material in *Choerotherium pygmaeum* (Depéret, 1892); Simpson (1945) moved *Choerotherium* Lartet, 1851 into the Tayassuidae and changed the generic name to *Taucanamo.* However, as noticed by Van der Made (1996a), the generic name *Choeromorus* Gervais, 1852 has priority over *Taucanamo*, but as *Taucanamo* has been widely used since 1945 (Ginsburg 1974; Pickford 1976; Pickford & Ertürk 1979; Chen 1984; Fortelius & Bernor 1990; Van der Made 1997a; Liu 2003), it will be applied here to promote nomenclatural stability as recommended by the *International Code of Zoological Nomenclature* (ICZN 1999: Art. 23). Depéret (1892) named the species *Choerotherium pygmaeum* for a small suoid from La Grive Saint-Alban (MN7-8; Isère, France), but Van der Made (1996a) demonstrated that the holotype belongs to the small suid genus *Albanohyus* erected by Ginsburg (1974) for the same material. However, the material from Steinheim as a whole can be referred to *Taucanamo* as a species different from the type species *Taucanamo sansaniense* (Chen 1984; Fortelius & Bernor 1990). The size difference between *T. sansaniense* from Sansan and the *Taucanamo* from Béon 1 is clear in the premolars and upper molars and slight in the lower molars (Fig. 10). Chen (1984) detailed the major differences between the material from Steinheim and Sansan, considered as two different species: the *Taucanamo* from Steinheim is slightly smaller; the P4 is less molariform; the upper molars are rectangular whereas in *T. sansaniense* they are quadrate; the Cm-P1 and P1-P2 diastemata are small; the talonid of p3 and p4 consist of an elevated cuspid with a clear elevated cingulum on the postero-external side; the talonid of m3 is shorter and simpler in *Taucanamo* from Steinheim. Later, Fortelius & Bernor (1990) suggested that *Taucanamo grandaevum* should be the valid name for the Steinheim material. In his revision of *Taucanamo*, Van der Made (1997a) agrees and extends the hypodigm of *T. grandaevum* to the material from La Grive and Anwill (MN7-8); he named *T. primum* for early material originating from MN4 localities (Artenay, Bézian, and Els Casots).

There is no question about *T. primum* being clearly different from *T. grandaevum*. On the one hand, the *Taucanamo* from Béon 1 and *T. primum* are not only coeval but also morphologically distinct: some clear morphological differences exist between the holotype from Artenay and comparable material from Béon 1: the lower molars are simpler in Béon 1, the cusps are smaller and more rounded in *T. primum*, the buccal cingulum is absent in

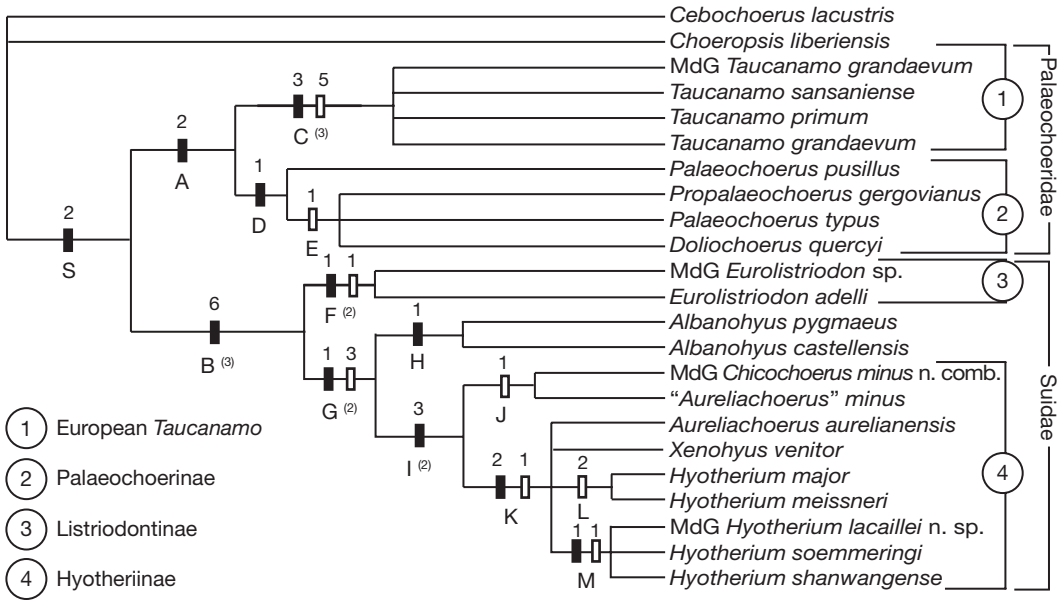

FIG. 12. — Phylogenetic relationships of the considered Suoidea: strict consensus of the 240 parcimonious trees (L = 72; Ci = 0.62; Ri = 0.86). Above black boxes figures the number of unambiguous synapomorphies, above the white boxes figures the number of ambiguous synapomorphies. Bremer support superior to 1 lies in brackets after the letter corresponding to the node.

Béon 1, and the pentaconid on m2-m3 is reduced in *T. primum* (Fig. 11). On the other hand, the *Taucanamo* from Béon 1 and *T. grandaevum* are distinct from a stratigraphical point of view, but very similar morphologically, thus justifying referring the Béon 1 material to *T. grandaevum*, and extending its stratigraphical range down to the middle Orleanian ELMA (MN4).

PHYLOGENETIC ANALYSIS

A phylogenetic analysis based on 44 dental, cranial, and postcranial characters was performed in order to define how small suoids from Béon 1 relate to other small European taxa. The present analysis is not intended to provide a complete picture of the phylogenetic relationships of the Suoidea. It rather supplies the basis for the systematics followed in this article. Some characters employed in this analysis were used by other authors in order to define specific/generic affinities of concerned taxa.

CHARACTER ANALYSIS

The outgroup includes the Eocene European dichobunoid *Cebochoerus lacustris* (Gervais, 1859) and the extant hippopotamid *Choeropsis liberiensis* (Morton, 1849). The four suoid taxa from Béon 1 were treated as terminal units to test their relationships with other Miocene European suoids. They are listed as "MdG *Eurolistriodon* sp. (Orliac in press)", "MdG *Hyotherium lacaillei* n. sp.", "MdG '*Chicochoerus*' *minus* (Golpe Posse, 1972) n. comb.", and "MdG *Taucanamo grandaevum* (Lartet, 1851)", "MdG" being intended for "Montréal-du-Gers".

Other suoids included in the analysis are:

– Hyotheriinae: *Hyotherium soemmeringi* (Meyer, 1829); *H. meisneri* (Meyer, 1829); *H. major* (Pomel, 1847); *Aureliachoerus minus* (Golpe Posse, 1972); *Aureliachoerus aurelianensis* (Stehlin, 1900); *Xenohyus venitor* Ginsburg, 1980. *Hyotherium shanwangense* Liu, Fortelius & Pickford, 2002 from the early middle Miocene of China (Liu *et al.* 2002) is also included in the analysis because of its morphological similarities with the *Hyotherium* from Béon 1;

– Cainochoerinae: *Albanohyus pygmaeus* (Depéret, 1892) and *Albanohyus castellensis* (Golpe Posse, 1977);
– Palaeochoeridae: *Palaeochoerus typus* Pomel, 1847; *P. pusillus* (Ginsburg, 1974); *Propalaeochoerus gergovianus* (Croizet *in* Blainville, 1846); *Taucanamo sansaniense* (Lartet, 1851); *T. grandaevum* (Fraas, 1870); *T. primum* Van der Made, 1997; *Doliochoerus quercyi* Filhol, 1882.

Although small Miocene suoids were once called "Old World peccaries", no extant peccary is included in the analysis. First, it is now accepted that these taxa do not belong to the Tayassuidae (Van der Made 1996a, 1997a; Liu 2003). Second, modern peccaries display convergent characters with Old World suids that could blur the whole phylogenetic image. For the selected characters, *Cebochoerus* and a hippopotamid display enough unambiguous primitive states for Suiformes that make the analysis of Miocene taxa meaningful (although, accordingly, non exhaustive).

Forty-four cranial, mandibular, and dental characters were controlled on these 23 terminal taxa. The data matrix consists of 42 binary and 2 unordered multistate characters (Appendix 3). Material and characters are listed in Appendices 1 and 2, respectively. Most characters are illustrated in Appendices 4 and 5.

The data were treated under the assumptions of unweighted parsimony, using PAUP 3.1 (Swofford 1993), with the exact "Branch & Bound" algorithm. The strict consensus of the 240 shortest trees (L = 70; CI = 0.65; RI = 0.87) is presented in Figure 12; only the unambiguous synapomorphies are listed and discussed hereafter. The distribution of character states at each node is detailed in a taxon/character matrix (Appendix 6).

Results and systematic implications

The phylogenetic analysis shows two main clades corresponding to the families Palaeochoeridae (clade A) and Suidae (clade B).

The clade A is defined by two non-ambiguous synapomorphies: the apex of the premolars is lingually recurved (12^1); the roots of the first lobe of lower molars are fused (14^0). Among Palaeochoeridae two clades can be recognised: the clade C, corresponding to the European representatives of *Taucanamo*, and the clade D corresponding to the Palaeochoerinae Matthew, 1924. The clade C is supported by eight unambiguous synapomorphies: the absence of metaconid on the p4 (5^1); the lack of postero-buccal basin on the p4 (8^1); lower molars bucco-lingually compressed (10^1); a premolar row longer than the molar row (13^1); a rounded P4 (28^1); a straight lingual wall on the upper molars (33^0); a mandible with a weak backwardly oriented coronoid process (35^1); a lack of canine flange (37^0). The relationships among *Taucanamo* are unresolved. The clade D, grouping *Propalaeochoerus*, *Palaeochoerus*, and *Doliochoerus* is defined by one non-ambiguous and non-homoplastic synapomorphy: the presence of a paraconid in the p4 (6^1) and corresponds to the Palaeochoerinae (Doliochoerinae Simpson, 1945).

The Suidae (clade B) are here supported by six non-ambiguous and non-homoplastic synapomorphies: there is a clear groove separating the prehypoconulid and the prehypocristid on the lower molars (18^1); the two cusps of each lobe of the lower molars are close to each other so that there is a demarcation between the cusps and the base of the crown (20^1); the ventral profile of the mandible widens posteriorly (34^1); there is a strong alveolar bulge on the buccal surface of the mandible, at the level of the m3 (36^1); the metapodials present a clear medial crest on the anterior surface of their distal trochlea (43^1) and the proximal surface of the Mc III bears a rounded posterior expansion (44^1). Among Suidae, the first offshoot (clade F) corresponds to *Eurolistriodon* and represents the Listriodontinae in this analysis as well. This clade is defined by a differentiation of an accessory cusp in the postprotocristid (4^1) and the unique shape of the crown of I1 with a metaconal part in the same plane as the paracone (22^1). The clade G includes both species of *Albanohyus* and Hyotheriinae on the basis of a lack of posterolingual basin on the p4 (8^1); a lack of p1-p2 diastema (9^1); a reduced groove separating the precristids (16^1) and a protoconule of the upper molar fused to the anterior cingulum (29^1). The monophyly of *Albanohyus* is here supported by one unambiguous synapomorphy: an important wear of the lingual surface of the I1 (23^1), this caracter state is also

found in *Cainochoerus*. The clade I represents the Hyotheriinae, and is defined by: p1 and p2 being of small size compared to p3-4 (2^1); the endocristids of the two anterior cusps of the m2-m3 being low and posteriorly oriented (19^1); and the presence of an antero-dorsal groove lining the anterior crest of the male upper canine (24^1).

Among Hyotheriinae, the genus *Aureliachoerus* is polyphyletic in its former content, i.e. including *A. aurelianensis* and "*A.*" *minus*. The species "*A.*" *minus* forms the clade J with "MdG *A. minus*" defined by one unambiguous synapomorphy: the presence of an internal basin of the first lophid of the lower molars (17^1). A monospecific genus is erected for the clade J: *Chicochoerus* n. gen.; the material from Béon 1 and Pellecahus is therefore assigned to *Chicochoerus minus* n. comb. *Chicochoerus* n. gen. is primitive in comparison to other European hyotheriines, including *A. aurelianensis*, as it lacks an accessory cusp in the p3 postprotocristid (4^1); a high and well developed postcristid in the lower premolars (11^1), and a wide endometacristid with incipient endometaconulid in the lower molars (15^1). The latter character state is found in *Hyotherium*, *Aureliachoerus aurelianensis*, and *Xenohyus*. Among the clade K, the species *H. soemmeringi*, *H. shanwangense*, and MdG *H. lacaillei* n. sp. form the clade M supported by a weak metaconid on the p4 (5^2) and by slender premolars (10^1). *H. lacaillei* n. sp. presents an original combination of characters with a P1 lingual to the CM alveolus (27^1) that justifies a separation at the specific level.

Other issues raised by the phylogenetic analysis

In the phylogenetic analysis performed by Liu (2003) the Palaeochoeridae appeared paraphyletic and the close relationship between *Taucanamo* and Palaeochoerids supported by Van der Made (1996a, 1997a) was rejected. *Palaeochoerus* was apart from the Schizochoerinae clade, i.e. (*Taucanamo* (*Schizochoerus*, *Yunnanochoerus*)), and shared a closer relation with other Suidae. In the present analysis, including the genera *Palaeochoerus*, *Propalaeochoerus*, and *Doliochoerus* as representatives of the Palaeochoerinae, the monophyly of the Palaeochoeridae is supported by two non-ambiguous and non homoplastic synapomorphies. It is noteworthy that the Palaeochoeridae are supported here contrary to Liu (2003). However, it is obvious that there are two taxonomic sample biases: the present analysis does not include *Schizochoerus* and *Yunnanochoerus* and the analysis of Liu (2003) did not include *Doliochoerus* and *Propalaeochoerus*. Yet, the scope of this paper was not defining the interrelationships of Suidae but highlighting some taxonomic aspects of small Miocene suoids from Europe. Further resolution of this systematic issue requires inclusion of representatives of the Asian (*Yunnanochoerus*, *Sinapriculus*, and *Eocenchoerus*) and African (*Cainochoerus*, *Kenyasus*) Miocene suids, as well as members of other subfamilies such as Tetraconodontinae and Suinae.

CONCLUSION

The revision of the small suoids from Béon 1 (Montréal-du-Gers, Gers, France) indicates the presence of two Hyotheriinae: *Hyotherium lacaillei* n. sp. and the small *Chicochoerus minus* n. comb. (Golpe Posse 1972) and of one member of the Palaeochoeridae, *Taucanamo grandaevum*. The new *Hyotherium* species, previously attributed to *H. soemmeringi*, differs from the latter by its globular upper P1-P2, by a P1 located lingually to the canine alveolus and by the lack of diastema between the first and second upper and lower premolars.

A new genus is erected for the species previously identified as *Aureliachoerus minus* present in the Spanish localities of Can Canals and El Canyet (Golpe Posse 1972), the Austrian localities of Oberdorf and Seegraben (Van der Made 1998), and the French localities of Béon 1 and Pellecahus. This genus, known throughout the Orleanian European Land Mammal Age (MN3-MN5), is defined by an asymmetrical p2 and by the presence of an internal basin in the first lophid of the lower molars. It is related to Hyotheriinae by p2 being of reduced size compared to p3-p4, a posterior orientation of the endocristids of the two anterior cusps of the m2-m3 and by the presence of an antero-dorsal groove lining the anterior crest of the male upper canine.

The locality of Béon 1 has yielded an original suoid faunal assemblage with two new species: *Eurolistriodon* sp. and *H. lacaillei* n. sp., closely related to the Spanish *Eurolistriodon adelli* and to the Chinese *Hyotherium shanwangense*, respectively. The suoid community of Béon 1 contains typical representatives of the middle Orleanian (MN4) *Chicochoerus minus* n. comb. and *Taucanamo grandaevum*.

Acknowledgements
We are grateful to all the persons who helped in the excavation of Béon 1, to the 380 students and teenagers who participated for 20 years in the field work. We are also grateful to the city of Toulouse, owner of the site and to Mr G. Bezerra, Mayor of Montréal-du-Gers, who discovered the first fossils at Béon 1. Many thanks to M. Philippe and D. Berthet (MHNL), A. Galobart Lorrente (IPS), S. Moyà Solà (IPS), P. Aurell i Garrido (IPS) for their help and access to collections and to P. Tassy (MNHN), and J. R. Boisserie (MNHN) for reading early versions of the manuscript. Many thanks to F. Escuiller for the lending of the hyotherine material from Grepiac. The two reviewers M. Pickford and J. Van der Made are thanked for constructive and thorough reviews of the manuscript. This work is supported by a MRT grant (ED 392) of the French ministère de la Recherche et de l'Enseignement supérieur.

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Submitted on 1st June 2006;
accepted on 5 October 2006.

APPENDIX 1

List of the taxa included in the phylogenetic analysis and of the corresponding checked material.

1. *Cebochoerus lacustris* (Gervais, 1859), skull and associated mandible (MNHN Qu 56-57), figured by Pearson (1927: text-figs 18-20, p. 413-415).
2. *Choeropsis liberiensis* (Morton, 1849), skull (MNHN 1982-10).
3. MdG *Hyotherium lacaillei* n. sp., material from Béon 1, Montréal-du-Gers, listed in the present article.
4. *Hyotherium major* (Pomel, 1847), material from Saint-Gérand-le-Puy (MNHN).
5. *Hyotherium soemmeringi* (Meyer, 1829), material from Georgensmünd figured by Meyer (1834: pl. II, fig. 9); material from Baigneaux-en-Beauce (MNHN); cast of the material from Sandelzhausen (BSPGM 1959 II 305), figured by Schmidt-Kittler (1971: pl. 11) and cast of the mandible BSPGM 1959 II 313.
6. *Hyotherium meisneri* (Meyer, 1829), material from Cetina de Aragon (Spain) figured by Van der Made (1994: pls 1-3, 4, 1-5, 7-13); material from Grépiac, private collections of F. Escuiller.
7. *Hyotherium shanwangense* Liu, Fortelius & Pickford, 2002, material from Shandong (China) figured by Liu *et al.* (2002: figs 4-6).
8. *Aureliachoerus aurelianensis* (Stehlin, 1900), material from Artenay (MNHN).
9. MdG *Chicochoerus minus* n. comb., material from Béon 1, Montréal-du-Gers, listed in the present article; the material from the contemporaneous locality of Pellecahus (Gers) is here associated to this taxa.
10. "*Aureliachoerus*" *minus* (Golpe Posse, 1972), material from El Canyet and Can Canals (IPS).
11. *Albanohyus pygmaeus* (Depéret, 1892), material from La-Grive-Saint-Alban (MHNL).
12. *Albanohyus castellensis* (Golpe Posse, 1977), material from Castell de Barberá (Spain) (IPS).
13. *Xenohyus venitor* Ginsburg, 1980, material from French localities of Faluns Savignéens of Anjou and Touraine, housed in the MNHN under the designation Fs.
14. MdG *Taucanamo grandaevum*, material from Béon 1, Montréal-du-Gers, listed in the present article.
15. *Taucanamo sansaniense* (Lartet, 1851), material from Sansan (MNHN).
16. *Taucanamo primum* Van der Made, 1997, type specimen from Artenay (Ar 5, MNHN).
17. *Taucanamo grandaevum* (Fraas, 1870), material from Steinheim (Germany), figured by Chen (1984: pl. 2, figs 4-6, pl. 3, figs 1-8); material from El Casots figured by Pickford & Moyá Solá (1994: figs 1-6); material from La Grive-Saint-Alban (MHNL).
18. *Propalaeochoerus gergovianus* (Croizet *in* Blainville, 1846), Gergovie (Puy-de-Dôme), holotype 4204, mandible Lim 518-519 (MNHN).
19. *Palaeochoerus pusillus* Ginsburg, 1974, Phosphorites du Quercy (MNHN); material from Germany figured by Hellmund (1992: pl. 4, figs 1, 2, pl. 5, figs 1-6, pl. 6, figs 1-8, pl. 7, figs 1-6, pl. 8, figs 1-5, pl. 10, figs 1-4).
20. *Palaeochoerus typus* Pomel, 1847, material from Saint-Gérand-le-Puy (MNHN); cast of the hemimandible figured by Hellmund (1992: pl. 2, fig. 1); material from Germany figured by Hellmund (1992: pl. 1, pl. 2, figs 1-3).
21. *Doliochoerus quercyi* Filhol, 1882, Phosphorites du Quercy (MNHN).
22. MdG *Eurolistriodon* sp., material from Béon 1, Montréal-du-Gers (Orliac in press).
23. *Eurolistriodon adelli* Pickford & Moyá Solá, 1995, material from Els Casots (IPS).

APPENDIX 2

List of characters used in the data matrix.

1. p1, shape: caniniform (0); premolariform (1) (character mentioned by Hellmund 1992).
2. p2, dimension of the tooth in comparison to p3-p4: slightly smaller (0); strongly reduced (1).
3. p2, shape of the tooth in lateral view: almost symmetric (0); clearly asymmetric with short/convexe anterior part and long/concave posterior part (1).
4. p3, differentiation of accessory cusps in the postcristid: absent (0); present (1).
5. p4, development of the metaconid: metaconid well developed and individualized (0); metaconid absent (1); metaconid weak (2).
6. p4, paraconid: absent (0); present (1).
7. p4, development of the preprotocristid: absent or very weak (0); important (1).
8. p4, lingual posterior basin: present (0); absent (1).
9. diastema between p1 and p2: present (0); absent (1).
10. Lower premolars, breadth: bucco-lingualy inflated (0); bucco-lingualy compressed (1).
11. Lower premolars, postprotocristid: low, which confers a concave profile to the distal part of the teeth (0); high, which confers to the tooth a roof shape in buccal view (1) (character to be considered on unworn teeth). This character has already been mentioned by Hellmund (1992: 18, in his comparison of *Dubiotherium* and *Hyotherium*).
12. Lower premolars, apex: straight (0); lingually sloping (1).
13. Cheek teeth, relative importance of premolar and molar: molar more developed than the premolars (0); premolars more developed than the molars (1). This character was mentioned by Van der Made (1996a).
14. Molar, roots: lower molars with mesial roots unfused and upper molars with buccal row unfused (0); lower molars with mesial roots fused and upper molars with buccal row fused (1). This character has already been mentioned by Ginsburg (1974) and Van der Made (1996a, 1997a).
15. m2-m3, endometacristid wide with incipient endometaconulid: absent (0); present (1).
16. m2-m3, groove separating the two anterior cusps, between the precristids: wide (0); narrow (1).
17. m2-m3, internal basin of the anterior lophid: absent (0); present (1).
18. m2-m3, groove separating the prehypoconulid and the hypoconid: absent (0); present (1).
19. m2-m3, endocristids of the mesial lobe: transverse and high (0); posterior and low (1).
20. lower molars, convergence of the protoconid and metaconid: absent (0): present (1). (This character is correlated with an inflexion of the crown delimiting the cusps from the base of the crown at the level of the lingual cusps).
21. I1, distal cusp: absent (0); present as a distinct cusp (1).
22. I1, shape of the crown: metacone situated in a lingual position compared to the paracone (0); metacone in the same plane as the paracone (1).
23. I1, abnormally important wear on the lingual surface: absent (0); present (1).
24. Upper canine, dorsal groove: absent (0); present (1).
25. Upper canine, ventral (or lingual) enamel band: absent (0); present (1); incipient (2).
26. P1-P2 diastema: present (0); absent (1).
27. P1, position of the tooth in respect to the upper canine: posterior to the canine (0); lingual to the canine (1).
28. P4, shape of the crown: wide bucco-lingualy (0); rounded (1).
29. Upper molars, protoconule: located in a distal position, between the two anterior cusps, integrated to the preprotocrista (0); located in a mesial position, intergrated into the mesial cingulum (1). This character has already been mentionned by Van der Made (1996a, b).
30. Upper molars, tetrapreconule: located mesial to the two posterior cusps (0); intercalated between the two posterior cusps, integrated into the prehypocrista (1).
31. M3, talonid: not developped as a distinct lobe (0); developped as a distinct lobe (1).
32. Upper molar, proportions: larger than long (0); longer than large (1).
33. Upper molar, lingual wall: straight (0); sloping (1).
34. Mandible, height of the horizontal ramus: reduced anterior to the vascular incisura (0); not reduced anterior to the vascular incisura (1).
35. Mandible, orientation of the anterior border of the the ascending ramus: subvertical (0); sloping posteriorly (1).
36. Mandible, infra alveolar bulge: absent (0); present (1).
37. Skull, canine flange: absent (0); present (1).
38. Skull, posterior border of the canine flange: bulged (0); not bulged (1).
39. Skull, postglenoid process: well developed (0); reduced (1).
40. Skull, external auditory meatus: open (0); closed (1).
41. Skull, outline of the occiput: trapezoid (0); contracted behind the auditory meatus (1).
42. Skull, posterior extension of the palate: anterior to the rear of the M3 (0); posterior to the rear of the M3 (1).
43. Metapodials, median crest extending onto the anterior surface of the distal articulation: absent (0); present (1).
44. Mc III, shape of the posterior process: sharp (0); rounded (1).

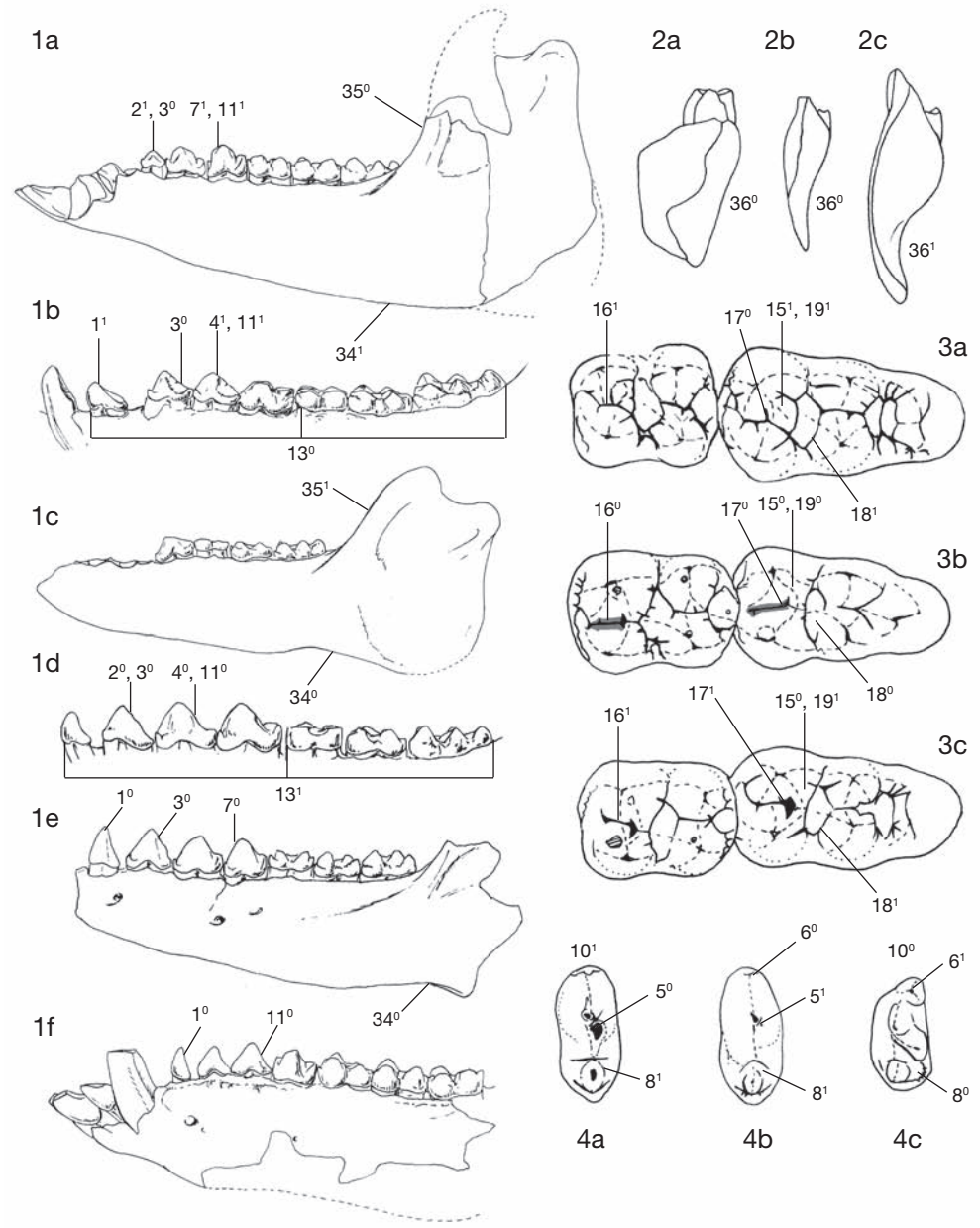
APPENDIX 3

Data matrix showing the distribution of 44 dental, cranial and postcranial characters among 23 taxa. "?" denotes unknown data and "-" refers to non applicable character.

Cebochoerus lacustris	100?0	0?000	?0-??	??000	????0	0000?	001?0	?0-00	00??
Choeropsis liberiensis	00000	00000	00000	0?-?-	-----	000--	10000	01000	0100
MdG *Hyotherium lacaillei* n. sp.	?1012	01111	10001	10111	10012	11010	?1110	1????	??11
H. major	11010	01100	10001	10111	?0012	01010	11110	1??11	1?11
H. soemmeringi	10012	01101	10001	10111	10012	00010	1111?	110??	????
H. meissneri	11010	01100	10001	1011?	00012	01010	1111?	?10??	?0??
H. shanwangense	11012	01101	10001	10111	10012	10010	111?0	?10??	?0??
Aureliachoerus aurelianensis	11010	01110	10001	10111	10012	?0010	11110	110??	?011
MdG *Chicochoerus minus* n. comb.	11101	01111	00?00	11111	???10	??010	1111?	1????	??11
"*Aureliachoerus*" *minus*	?????	?????	???00	11111	?????	??0??	?????	?????	????
Albanohyus pygmaeus	?????	????0	???00	1?101	00101	???10	111??	?????	??11
Al. castellensis	10000	00110	00000	10101	00101	10010	111??	1????	????
Xenohyus venitor	11?10	0?110	?00?1	10111	10???	??010	111??	?????	????
MdG *Taucanamo grandaevum*	00001	00101	01?10	00000	???00	???01	010??	0????	????
T. sansaniense	00001	00101	01110	00000	00000	10101	01001	00-01	1100
T. primum	00001	00101	01110	00000	?????	?????	?1?0?	0????	????
T. grandaevum	00001	00101	01110	00000	???00	001??	01001	00?01	11?0
Propaleochoerus gergovianus	0??00	1001?	010?0	11?00	?????	?????	???0?	0????	??00
P. pusillus	00??0	10000	01010	?0?00	00000	??001	001??	?????	????
Paleochoerus typus	00??0	10000	01010	1100?	000??	10001	00100	0110?	??0?
Doliochoerus quercyi	00000	10000	01010	11000	00000	10001	0010?	01101	?10?
MdG *Eurolistriodon* sp.	10010	01000	00000	00101	01001	00000	11110	11001	1111
E. adelli	10010	01000	00000	00101	01001	00000	11110	11001	1111

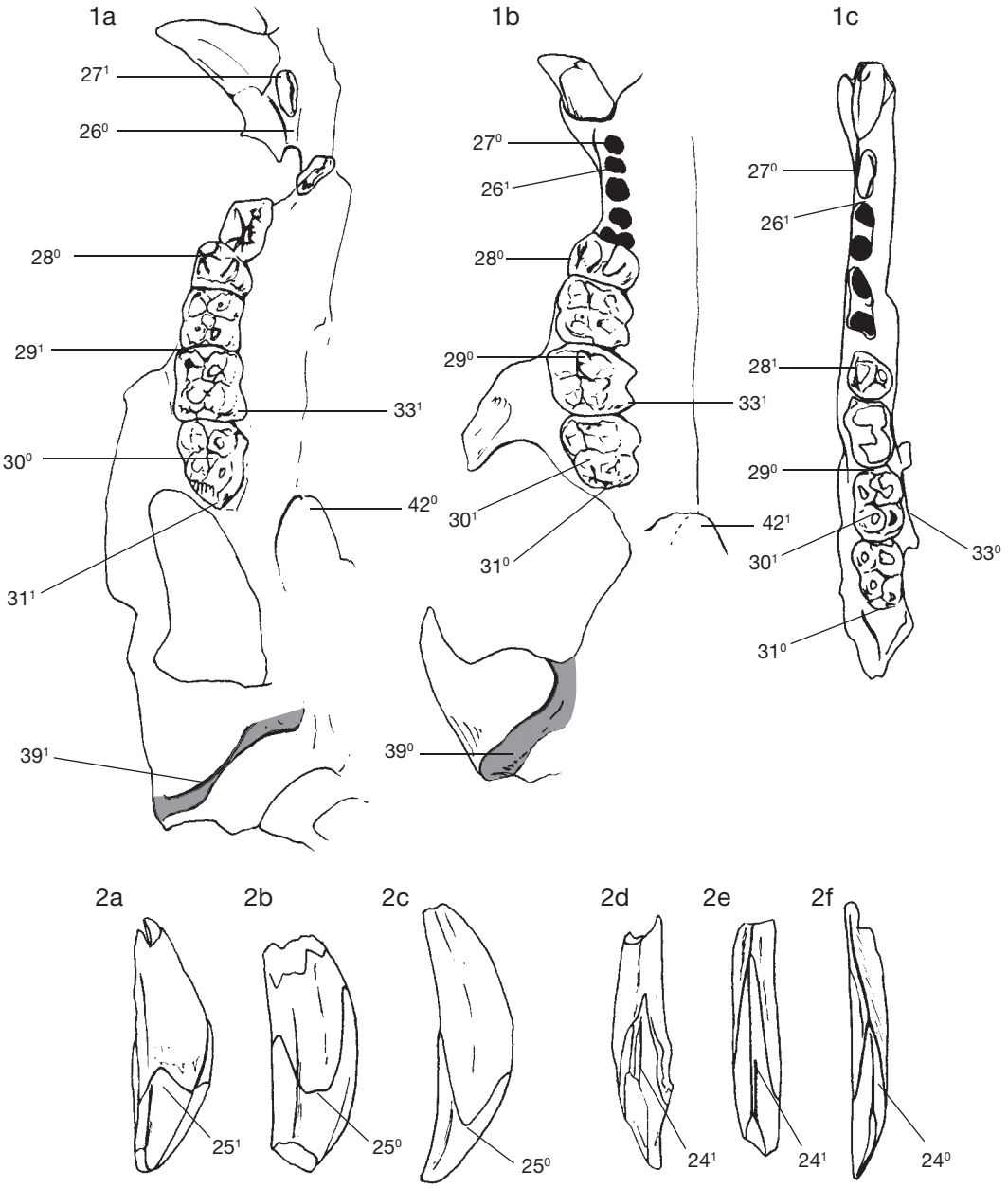
APPENDIX 4

Illustration of most of the characters from the mandible and lower dentition listed in Appendix 2: **1**, lateral view of the madibule of: **1a**, *Aureliachoerus aurelianensis* (reconstructed from the specimens MNHN Ar 2662, 2663, 2822); **1b**, *Hyotherium soemmeringi* (MNHN, cast 1959 II 313); **1c**, *Taucanamo sansaniense* (MNHN Sa 4661); **1d**, detail of dentition of *T. sansaniense* (MNHN Sa 4663); **1e**, *T. primum* (MNHN Ar 5); **1f**, *Doliochoerus quercyi* (MNHN Qu 16585a); **2**, posterior view of the left horizontal ramus of the mandible of: **2a**, *D. quercyi*; **2b**, *T. primum*; **2c**, *H. major* (MNHN SG 3305); **3**, structure of lower m2-m3 of: **3a**, *H. lacaillei* n. sp.; **3b**, *T. sansaniense*; **3c**, *Chicochoerus minus* n. comb.; **4**, occlusal view of p4 of: **4a**, *H. soemmeringi*; **4b**, *T. sansaniense*; **4c**, *D. quercyi*.



APPENDIX 5

Illustration of most of the characters from the skull and upper dentition listed in Appendix 2: **1**, occlusal view of skulls and partial maxillar of: **1a**, *Hyotherium major* (SMNS 44884); **1b**, *Palaeochoerus typus* (NHM 34961a); **1c**, *Taucanamo sansaniense* (MNHN Sa 4665); **2**, upper canine of: **2a**, **2d**, *H. major* (MNHN SG 3618); **2a**, lingual view; **2d**, anterior view; **2b**, **2e**, *Chicochoerus minus* n. comb. (MHNT Béon E3 894); **2b**, lingual view; **2e**, anterior view; **2c**, **2f**, *T. grandaevum* (MHNT Béon E3 86); **2c**, lingual view; **2f**, anterior view.



APPENDIX 6

Taxon/Character matrix. Reconstructed character states for internal nodes of the strict consensus figured in Figure 12. Character-state optimization = accelerated transformation (ACCTRAN). Length of the consensus = 72; Ci = 0.62; Ri = 0.86. Letters refer to the nodes of the Figure 12.

S	00000	00000	00000	00000	00000	10000	01100	01001	1100
A	00000	00000	01010	00000	00000	10001	01100	01101	1100
B	10000	01000	00000	00101	00001	10000	11110	11001	1111
C	00001	00101	01110	00000	00000	10101	01001	00101	1100
D	00000	10000	01010	10000	00000	10001	00100	01101	1100
E	00000	10000	01010	11000	00000	10001	00100	01101	1100
F	10010	01000	00000	00101	01001	00000	11110	11001	1111
G	10000	01110	00000	10101	00001	10010	11110	11011	1011
H	10000	00110	00000	10101	00101	10010	11110	11011	1011
I	11000	01110	00000	10111	10010	10010	11110	11011	1011
J	11101	01111	00000	11111	10010	10010	11110	11011	1011
K	11010	01110	10001	10111	10012	10010	11110	11011	1011
L	11010	01100	10001	10111	00012	01010	11110	11011	1011
M	11012	01101	10001	10111	10012	10010	11110	11011	1011