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Small suoids from the Miocene of Europe and Asia

Los suoideos de talla pequeña del Mioceno de Europa y Asia

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ABSTRACT

The history of study of small suoids from the Miocene of Eurasia is complex for several reasons: scarcity of fossil material, a high degree of dental convergence and parallelism between closely and distantly related lineages, and frequent misattribution of fossils, resulting in the gradual development of a confusing taxonomy. Changes in taxonomy above the genus level, have added to the complexity; European lineages classified in Suidae in 1924 are now arranged into three separate families; Suidae, Palaeochoeridae and Sanitheriidae. Recent studies have considerably clarified the situation, but there remain several problematic issues to resolve, especially among the Palaeochoeridae. The fossil register of some taxa is limited, so it is necessary to put on record newly recognised specimens in order to fill out our knowledge concerning them. This paper includes previously undescribed material of Palaeochoeridae and small Suidae, as well as reinterpretation of some fossils published in "obscure" scientific journals. The latter include some taxa that have priority over more recently proposed names. A systematic revision of these forms is carried out, and the paper ends with a proposal for a revised taxonomy of the Palaeochoeridae, a family that has recently taken on importance in the debate about the origins of Hippopotamidae.

Keywords: Suoidea, Palaeochoeridae, Suidae, Miocene, Eurasia, Taxonomy, Systematics

RESUMEN

La historia del estudio de los suoideos de talla pequeña del Mioceno de Eurasia es compleja por varias razones: la escasez de material fósil, un grado alto de convergencia y paralelismo dental entre linajes cercana y lejanamente relacionados, y la frecuente errónea identificación de los fósiles, teniendo como resultado el desarrollo gradual de una taxonomía confusa. Los cambios en la taxonomía por encima del nivel de género, han contribuído a esta complejidad; linajes europeos clasificados como Suidae en 1924 ahora se reparten en tres familias separadas; Suidae, Palaeochoeridae y Sanitheriidae. Estudios recientes han clarificado considerablemente la situación, pero quedan varios asuntos problemáticos por resolver, especialmente en el caso de los Palaeochoeridae. El registro fósil de algunos taxones es limitado, así que es necesario recopilar los especímenes actualmente reconocidos para completer nuestro conocimiento con respecto a ellos. Este trabajo incluye material no descrito previamente de Palaeochoeridae y pequeños Suidae, así como la reinterpretación de algunos fósiles publicados en revistas científicos poco accesibles. Entre estos últimos se incluyen algunos taxones que tienen prioridad sobre nombres propuestos recientemente. Se lleva a cabo una revisión sistemática de estas formas, y se finaliza con una propuesta de revisión taxonómica de Palaeochoeridae, una familia que ha tomado recientemente gran importancia en el debate acerca de los orígenes de Hippopotamidae.

Palabras clave: Suoidea, Palaeochoeridae, Suidae, Mioceno, Eurasia, Taxonomía, Sistemática

Introduction

The aim of this paper is to review the systematic status of the hypsorhizic Early Miocene palaeochoerids of Europe and the lophodont Middle and Late Miocene palaeochoerids and suids of Eurasia (Fig. 1, Table 1). It complements the studies of Hellmund (1992) on the bunodont late Oligocene to basal

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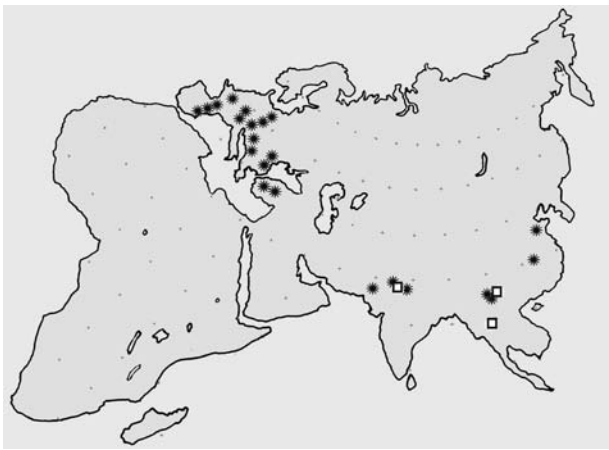

Fig. 1.—Distribution of lophodont Palaeochoeridae in Eurasia (black stars) and the suid *Lophochoerus* (squares). NB square symbol Southern China is based on fossils from Chinese Drug Stores (Von Koenigswald, 1963), so is approximate.

Miocene palaeochoerids of Europe, and the studies of Van der Made (1997a, 1997b, 1998, 2010) on the European Early and Middle Miocene palaeochoerids. There remain several important collections to study, including a fine sample of *Propalaeochoerus elaverensis* from the type locality Coderet, France.

It is noted that Palaeochoeridae have been linked to the origin of Hippopotamidae (Pickford, 2008) so a more complete understanding of the family is essential, particularly because some researchers consider that hippopotamids emerged from Anthracotheriidae (Boisserie *et al*., 2005).

Many suoid lineages possess bunodont dentitions, but there are several groups that developed highly lophodont cheek teeth independently from each other, resulting in a plethora of convergences, historically causing confusing between perissodactyls, primates and suoids. In most instances, the systematic and phylogenetic relationships of these lophodont lineages were initially misunderstood. In the case of the suid *Listriodon*, isolated molars were thought by early workers to belong to tapir-like perissodactyls (*Tapirotherium blainvilleanum* Lartet (1851), *Tapirus pentapotamiae* Falconer (1868)) until more complete fossils were found, which showed their suid affinities. Dental and mandibular remains of small palaeochoerids have on occasion been named after their resemblances to lemurs (*Sus lemuroides* Blainville, 1847, based on a mandibular symphysis of *Choeromorus sansaniense*, transferred to Pachysimia by Lydekker, 1884) or cercopithecids, as shown by the attribution of their fossils to *Colobus grandaevus* by Fraas (1870) and *Macaca youngi* by Gu Yumin (1980). When specimens of *Schizochoerus vallesensis* Crusafont & Lavocat (1954) were first described, they were interpreted to represent listriodonts (listed as *Listriodon* n?. gen. by Crusafont & Villalta, 1948), but Golpe-Posse (1972a, 1972b) realised that the species was so divergent from *Listriodon* that she erected a subfamily Schizochoerini, for it (see discussion in Van der Made, 2010, concerning the validity of this suprageneric name). The genus was transferred to Palaeochoeridae (at the time known as Old World Tayassuidae) by Pickford (1978). When specimens of *Namachoerus* Pickford (1995) were first described, they were interpreted to represent a small sanitheriid (*Xenochoerus moruoroti* Wilkinson, 1976) before being transferred to the listriodont genus *Lopholistriodon* (Pickford & Wilkinson, 1975) itself initially confused with a tapir (Aguirre & Leakey, 1974). When more complete maxillae and mandibles became available for study, they showed that, unlike *Lopholistriodon*, the species did not share the morphology of the skull with *Listriodon*; hence the decision to erect a separate genus, *Namachoerus*, and a separate subfamily Namachoerinae (Pickford, 1995) within the Suidae. When dental remains of *Anthraconema dangari* Prasad (1970) were first described, they were interpreted to belong to anthracotheres, until Pickford (1978) realised that this species showed strong resemblances to *Schizochoerus* (now *Schizoporcus*). Another lineage from the Indian subcontinent was initially thought to represent the palaeochoerid genus *Taucanamo*, but the material was later put into *Schizochoerus* (*S. gandakasense*) by Pickford (1978) because it was more lophodont than the former genus. In the same paper, Pickford (1978) transferred Prasad's species to *Schizochoerus* as the combination *Schizochoerus dangari* (Prasad, 1970). Han Defen (1983, 1985) first attributed small lophodont suoid teeth from Lufeng, Yunnan, to *Lophochoerus*, a small tetraconodont suid, but it was later realised that they represent a lophodont palaeochoerid for which Van der Made & Han (1994) erected the genus *Yunnanochoerus*. The latter authors did not discuss the status of Prasad's material from India (it is poorly illustrated) but it is now clear that the holotype and additional previously undescribed fossils from the type locality (Hari Talyangar, India) belong to the same genus and species. Thus *Yunnanochoerus* Van der Made & Han (1994) is a junior synonym of *Anthraconema* Prasad (1970). However, *Anthraconema* Prasad

Table 1.—**Distribution of lophodont Palaeochoeridae in Eurasia arranged by country (Vos *et al.*, 2007, recorded *Taucanamo*? / *Yunnanochoerus* at Kastelios Hill 2 (MN 9-10), Crete. The material basis for this listing seems not to have been published)**

Locality	Biozone	Age Ma	Taxon (this paper)	Reference
Hari Talyangar, India	MN 12	ca 7-8	*Yunnanochoerus dangari*	Prasad, 1970, this paper
Gandakas, Pakistan	MN 11	ca 9-8	*Yunnanochoerus gandakasensis*	Pickford, 1977
Chinji, Pakistan	MN 7/8	ca 12	*Pecarichoerus orientalis*	Colbert, 1933, this paper
Bugti, Pakistan	MN 4	ca 16	*Pecarichoerus sminthos*	Forster-Cooper, 1913
Paali D-C2, Pakistan	MN 4	ca 17	*Pecarichoerus sminthos*	Orliac *et al*., 2010b
Lufeng, China	MN 12	ca 7	*Yunnanochoerus lufengensis*	Van der Made & Han, 1994
Yuanmou, China	MN 13	ca 6	*Yunnanochoerus gandakasensis*	Qi *et al*., 2006; this paper
Sihong, China	MN 4	ca 16	*Pecarichoerus sminthos*	This paper
Xiaodian, China	MN 7	ca 16	*Pecarichoerus sminthos*	Gu Yumin, 1980
Chiang Muan, Thailand	MN 8	ca 11	*Pecarichoerus sminthos*	Pickford *et al*., 2004
Sinap, Turkey	MN 9	ca 10	*Schizoporcus arambourgi*	Ozansoy, 1965; Van der Made, 1997a
Yassiören, Turkey	MN 9	ca 10	*Schizoporcus vallesensis*	Ozansoy, 1965
Çandir, Turkey	MN 6	ca 13.5	*Pecarichoerus anatoliensis*	Van der Made, 1997a
Inönu, Turkey	MN 6	ca 13.5	*Choeromorus inonuensis*	Pickford & Ertürk, 1979
Paşalar, Turkey	MN 6	ca 13	*Choeromorus inonuensis*	Pickford & Ertürk, 1979
Nsebar, Bulgaria	MN 9	ca 10.5	*Schizoporcus vallesensis*	Nikolov & Thenius, 1967
Kalfa, Moldova	MN 9	ca 10.5	*Schizoporcus vallesensis*	Lungu, 1971, 1974
Münzenberg (Leoben) Austria	MN 5	ca 14.5	*Pecarichoerus orientalis*	Zdarsky, 1909; Van der Made, 1998
Göriach, Austria	MN 6	ca 13.5	*Pecarichoerus orientalis*	Van der Made, 1997a
Neudorf, Czech Republic	MN 6	ca 13.5	*Pecarichoerus orientalis*	Zapfe, 1983
Sandelzhausen, Germany	MN 6 (5)	ca 14	*Pecarichoerus orientalis*	Van der Made, 1998
Steinheim, Germany	MN 7	ca 12.5	*Choeromorus grandaevus*	Chen Guanfang, 1984; Fraas, 1870
Petersbuch 2, Germany	MN 4	ca 16	*Pecarichoerus primus*	Van der Made, 2010
Thannhausen, Germany	MN 6	ca 13.5	*Choeromorus inonuensis*	Van der Made, 2010
Anwil, Switzerland	MN 8	ca 12	*Choeromorus grandaevus*	Van der Made, 2010
Przeworno 2, Poland	MN 8	ca 12	*Choeromorus grandaevus*	Van der Made, 2010
Mala Miliva, Serbia	MN 5	ca 14.5	*Pecarichoerus orientalis*	Petronijevic, 1967
Prebreza, Serbia	MN 6	ca 14.5	*Pecarichoerus orientalis*	Pavlovic, 1969
Artenay, France	MN 4	ca 16	*Pecarichoerus primus*	Mayet, 1908
Bézian, France	MN 4	ca 15.5	*Pecarichoerus primus*	Ginsburg & Bulot, 1987

Table 1 *(continuation).*—**Distribution of lophodont Palaeochoeridae in Eurasia arranged by country (Vos *et al.*, 2007, recorded *Taucanamo*? / *Yunnanochoerus* at Kastelios Hill 2 (MN 9-10), Crete. The material basis for this listing seems not to have been published)**

Locality	Biozone	Age Ma	Taxon (this paper)	Reference
Sansan, France	MN 6	ca 13.5	*Choeromorus mamillatus*	Gervais, 1850
La Grive, France	MN 7/8	ca 12	*Choeromorus grandaevus*	Van der Made, 2010
Bonnefond, France	MN 7	ca 12.5	*Choeromorus inonuensis*	Van der Made, 2010
Castelnau d'Arbieu, France	MN 5	ca 14.5	*Choeromorus inonuensis*	Van der Made, 2010
Lavardens, France	MN 5	ca 14.5	*Choeromorus mamillatus*	Van der Made, 2010
Béon, (Montréal), France	MN 4	ca 15.5	*Choeromorus grandaevus*	Orliac *et al.*, 2006; Van der Made, 2010
Baigneaux en Beauce, France	MN 4	ca 15.5	*Pecarichoerus orientalis*	Van der Made, 2010
Els Casots, Spain	MN 4	ca 16	*Pecarichoerus primus*	Pickford & Moyà Solà, 1994
Bunõl, Spain	MN 4	ca 16	*Pecarichoerus primus*	Van der Made *et al.*, 1998
Viladecaballs (Can Purull, La Tarumba) Spain	MN 10	ca 10	*Schizoporcus vallesensis*	Crusafont & Lavocat, 1954

(1970) is pre-occupied by *Anthraconema* Zur Strassen (1904) a free living nematode, itself a synonym of *Siphonolaimus* De Man (1893). Thus *Yunnanochoerus* is the valid name for this genus of palaeochoerid.

In a seminal paper, Van der Made (1996) pointed out that small suids and palaeochoerids from the Miocene of Europe had for many years been confused with each other, partly due to their similar dimensions, but also due to superficial similarities in the occlusal morphology of their cheek teeth. He pointed out the features which distinguished the two groups from each other (notably cheek tooth radicular and crown morphology and some post-cranial characters) and provided a detailed list of localities at which the various species occurred, results which were recently extended by the same author (Van der Made, 2010). Nevertheless, there remain several residual problems concerning the nomenclature of the palaeochoerids in particular, which this contribution attempts to resolve.

The hypsorhizic palaeochoerids *Lorancahyus daamsi* and *Lorancahyus hypsorhizus* are extremely rare, each having previously been recorded from a single Spanish locality, but material from a second locality in France (MN 2) is described herein. The fossils indicate a possible descendant relationship from the basal Early Miocene lineage *Propalaeochoerus pusillus* (MN 1).

The Middle and Late Miocene lophodont palaeochoerid suoids of Europe and Asia have long been in need of taxonomic revision. The first described species from Asia was *Microbunodon sminthos* Forster-Cooper (1913, 1924) from Bugti, Pakistan, initially interpreted as an anthracothere. It was followed by *Pecarichoerus orientalis* Colbert (1933) from Chinji, Pakistan, interpreted as a peccary. Then came *Anthraconema dangari* Prasad (1970) from Hari Talyangar, India, thought by its discoverer to be an anthracothere (*Anthraconema* Prasad is a homonym of *Anthraconema* Zur Strassen, 1904). A genus name, *Yunnanochoerus* Van der Made & Han (1994) is available for this taxon. The fourth species described from Gandakas in the Potwar Plateau, Pakistan, was initially attributed to *Taucanamo gandakasense* Pickford (1977) and then to *Schizochoerus*. The fifth described species was "*Macaca*" *youngi* Gu Yumin (1980) from Xiaodian, Hubei, China, initially thought to be a monkey, which was followed by the sixth, *Yunnanochoerus lufengensis* (Han, 1983) from Lufeng, Yunnan, China. More complete material of *Yunnanochoerus dangari* from the type locality (Hari Talyangar, India) described herein reveals that the Late Miocene Asian species are comfortably accommodated within a single genus, for which the genus name with priority after taking into account the homonymy of *Anthraconema* Prasad (1970) is *Yunnanochoerus*. Middle

Miocene *Pecarichoerus orientalis* is so similar in morphology and dimensions to *Schizoporcus muenzenbergensis* (Van der Made, 1998; Orliac *et al*., 2010b) that I consider the latter to be a synonym of the former. *Yunannochoerus* differs from *Pecarichoerus* (including the Asian material of what used to be called *Schizochoerus*) in possessing molar lophids that are further apart, and it has more enlarged, elongated premolars and a p/4 with one main cusp (Van der Made & Han, 1994). *Yunnanochoerus* is a lophodont Palaeochoeridae, probably descended from a slightly more bunodont form such as *Choeromorus grandaevus*, whereas the *Schizoporcus* lineage is more likely to have been derived from a separate bunodont lineage such as *Pecarichoerus primus*.

A tooth from Chiang Muan, Thailand previously attributed to *Pecarichoerus sminthos* is here attributed to the small suid species *Lophochoerus nagrii*, and a mandible from Przeworno, Poland initially attributed to *Taucanamo* is identified as the small suid *Albanohyus*. In order to augment our understanding of European suids, other material from various sites is included and fossil material previously published in "obscure" scientific journals is re-illustrated to make them more accessible to Western scholars.

A revised taxonomy of Neogene Palaeochoeridae ends the paper.

Materials and methods

Dental nomenclature is based on Pickford (1978, 1988). Lower molars are abbreviated to m/1, m/2 and m/3 for the first, second and third teeth respectively, upper molars are M1/, M2/ and M3/, likewise for premolars where p/1 or P1/ are used.

In the synonymy lists I have been guided by Matthews (1973). The year of publication to the left of the taxon can be in italic (*2010*) which implies a mention of the species but without description or illustration, or in roman (2010) which implies that the work contributes to our knowledge of the species. The year can be preceded by an asterisk (*1992) meaning that publication of a name in this work can be regarded as valid in terms of the ICZN, earlier mentions of the name are to be regarded as nomina nuda, or by lower case letter 'v' (vidimus: v1992) meaning that I have seen the specimens mentioned in the paper, and a lower case 'p' (partim: p1870) meaning that the reference applies only in part to the species (on occasion referred to as a 'gryphon' taxon (Van der Made, 2010)).

The geochronology of the species mentioned herein is based predominantly on the European Land Mammal Zonation (Mein, 1990; Rössner & Heissig, 1999) (MN Zones) some of which have been correlated to Asia (India, China). Most authors agree about the position of most of the localities within this zonation, but there are a few localities such as Castelnau d'Arbieu and Sandelzhausen which are positioned in different zones by different authors. For these cases I have taken the estimates published in Rössner & Heissig (1999).

Abbreviations

BSPG – Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany; CMu – Chiang Muan, Thailand; FSL – Faculty of Science, University of Lyon: GSI – Geological Survey of India, Calcutta; GSP – Geological Survey of Pakistan, Quetta; IPS – Institut Paleontologic Sabadell, Spain; IVPP V – Vertebrate collection, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; MNCN – Museo Nacional de Ciencias Naturales, Madrid; MNHN – Muséum National d'Histoire Naturelle, Paris; MTA – Maden Tetkik ve Arama, Ankara, Turkey; NHM - Natural History Museum, London; PDYV – Yunnan Institute of Archaeology, China; SG – St Gérand-le-Puy; SLJG – Steiermärkisches Landesmuseum Joanneum, Graz, Austria; SMF – Senckenberg Museum, Frankfurt; SMNS – Staatliches Museum für Naturkunde in Stuttgart; TGPI – Institut Pedagogique de l'Etat de Tiraspol; Yas – Yassiören, Turkey.

Systematic Descriptions

Family Palaeochoeridae Matthew, 1924
Genus *Lorancahyus* Pickford & Morales, 1998
Species *Lorancahyus daamsi* Pickford & Morales, 1998

Material: MNHN SG 3603, right mandible from St Gérand-le-Puy, France.

Description: MNHN SG 3603 is a right mandible containing worn p/3-p/4 and m/2, with the alveoli of the canine, p/1-p/2, and m/1 and the mesial part of the alveolus of m/3. There are several unusual features about this specimen. There are short diastemata between the canine, p/1, p/2 and p/3. The p/1 and p/2 are small teeth so that the distance between the rear of the canine alveolus and the front of the p/3 is only 14 mm, which is extremely short in a suoid context. The jaw is also quite slender and gracile, even at the level of the m/2.

There is a prominent mental foramen located about 1/3 of the depth of the jaw beneath the alveolar margin at p/1 level. There are several other nutritive foramina, one behind the mental foramen, and four others lower down the jaw beneath p/3, p/4, m/1 and m/2. In ventral view, the base of the mandible is sharp-edged from the genial fossa back to the level of the p/4, after which it is rounded. The depression that occurs above this sharp edge extends from the genial fossa back toward the lingual fossa beneath the molars. The broken section of the mandible at the rear of m/2 shows the presence of a large mandibular canal occupying almost half the height of the mandible.

The mesial and distal roots of m/2 are solidly fused well beneath cervix, although the alveolus of m/1 indicates that its mesial and distal roots were separated from about cervical level. In all three molars the buccal and lingual roots were fused throughout their height, as in Palaeochoeridae in general.

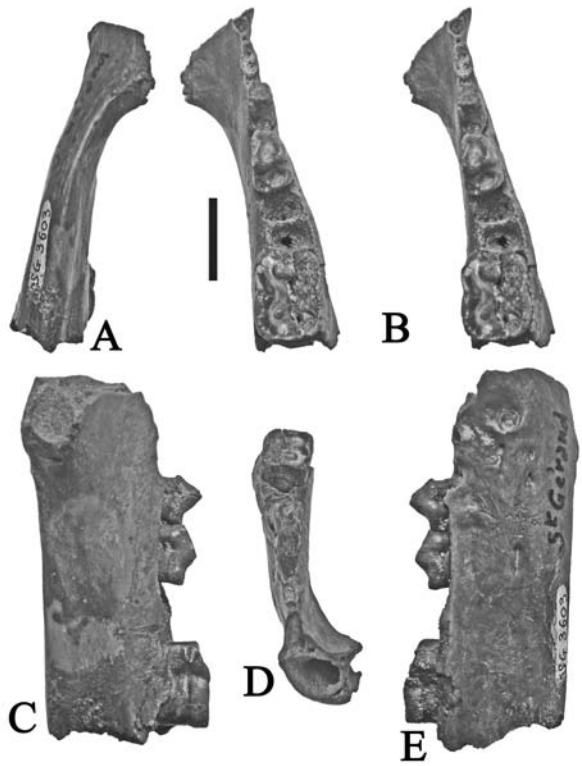

Fig. 2.—MNHN SG 3603, right mandible containing p/3-p/4 and deeply worn m/2, plus alveoli of canine, p/1-p/2 and m/1, *Lorancahyus daamsi*, A) ventral, B) stereo occlusal, C) lingual, D) anterior oblique and E) buccal views (scale bar : 10 mm).

The canine alveolus is deep, extending as far back as the genial fossa and it is slightly tilted laterally, and this causes a swelling in the lateral profile of the mandible mesial to the p/1. The p/1 was simple rooted, but the p/2 possessed two roots that were fused throughout their height.

The p/3 is worn to the stage where little morphology remains, but it is possible to discern that it has a single main cusp behind which is an expanded distal part showing a low disto-buccal cusplet. The p/4 is deeply worn, but it had a lingual cusp (protoconid) close to the buccal main cusp, as shown by a shallow groove on the lingual side of the crown. There was a prominent disto-buccal cuspid, and on its lingual side a shallow distal shelf. The m/2 is deeply worn to the stage where the crown has almost disappeared, leaving just a ring of enamel surrounding a large dentine lake. The dentine lake shows secondary dentine infilling what used to be pulp cavities, a phenomenon that characterises many palaeochoerids such as *Propalaeochoerus, Lorancahyus*, and *Palaeochoerus*, which endure heavy wear on the cheek teeth.

Discussion: The m/2 dimensions in the mandible MNHN SG 3603 are similar to those in a mandible (SMNS 20272) of *Propalaeochoerus pusillus* from Tomerdingen, Germany, described by Hellmund (1992, pl. 4, fig. 1) but the anterior part of the mandible containing the premolars and canine is considerably shorter than in *P. pusillus*. The planum alveolare is steeper in the St Gérand-le-Puy specimen than in the Tomerdingen one, which indicates a much shorter muzzle in SG 3603 than in the German specimen. Lower molars of *Propalaeochoerus pusillus* from Tomerdingen, show precocious development of root fusion in the m/3 (Hellmund, 1992, pl.10, fig. 3), especially the roots beneath the entoconid, hypoconid and hypoconulid, but there remains a slit between these roots and the one beneath the protoconid - entoconid cusp pair. These specimens suggest a possible ancestor – descendant relationship between *Propalaeochoerus pusillus* (MN 1) (Hellmund, 1992) and *Lorancahyus daamsi* (MN 2a) (Pickford & Morales, 1998).

Van der Made (2010, p. 114) wrote that the type material of *Lorancahyus daamsi* may well represent the same species as *Palaeochoerus typus*. The St Gérand-le-Puy specimen indicates that this possibility can be rejected. The differences in mandibular morphology are too great for them to be classified in a single species, even if the molar morphology is somewhat comparable.

The original description of *Lorancahyus daamsi* was based on material from a unique site at Moheda in Spain correlated to MN 2a (Pickford & Morales, 1998). The mandible from St Gérand-le-Puy housed at the Muséum National d'Histoire Naturelle is comparable in dimensions and morphology to the holotype from Moheda. The discovery of this species in France enlarges its known distribution and confirms the biochronological correlation between the two sites.

Species *Lorancahyus hypsorhizus* Pickford & Morales, 1998

Material: FSL, right mandible fragment containing m/2-m/3, distal left humerus, left talus.

Description: The right mandible of *Lorancahyus hypsorhizus* (Fig. 3) housed at the University of Lyon was found at St Gérand-le-Puy, France. The jaw contains moderately worn m/2 and m/3. The roots of m/2 and m/3 are solidly fused from side to side and from mesial to distal, the crowns are simplified with the valleys close together, and in the m/3 there is strong backward flare of the hypoconulid and third root. The mesial and distal fovea would have been small and shallow, having been eradicated even in slightly worn teeth. The lingual and buccal notches are narrow but deep. The third root of the m/3 is solidly fused to the first and second ones. Measurements are provided in Table 2.

From the same site there are a distal left humerus and a left talus (Fig. 3C). The humeral articulation is 14.6 mm in mediolateral diameter, and the total breadth of the distal end is 15.4 mm. The capitulum is swollen, almost ball-like and the lateral crest is low but sharp. The supracondylar fossae are deep on both the posterior and anterior aspects with perforation between them. This morphology indicates the probability of extreme flexion and extension movements in the elbow joint of *Lorancahyus*, while the ball-shaped zona conoidea and the sharpness of the lateral and medial crests indicate a strongly stabilised joint.

The talus has an extremely broad navicular facet (Fig. 3C2), as is usual in palaeochoerids and tayassuids, unlike the narrower facet that occurs in suids, anthracotheres and hippopotamids. In posterior aspect it has the characteristic bent shape that is found in Suiformes. The external length is 23.6 mm, internal length – 22.6 mm, proximal breadth – 11.2 mm, distal breadth – 13.0 mm.

Table 2.—**Measurements (in mm) of the teeth of *Lorancahyus hypsorhizus* (FSL and LO) and *Lorancahyus daamsi* (MOH and SG) (+ = measurements are provided for the alveolus of m/1, the crown would be somewhat larger than these measurements)**

Catalogue	Tooth	Mesio-distal breadth	Bucco-lingual breadth	Data source
FSL	m/2 right	10.5	8.7	Own
	m/3 right	15.3	8.9	
MNCN LO 3862	m/2 right	10.4	8.4	Pickford & Morales, 1998
	m/3 right	12.4	7.9	
MNCN LO 3864	m/1	10.0	7.0	Pickford & Morales, 1998
MOH 16	m/2 left	10.2	10.0	Pickford & Morales, 1998
MNHN SG 3603	p/3 right	7.1	3.9	Own
	p/4 right	8.2	5.3	
	m/1 alveolus	8+	6+	
	m/2 right	11.6	9.0	

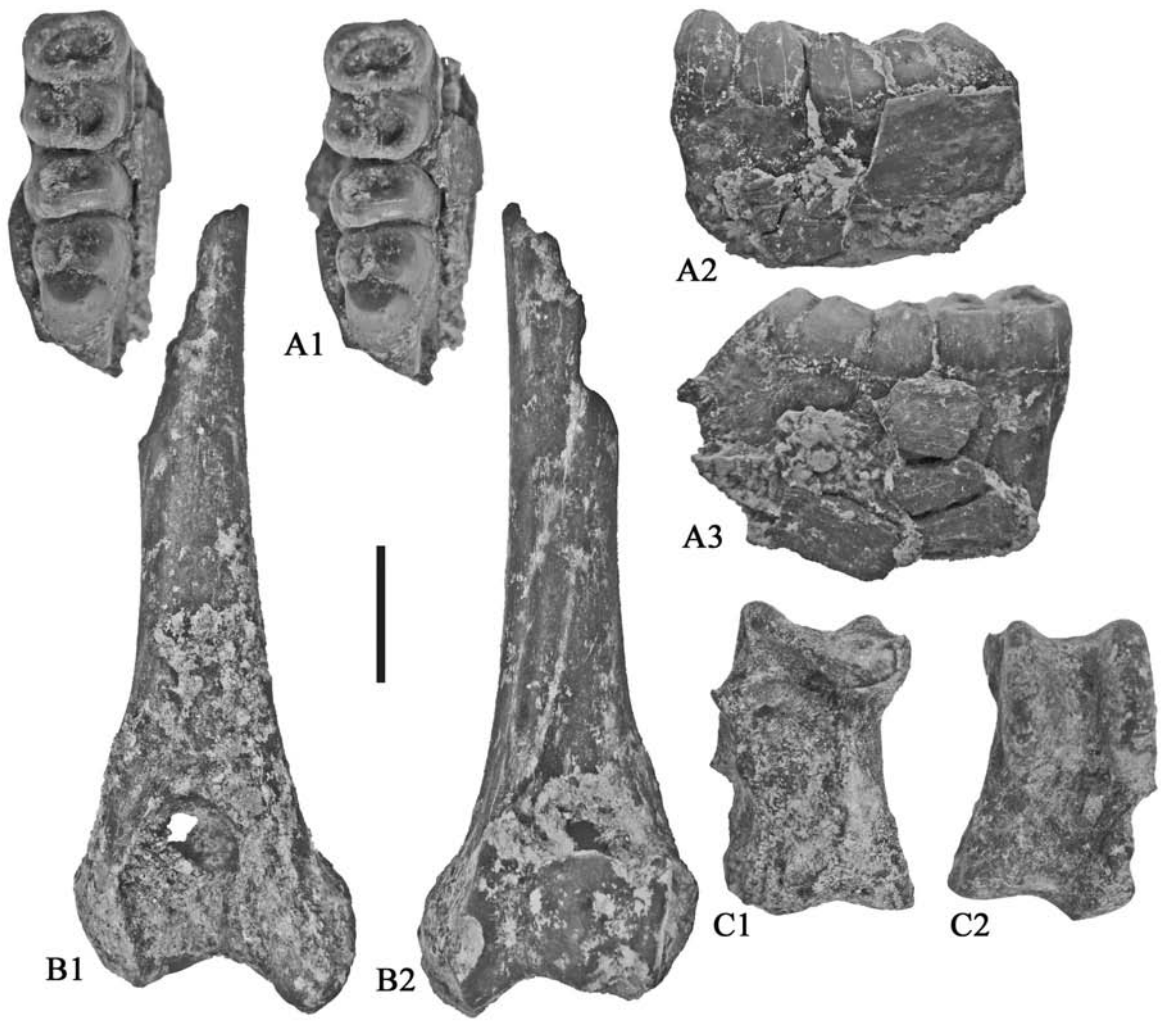

Fig. 3.—*Lorancahyus hypsorhizus* from St Gérand-le-Puy, France. A) right mandible containing m/2 and m/3, A1) stereo occlusal, A2) lingual and A3) buccal views; B) distal left humerus, B1) posterior, B2) anterior views, C) left talus, C1) posterior, C2) anterior views (scale bar : 10 mm).

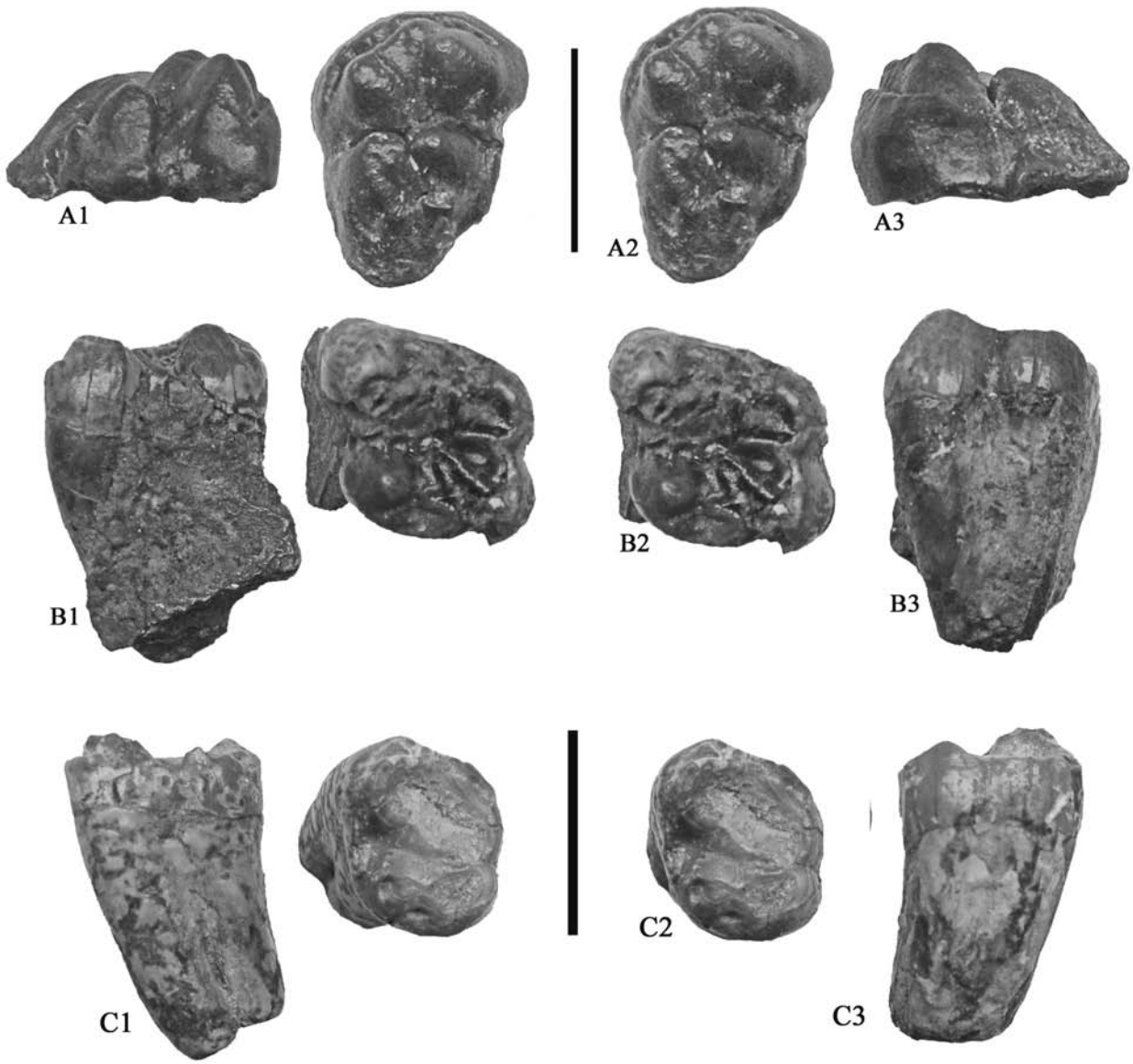

Fig. 4.—A) MNCN 35306, rootless left M3/ from Cetina de Aragon, Spain, attributed to *Propalaeochoerus* cf *pusillus*. The cusps are more crowded and puffier than is the case in upper molars of *Lorancahyus hypsorhizus* (B, C) but the tooth is compatible in dimensions with this taxon (scale : 10 mm).

Discussion: Van der Made (2010, p. 114) suggested that *Lorancahyus hypsorhizus* is related to what he called *Propalaeochoerus* sp. A. from Cetina de Aragòn (Van der Made, 1994) and problematic material from Navarette (Van der Made, 1990). The only palaeochoerid tooth from Cetina is a rootless upper third molar (12.7 x 11.6 mm) which makes comparisons with the Loranca and St-Gérand fossils difficult. At first view, the suggestion by Van der Made (2010) is not impossible, however, as isolated, worn upper molars from Loranca measure 10 x 10.5 mm and 9.7 x 8.6 mm respectively (Pickford & Morales, in Pickford, 1993) compatible in dimensions with the Cetina M3/. The main difference between the upper molar from Cetina de Aragon and the intermediate upper molars from Loranca is that in the latter specimens the cusps are more isolated from each other and less voluminous, unlike the crowded puffy cusps that occur in the specimen from Cetina (Fig. 4). From this it is concluded that the Cetina tooth does not belong to *Lorancahyus* but to *Propalaeochoerus* cf *pusillus*.

The specimens from Navarette consist of a maxilla with canine in situ and alveoli of P1/ and P2/ separated by a short diastema (7mm). There is a very short gap between the canine and the P1/ alveolus (2 mm). The canine is bucco-lingually compressed, is implanted vertically in the maxilla and has a vertical mesial wear facet. The maxilla is swollen above and behind the canine, forming a canine boss, with a niche mesially

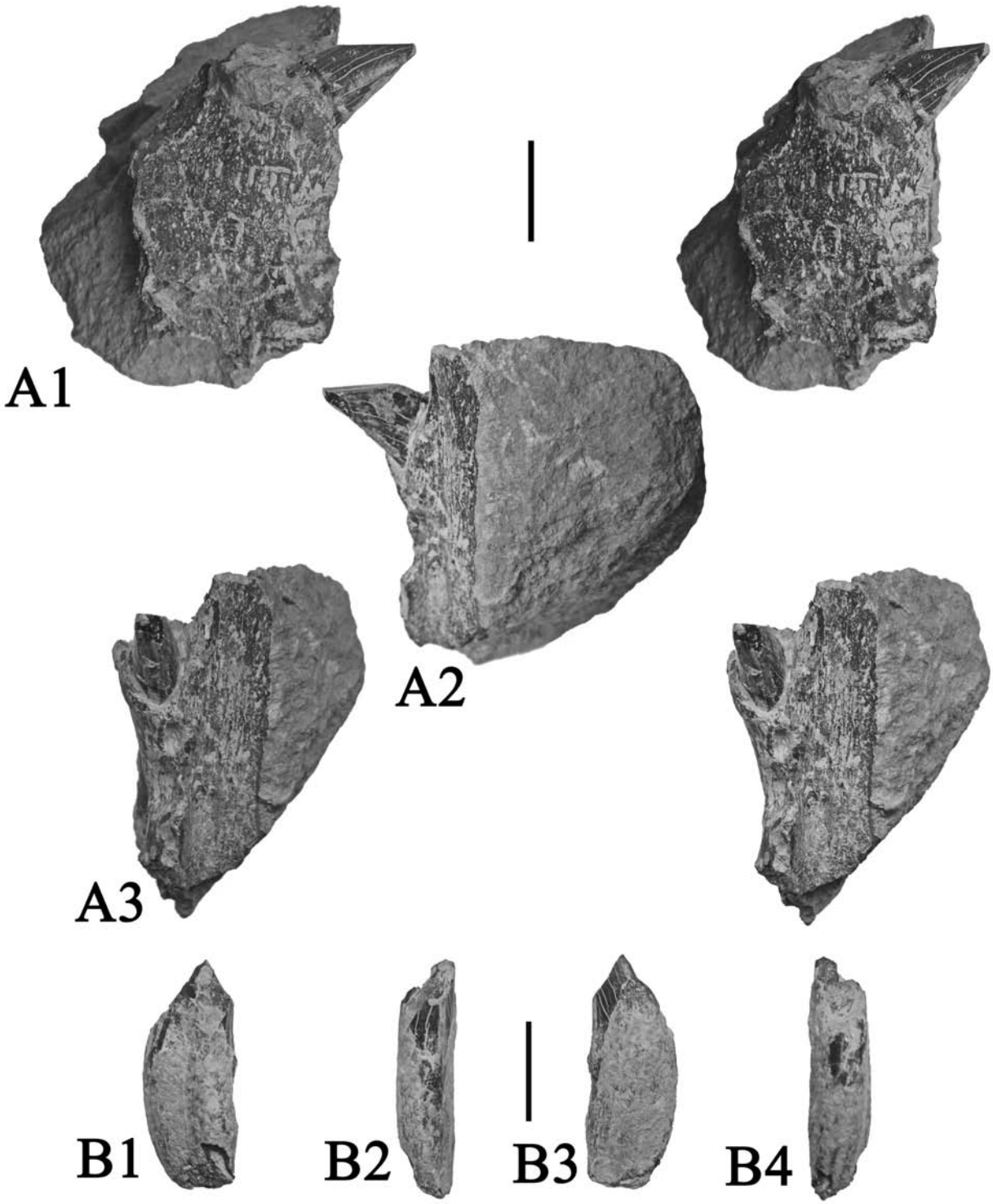

Fig. 5.—Small palaeochoerid from Navarette, Spain - A) right maxilla containing the canine; A1) stereo buccal, A2) lingual and A3) stereo occlusal views; B) left upper canine, B1) lingual, B2) distal, B3) buccal and B4) mesial views. (Scale : 10 mm).

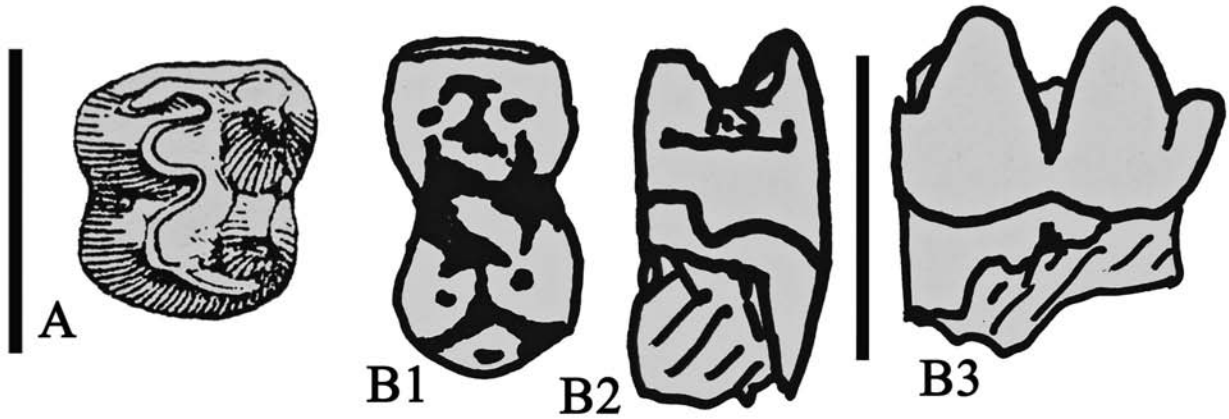

Fig. 6.—*Pecarichoerus sminthos* from China. A) holotype left upper molar of *Macaca youngi* from Xiaodian, Hubei, occlusal view (from Gu Yumin, 1980); B) right m/1 or m/2 of *P. sminthos* from Sihong, China, stored in the IVPP, Beijing, B1) occlusal, B2) mesial and B3) lingual views (scale bars: 10 mm).

for the lower canine. The lateral surface of the maxilla has a prominent depression above the P2/. The inter-maxillary suture is preserved and measurements of the specimen indicate that the inter-canine palatal breadth was ca 18 mm. There is a prominent palatal groove running from mesial to distal alongside the tooth row, as in *Schizoporcus arambourgi* (Fig. 11) and the surface of the bone on the lingual side of the groove shows low transverse ridges or swellings which make for an undulating rather than a flat palatal surface.

The canine in the maxilla measures 7.5 x 5.3 mm (md x bl) and has 9.7 mm of exposed crown height. The isolated canine measures 8.8 x 5.6 mm (md x bl) but the total height cannot be ascertained due to damage to the apex. It shows a clear distal crest and in both canines the enamel is thin.

The Navarette suoid specimens are interesting, but without knowledge of the premolars and molars it is not possible to suggest a convincing identification other than that they represent palaeochoerids.

Genus *Pecarichoerus* Colbert, 1933
Species *Pecarichoerus sminthos* (Forster-Cooper, 1913)

Material: Isolated lower molar from Shanwang, China housed in the IVPP, Beijing (Li *et al*., 1984); isolated upper molar from Xiaodian, China (Gu Yumin, 1980).

Description: Pecarichoerus was listed in the fauna from the Shanwang Formation (Hsiehchiao (Xiacaowan)) by Li *et al*., (1984). A lightly worn lower molar from Sihong (Fig. 6b) housed in the IVPP, Beijing is provisionally attributed to this species. The tooth consists of four, tall pointed cusps arranged in two pairs, accompanied by a well formed centrally positioned hypoconulid. The roots beneath each lophid are fused medio-laterally and in lateral view are close together. There is a tiny basal pillar in the median transverse valley between the protoconid and hypoconid. The metaconid shows a weak zygodont cristid. The mesial cingulum is not attached to the anterior accessory cusplet. The precristids of the protoconid and metaconid fuse with the anterior accessory cusplet, enclosing a mesial fovea. The postcristids from the protoconid and metaconid meet in the midline of the tooth to close off the rear of the mesial fovea. The sagittal valley between the protoconid and metaconid is deep. The metaconid has a centrally directed cristid that swells basally to form a small cuspid that partly blocks the mesial fovea. The precristid of the hypoconid joins a low median accessory cusplet which partly blocks the median transverse valley. The entoconid is isolated at its apex and, like the hypoconid, shows weak Fürchen. The sagittal valley between the hypoconid and entoconid is deep. The hypoconulid overhangs the cervix distally. The cusps are tall relative to the occlusal dimensions of the tooth (8.4 mm tall at the metaconid which is greater than the breadth of the tooth, 7.1 mm at metaconid).

The upper molar from Xiaodian, China, holotype of *Macaca youngi*, is a small tooth with moderately worn lingual cusps and unworn buccal ones (Fig. 6a). The mesial cingulum is broad bucco-lingually and narrow mesio-distally. The buccal cusps are isolated from the lingual ones until near their bases. The protocone has a prominent obliquely oriented preprotocrista and the hypocone has a strong obliquely directed precrista that reaches the protocone and an oblique postcrista that extends to the rear of the metacone. The buccal cusps are distinctly smaller than the buccal ones, as in the type species from Chinji.

Discussion: The Xiaodian tooth is not that of a cercopithecid as thought by its describer (Gu Yumin, 1980) but is from a palaeochoerid. As an M1/ it has the right dimensions to belong to *Pecarichoerus orientalis* of which the M1/ is unknown (the supposed M1/ described by Colbert, 1933, is in fact the M2/). As an M2/ the Xiaodian tooth has comparable dimensions to *Choeromorus grandaevus* which is similar to *Pecarichoerus sminthos* (Forster-Cooper, 1913) from Bugti, Pakistan (Pickford, 1987). Given that its meristic position is unknown it is here referred with some doubt to *Pecarichoerus sminthos*. Previously, Pickford (1987) considered that the fossils from Bugti, Chinji and Hubei could belong to a single species, but with the better samples now available, especially those from Europe (Van der Made, 2010), it is clearer that the bulk of palaeochoerid fossils from Bugti, Chinji, Sihong and Xiaodian belong to a species smaller than *Pecarichoerus orientalis*, although the

Table 3.—**Measurements (in mm) of the upper molars of Eurasian Palaeochoeridae**

Catalogue	Tooth	Mesio-distal length	Bucco-lingual breadth	Data source
GSI K16/341 Chinji, Pakistan	M3/ left	13.4	10.4	Own, 2007
AMNH 29955 Chinji, Pakistan	P4/ right M2/ left M3/ left M3/ right	11.6 13.5 14 13.9	9.0 12.5 12 11.6	Estimated from figure Colbert, 1933 (as M1/) Colbert, 1933 Estimated from figure
SMF 6396	M3/ left	12.1	9.6	Own, 2011
Paali Nala C2 Pakistan	M1/ right M2/ left	9.0 10.2	8.4 9.0	Orliac *et al*., 2010b
Xiaodian, Hubei, China	M1/ or M2/ left	9	8.1	Gu Yumin, 1980
Lufeng, China	M3/	13.3	10	Van der Made & Han, 1994
MF/1711/80 Przeworno, Poland	M1/ M2/ M3/	8.2 9.5 11.2	7.4 9 9	Kubiak, 1981
BSPG 1959 II 8216 Sandelzhausen, Germany	M1/ left M2/ left M3/ left M1/ right M2/ right M3/ right	10.5 12.2 13.9 10.1 12.1 13.9	10.1 11.5 — 10.2 11.3 11.2	Van der Made, 2010
BSPG 1959 II 275 Sandelzhausen, Germany	M1/ right M2/ right	— 12.7	9.9 11.2	Van der Made, 2010
BSPG 1959 II 272	M1/ left	10.2	9.9	Van der Made, 2010
BSPG 1959 II 280	M2/ left	12.8	11e	Van der Made, 2010
BSPG 1959 II 8918	M2/ left	13.6	12.3	Van der Made, 2010
Neudorf, Czech Republic	M2/	12.5	11.5	Zapfe, 1983
Neudorf, Czech Republic	M3/	16	11.4	Zapfe, 1983
SLJG 56699 Münzenberg, Austria	M2/ M3/	12.0 12.4	11.1 10.6	Van der Made, 1998 (Thenius, 1956, Leoben)
Paşalar, Turkey	M1/	11.0	9.0	Fortelius & Bernor, 1990
Paşalar, Turkey	M1/	10.7	9.4	Fortelius & Bernor, 1990
Paşalar, Turkey	M2/	11.8	9.8	Fortelius & Bernor, 1990
Paşalar, Turkey	M2/	10.8	9.2	Fortelius & Bernor, 1990
Paşalar, Turkey	M2/	10.4	9.6	Fortelius & Bernor, 1990
AK 13.4 Inönu, Turkey	M1/ M2/	10.9 12.2	8.9 10.6	Van der Made, 2003a
MTA 1953 Sinap, Turkey	M1/ left M2/ left M3/ left M2/ right M3/ right	13.6 17.0 20.1 16.5 19.4	12.1 14.3 14.9 14.6 14.9	Van der Made, 2003b

Table 3 *(continuation).*—**Measurements (in mm) of the upper molars of Eurasian Palaeochoeridae**

Catalogue	Tooth	Mesio-distal length	Bucco-lingual breadth	Data source
MNHN 3337	M1/ left	18.8	16.3	Van der Made, 2003b
Yassiören, Turkey	M2/ left	22.2	19.4	
	M3/ left	27.2	20.4	
	M1/ right	18.3	16.4	
	M2/ right	22.1	19.8	
	M3/ right	27.8	—	
TGPI I-782-785	M1/ left	16.0	12.0	Lungu, 1971, 1974
Kalfa, Moldova	M3/ right	24.0	19.0	
Anwil, Switzerland	M1/ left	8.5	7.3	Own, 2010 (from casts)
	M2/ left	10.0	8.0	
	M3/ left	11.5	8.4	
	M2/ right	10.2	8.0	
SMNS 9901	M1/ left	9.1	7.0	Chen, 1984
Steinheim, Germany	M2/ left	10.2	8.0	
	M1/ right	9.0	7.0	
	M2/ right	10.2	8.0	
	M3/ right	11.1	7.8	
SMNS 12962	M1/ left	9.9	8.5	Own, 2010
Steinheim, Germany	M2/ left	10.8	9.1	
	M3/ left	11.9	9.4	
	M1/ right	10.3	8.2	
	M2/ right	11.1	9.1	
SMNS 13234	M1/ left	8.7	7.7	Own, 2010
Steinheim, Germany	M2/ left	10.0	8.3	
	M3/ left	11.4	8.6	
	M1/ right	8.8	7.0	
	M2/ right	10.5	7.8	
	M3/ right	11.4	8.3	
SMNS 10801	M1/ left	8.5	8.3	Own, 2010 (worn specimen)
Steinheim, Germany	M2/ left	9.6	8.5	
Béon, France	M2/	10.4	9.4	Orliac *et al.*, 2006
	M3/	11.0	9.1	
Viladecaballs, Spain	M1/ left	18.0	14.2	Crusafont & Lavocat, 1954

one from Xiaodian might belong to *P. orientalis*, depending on its meristic position. The same applies to recently described fossils from Paali Nala, Pakistan (Orliac *et al.*, 2010b) which likely represent *P. sminthos*. This suggestion accords with the biostratigraphic age estimate of Xiaodian, as being equivalent to Shanwang, China (Qiu & Qiu, 1995).

Species *Pecarichoerus orientalis* Colbert, 1933

Material: GSI K16/341, isolated left M3/ from Chinji, housed in the GSI Calcutta, India; SMF 6396, isolated left M3/ housed in the Senckenberg Museum, Frankfurt., Germany.

Description: GSI K16/341 is an isolated left M3/ from Chinji (Fig. 7A). It is moderately deeply worn, but retains some critical morphology of the rear loph showing that the metacone is isolated from the neighbouring cusps at its apex and most of its height and is reduced in size relative to the hypocone. The hypocone sends a strong postcrista disto-buccally which ends behind the metacone, from which it is separated by a deep cleft. The main part of the hypocone is slightly behind the level of the metacone. The protocone is deeply worn and at its base it is distinctly larger than the paracone and is slightly behind it, giving the tooth a slightly trapezoidal outline. There is a bucco-lingually extensive mesial cingulum. In the base of the buccal notch, there is a low basal pillar, and there is another low cusplet in the notch between the metacone and the distal cingulum, in the disto-buccal corner of the crown.

SMF 6396, a left M3/ from Chinji stored in the Senckenberg Museum, Frankfurt, is in medium wear, and shows a well formed basal cusplet in the lingual end of the median transverse valley (Fig. 7B). The roots are fused for about 5 mm beneath thr cervix as in European specimens of the species.

Discussion: GSI K16/341 and SMF 6396 are similar in morphology to the M3/ in the holotype of *Pecarichoerus orientalis*

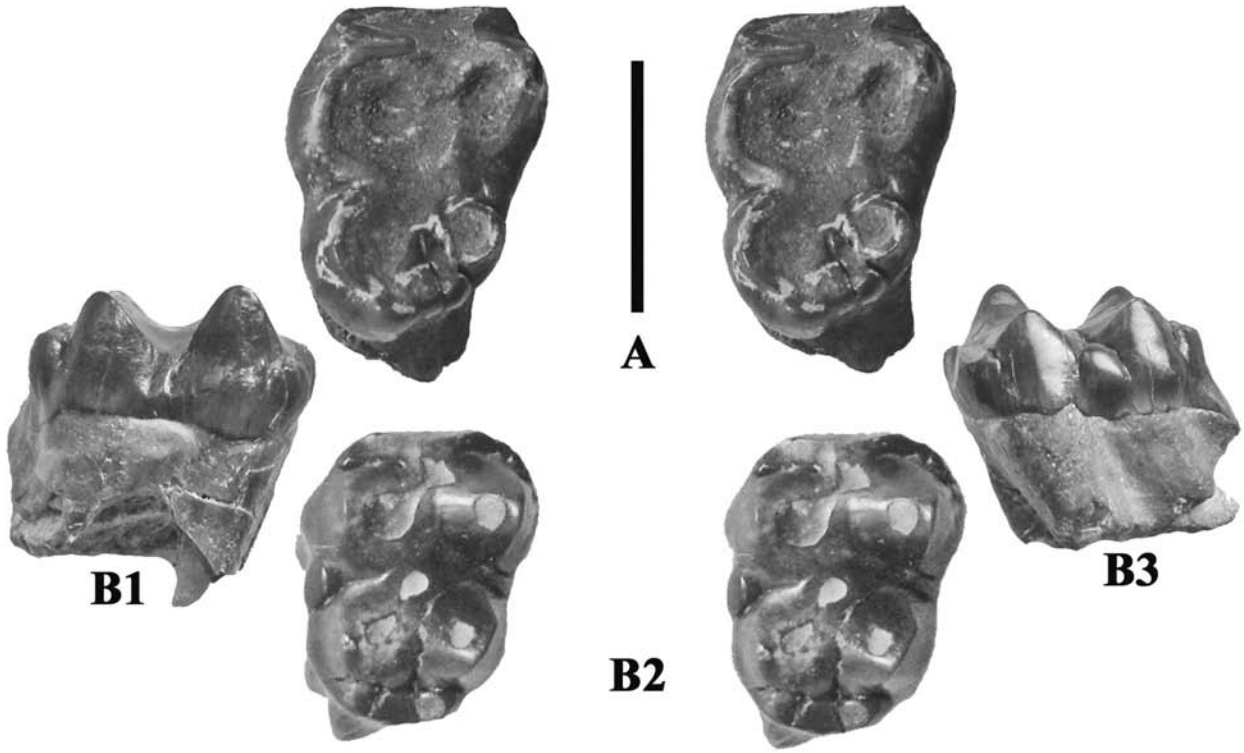

Fig. 7.—*Pecarichoerus orientalis* from Chinji, Pakistan, A) GSI K16/341, left M3/, stereo occlusal view, B) SMF 6396, left M3/, B1 – buccal, B2 – stereo occlusal, and B3 – lingual views (note the fused roots) (scale: 10 mm).

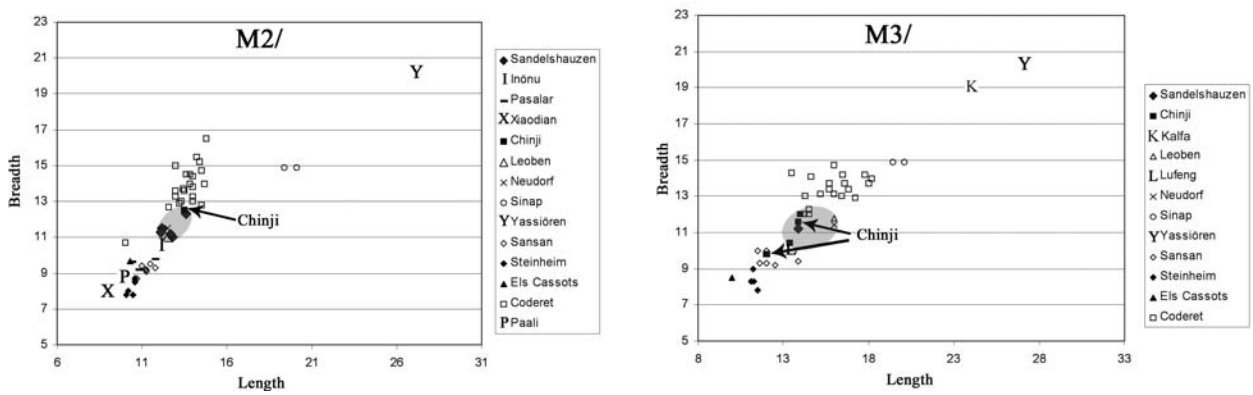

Fig. 8.—Bivariate plots of upper second and third molars of Palaeochoeridae. Note that the fossils from Chinji, Pakistan (*Pecarichoerus orientalis*) plot close to those from Sandelzhausen, Leoben and Neudorf (grey ovals) previously classified as *Schizoporcus muenzenbergensis*, but here considered to belong to the same species as that from Chinji. The Xiaodian tooth is here plotted as an M2/, but it could be an M1/ of *Pecarichoerus orientalis* instead.

Colbert (1933) but it are slightly narrower. What is intriguing is that the morphology is close to that of *Schizoporcus muenzenbergensis* (Van der Made, 1998). Not only is the morphology close, but the dimensions are almost identical (Fig. 8) indicating the probability that the Chinji species and that from Münzenberg and Sandelzhausen are the same. The Chinji species shows a small prehypocone crista in the M2/, a structure that is also present in specimens from Sandelzhausen, Germany (BSPG 1959 II 8216, skull) (this feature is obliterated in heavily worn specimens). The M3/ in the Sandelzhausen skull is very similar to that of the Chinji holotype (Fig. 9), and the basic structure is close to that of the new specimen described above (GSI K 16/341) (Fig. 10) allowing for the deeper wear in the latter specimen. The two buccal cusps (paracone and metacone) are noticeably smaller than the two lingual cusps (protocone and hypocone) and the mesial and distal cingula are

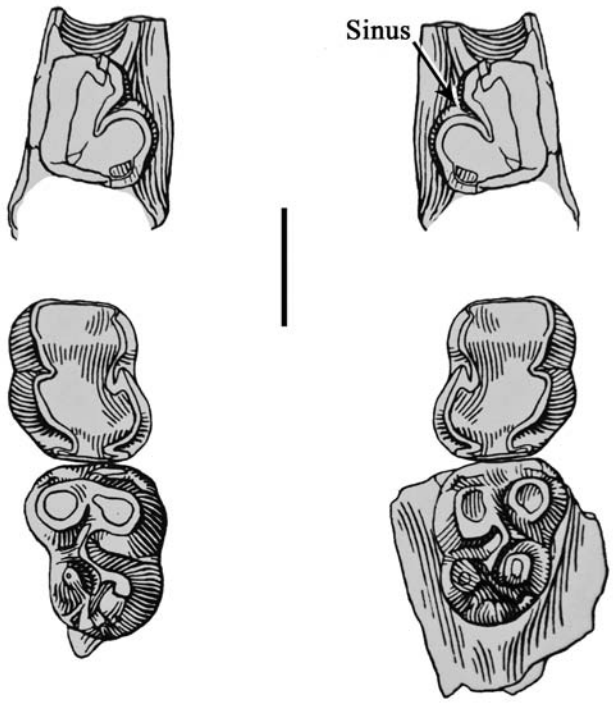

Fig. 9.—Reinterpretation of AMNH 29955, right P4/, left M2/ (not M1/) and left and right M3/, holotype of *Pecarichoerus orientalis* Colbert (1933) from Chinji, Pakistan (scale: 10 mm) image modified from Colbert, 1933). Note the distally oblique lingual sinus in P4/ (pale arrow in top right figure).

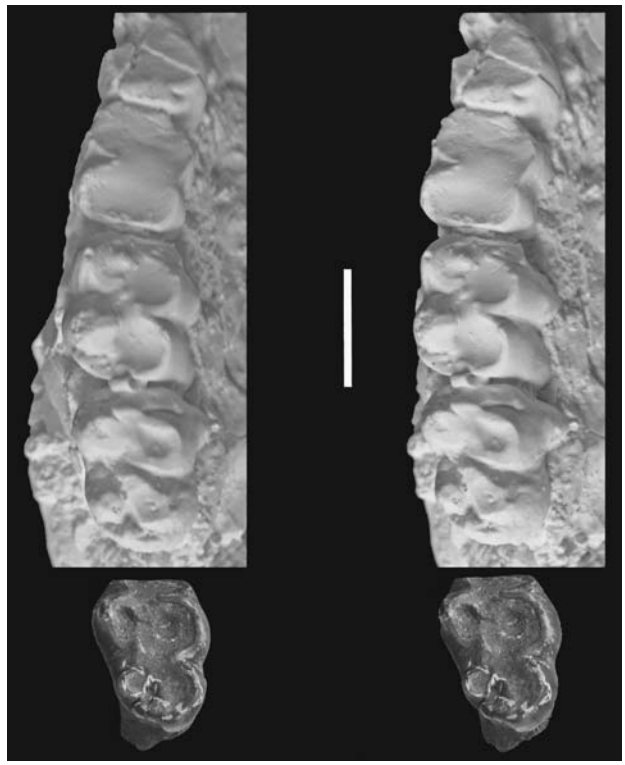

Fig. 10.—Comparison of palaeochoerid upper molars from Sandelzhausen (upper row) and Chinji (lower row). Upper row, stereo occlusal view of right cheek teeth of BSPG 1959 II 8216 (cast); lower row, stereo occlusal view of GSI K16/341 left M3/ (reversed).

strongly developed, the distal one curving round towards the rear of the metacone. The protocone and hypocone have robust crista tending mesio-centrally, so that with wear the cusps take on an ovoid contour, pointed obliquely mesially. These two cusps are not opposite the paracone and metacone, but lie slightly distally.

The P4/ from Chinji described by Colbert (1933) is worn and damaged buccally, but the preserved parts show the same basic morphology as the material from Sandelzhausen (Van der Made, 2010), especially the lingual valley (or sinus) entering the tooth at a markedly oblique angle pointing towards the rear. This cleft separates the distally positioned protocone from the buccal main cusp and there is a prominent distal cingulum (Fig. 9). This morphology differs radically from that observed in *Choeromorus grandaevus* (Fig. 24, 28).

Colbert (1933, 1935) interpreted the worn upper molar from Chinji as an M1/, possibly on account of the much greater degree of wear than in the M3/. However, its dimensions suggest that it is an M2/, and comparison with material from Sandelzhausen, Germany, reveals that the wear gradient in this lineage is indeed steep. For example, the skull BSPG 1959 II 8216 has a similar wear gradient (Van der Made, 2010, fig. 1) as the Chinji holotype of *Pecarichoerus orientalis*. The similarity between these specimens is striking, even down to details of cusp morphology, cingulum development and wear pattern. There can be little doubt that they are closely related, perhaps even conspecific, the stance adopted here.

Genus *Schizoporcus* Van der Made, 2010
Type species *Schizochoerus vallesensis* Crusafont & Lavocat, 1954
Species *Schizoporcus vallesensis* (Crusafont & Lavocat, 1954)

Holotype: Mandible fragments from Can Purull (Viladecaballs), near Sabadell, Catalunya, Spain.

Material from Turkey: When Ozansoy (1965) described a mandible (the holotype of *Schizochoerus arambourgi*) he kept some specimens in open nomenclature - a palate with P3/-M3/ on both sides, a second palatal fragment containing what he considered to be three permanent premolars and a deciduous premolar, an isolated canine and an upper incisor. He attributed the latter specimens to *Schizochoerus* cf *arambourgi*. His motive for creating a new species for the Yassiören mandible was related to the appreciable difference in dimensions between it and the holotype mandible of *Schizochoerus vallesensis*. The teeth in the palate and maxilla, in contrast are more similar in dimensions to the Spanish material, which is admittedly, rather poorly known (a single M1/).

Re-examination of the specimens reveals that the maxilla fragment does indeed carry the three anterior permanent premolars (the P2/ is represented by its roots only), but that in addition, there is an accessory premolar between the P1/ and the canine alveolus (Fig. 11).

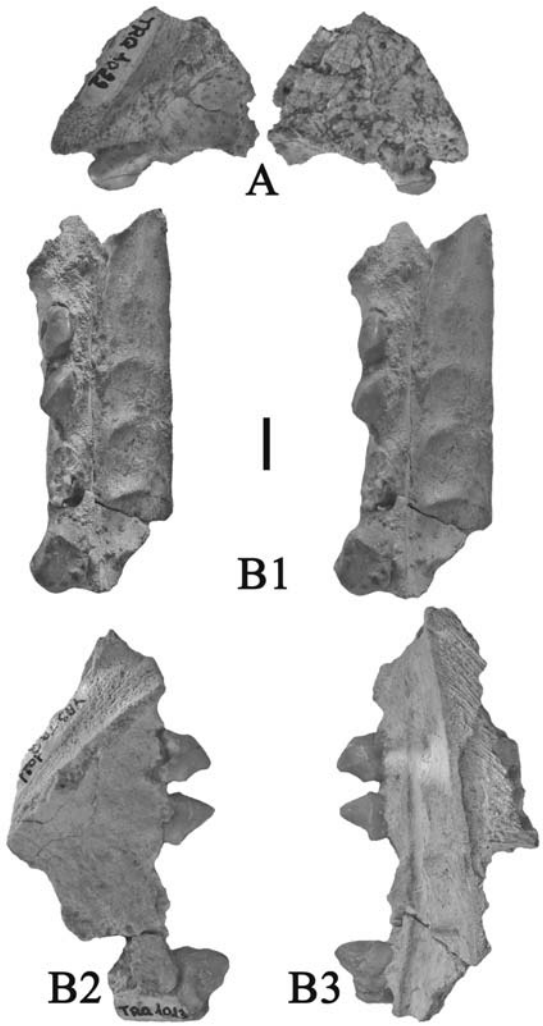

Fig. 11.—A) MNHN TRQ 1022, right premaxilla containing I3/, canine niche and part of canine alveolus, B) MNHN Yas 28 and Yas 30 (TRQ 1013 and 1011), maxilla of *Schizoporcus vallesensis* from Yassiören, Turkey, with P3/, root of P2/, P1/ and P^{acc}/, and parts of the canine alveolus. A) lingual and labial views, B1) stereo occlusal, B2) buccal and B3) lingual views (scale : 10 mm).

Ozansoy (1965) argued that the tooth in front of the P1/ was a retained deciduous premolar. However, apart from its smaller dimensions, in its morphology, enamel thickness and root morphology, it closely resembles the permanent tooth behind it, and I take it to represent an accessory permanent tooth.

The presence of accessory premolars is extremely rare among artiodactyls, but they are known to be characteristic of the anthracothere genus *Libycosaurus* from Northern and Equatorial Africa (Pickford, 1991, 2005, 2006). Until now their presence in other suiformes has not been documented. Van der Made (2003, Table 13.3) provided measurements of the two anterior teeth in the maxilla, but he thought they were P1/ and P2/ (his measurements labelled P1/ pertain to the P^{acc}/ and those labelled P2/ pertain to the P1/). Note also that the measurements of the lower teeth that he labelled *Schizochoerus*

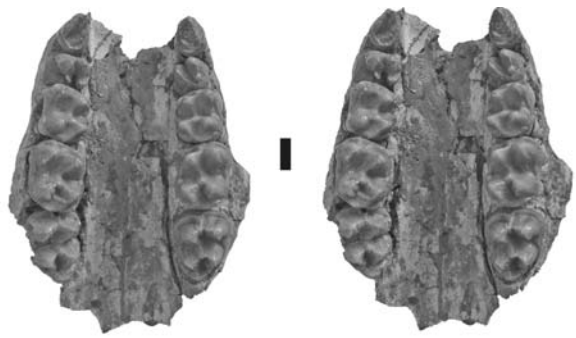

Fig. 12.—MNHN Yas 3337 (TRQ 1018), palate of *Schizoporcus vallesensis* from Yassiören, Turkey, with left and right P3/-M3/, stereo occlusal view (scale : 10 mm).

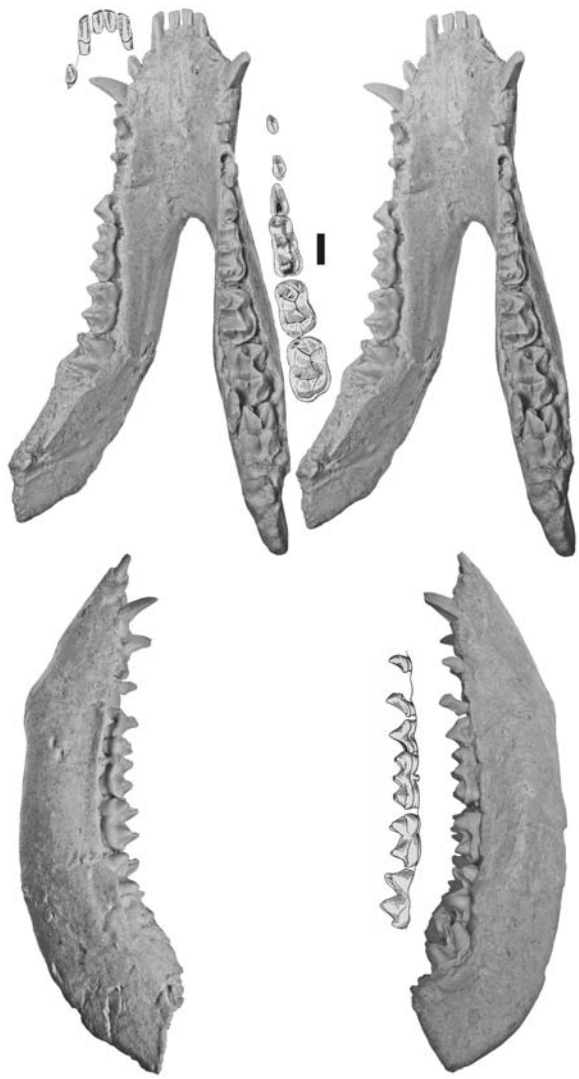

Fig. 13.—Cast of the Nsebar, Bulgaria, mandible with mixed dentition of *Schizoporcus vallesensis*, left lateral, stereo occlusal and right lateral views (drawings are from Nikolov & Thenius (1967) (scale bar – 10 mm). The right m/3 has been exposed since the specimen was described by Nikolov & Thenius (1967).

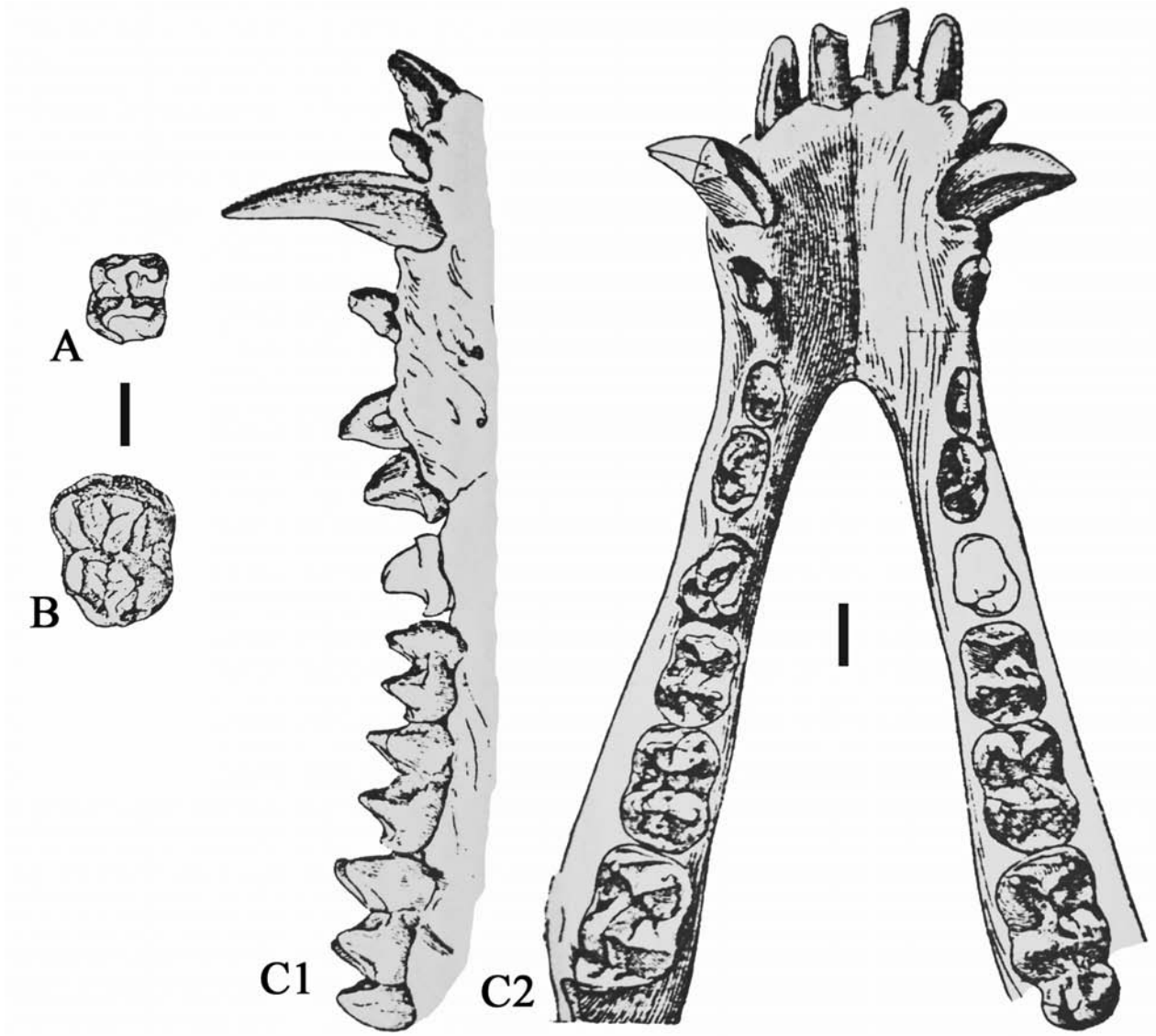

Fig. 14.—TGPI I-782-785, A) left M1/ occlusal view, B) right M3/ occlusal view, and C) mandible of *Schizoporcus vallesensis* from Kalfa, Moldova, C1) buccal view of right mandible, C2) occlusal view (image modified from Lungu, 1981, figs 1-3). Note the strongly fused symphysis in this young individual (scale bar : 10 mm).

sinapensis (Van der Made, 2003, Table 13.1) are from the holotype mandible of *Schizoporcus arambourgi*, which the author considers to be a synonym of *Schizoporcus vallesensis* (Van der Made, 2010). If the mandible really does represent the same species as *S. sinapensis*, then the latter name is a junior synonym of *S. arambourgi*. However, the species name in Van der Made's (2003a) Table 13.1 is likely a lapsus – *vallesensis* was probably meant. Nevertheless, the holotype mandible of *Schizoporcus arambourgi* is appreciably smaller than specimens of *S. vallesensis* from Spain, Bulgaria and Moldova (Ozansoy, 1965; Crusafont & Lavocat, 1954; Nikolov & Thenius, 1976; Lungu, 1971) and it is compatible in dimensions with the holotype snout of *Schizoporcus sinapensis*. In this paper it is considered to be a valid species (see below).

Species *Schizoporcus arambourgi* (Ozansoy, 1965)

Holotype: MNHN Yas 27 (TRQ 1010), juvenile mandible with mixed dentition, from Yassiören, Turkey.

Reassessment of fossils from Turkey: Pickford (1978) described a snout with almost complete dentition from Sinap, Turkey, and attributed it to *Schizochoerus* cf *gandakasensis*. It was refigured by Pickford & Ertürk (1979) and was briefly mentioned by Van der Made & Han (1994). Van der Made (1997a) created a new species on the basis of the specimen and he provided measurements (Van der Made, 2003b). The genus name was changed to *Schizoporcus* by Van der Made (2010) because *Schizochoerus* Crusafont & Lavocat, 1954, was preoccupied.

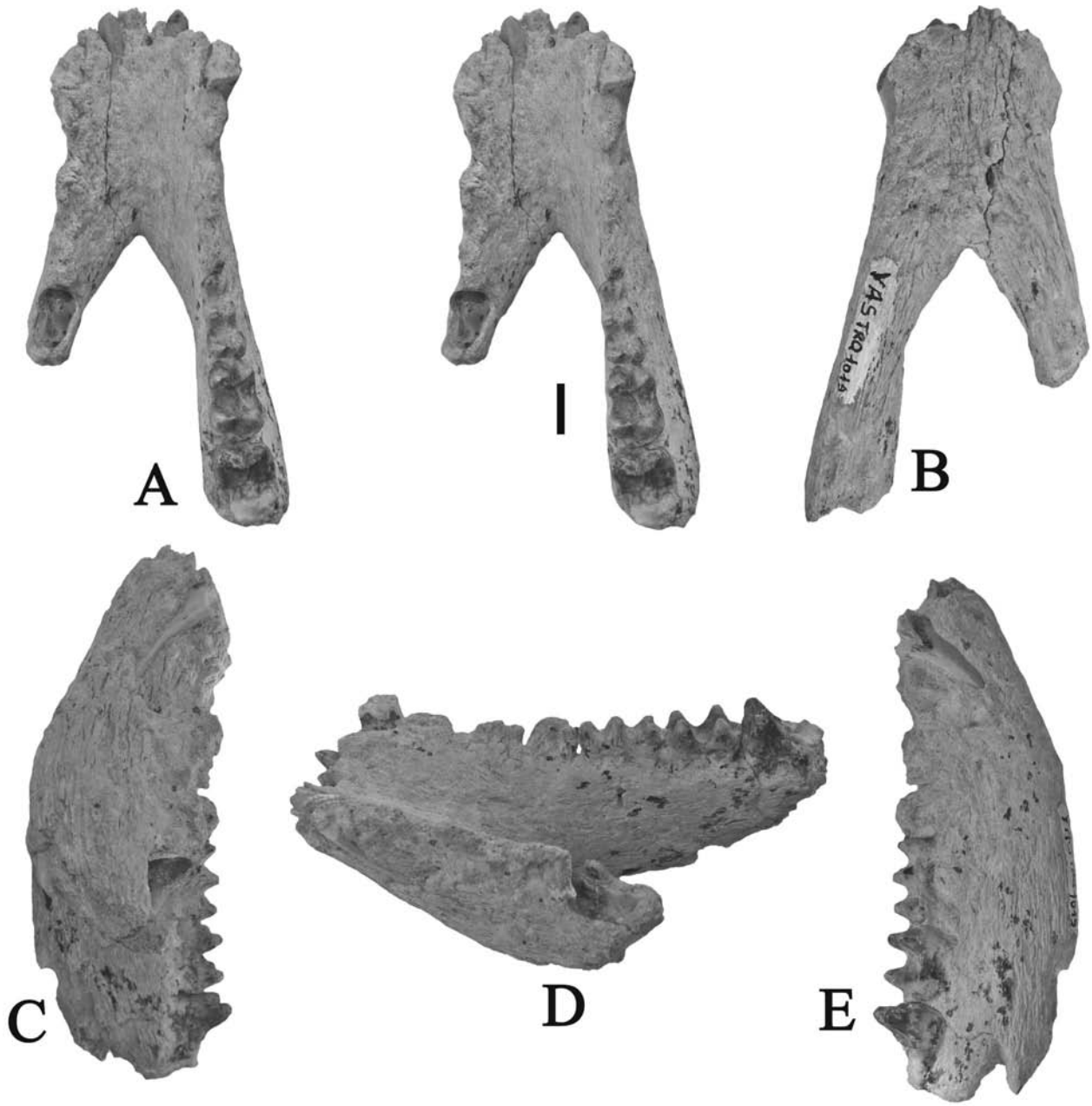

Fig. 15.—MNHN Yas 27 (TRQ 1010), mandible of *Schizoporcus vallesensis* from Yassiören, Turkey, containing permanent incisors in crypto, d/3, d/4, m/1 and part of m/2 in occlusion and left p/4 in crypto, A) stereo occlusal, B) ventral, C) left lateral, D) oblique occlusal and E) right lateral views. Note the completely fused symphysis in this juvenile individual (scale : 10 mm).

Re-analysis of the dimensions of all the fossils currently classified in *Schizoporcus* reveals that the holotype mandible of *S. arambourgi* is indeed substantially smaller than material attributed to *Schizoporcus vallesensis*, not only from the type locality, but also from Bulgaria and Moldavia (Crusafont & Lavocat, 1954; Nikolov & Thenius, 1067; Lungu, 1971).

The dimensions of the upper and lower molars of *Schizoporcus* show the usual relationships found widely in bunodont suiforms, the lower molars are usually somewhat longer but narrower than their upper counterparts. Plots of the upper and lower molars reveal that the lower teeth of *Schizoporcus arambourgi* are too small to represent the same species as *Schizoporcus vallesensis*, but that they are compatible with the upper teeth in the holotype snout of *Schizoporcus sinapensis*. It is therefore concluded that *S. sinapensis* (Van der Made, 1997a) is a junior synonym of *S. arambourgi* (Ozansoy, 1965). Earlier mentions of the species *S. arambourgi* by Ozansoy (1957a, 1957b) are nomina nuda (Van der Made, 1997a).

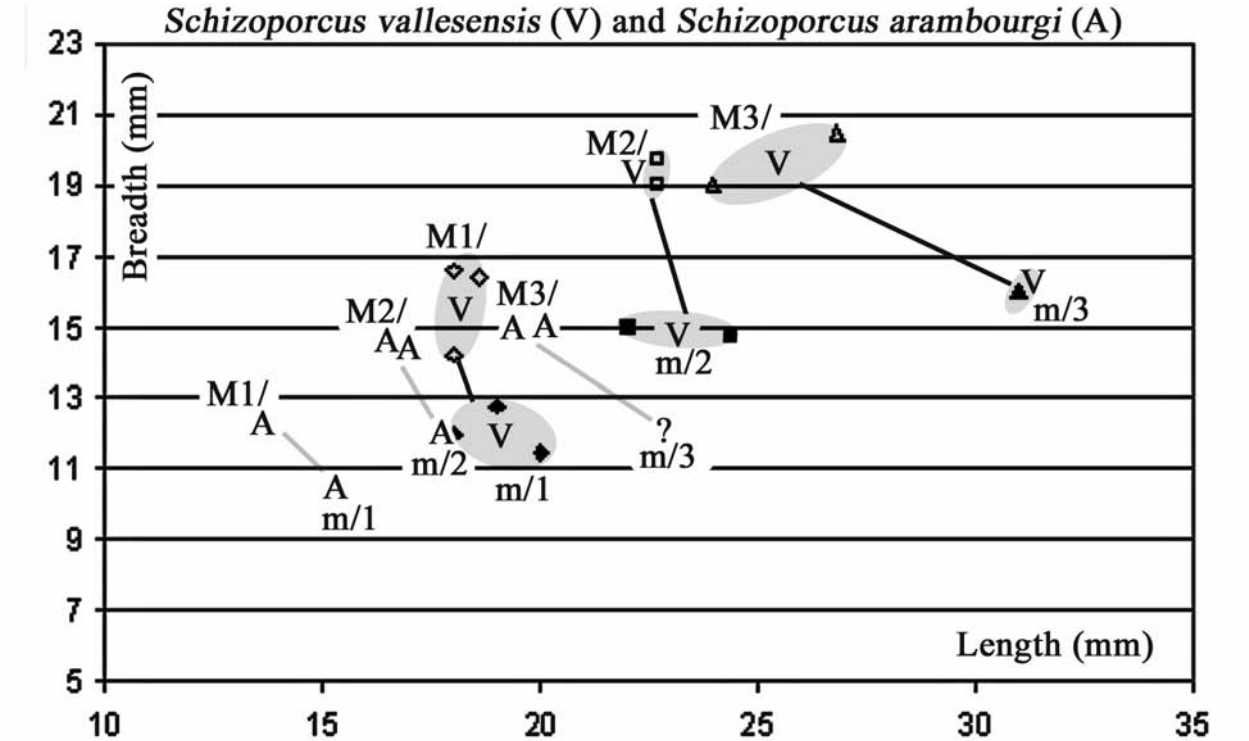

Fig. 16.—Relationship between upper and lower molars of species of *Schizoporcus* (V – *Schizoporcus vallesensis*, A – *Schizoporcus arambourgi*). The holotype mandible of *S. arambourgi* is compatible in size with the holotype snout of *S. sinapensis*, indicating that the two species are synonyms (? signifies that the m/3 of *S. arambourgi* is unknown, but that it is likely to have approximately the dimensions indicated on the basis of the size of the m/2).

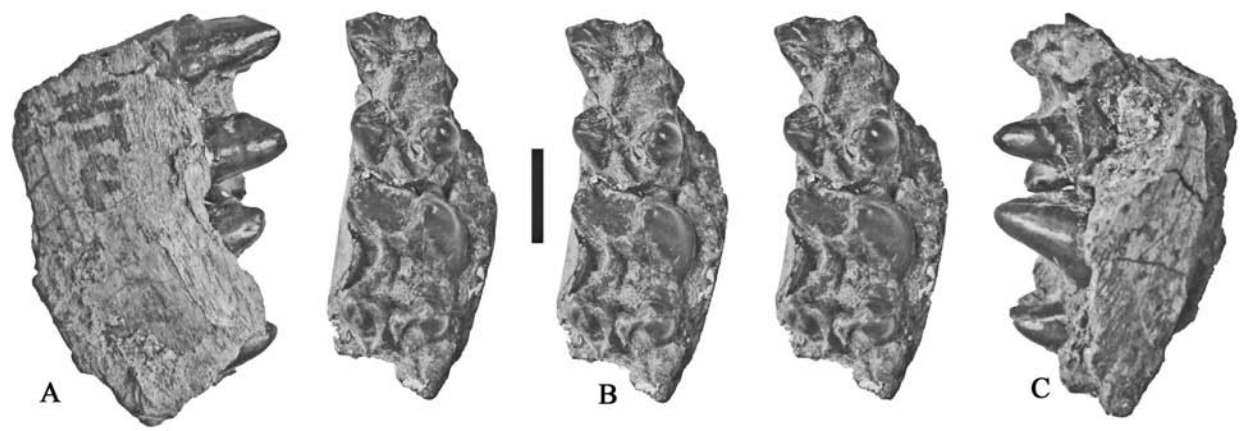

Fig. 17.—GSI Htu, left mandible fragment containing m/2 and m/3 (erupting) of *Yunnanochoerus dangari* (Prasad, 1970) from Hari Talyangar, Himachal Pradesh, India, A) lateral view, B) stereo occlusal views, and C) medial views (scale bar: 10 mm).

Genus *Yunnanochoerus* Van der Made & Han, 1994
Species *Yunnanochoerus dangari* (Prasad, 1970)

Material: GSI K15/247+249, right mandible fragment containing m/1-m/2, GSI Htu, left mandible fragment containing m/2-m/3, both from Hari Talyangar, India.

Description: The teeth in the two mandible fragments from Hari Talyangar, India are lightly worn or unworn but have suffered slight damage (missing enamel flakes). Specimen GSI Htu is a juvenile in which the m/3 is erupting; GSI K15/247+249 is adult with lightly worn m/1 and m/2.

The m/1 and m/2 have four tall, pointed cusps arranged into two transverse pairs (Fig. 17, 18). The preprotoconid cristid is prominent and curves medially to close off a deep mesial fovea located between the protoconid and metaconid. The premetaconid cristid is weak (in specimen GSI HTu this cuspid is miss-

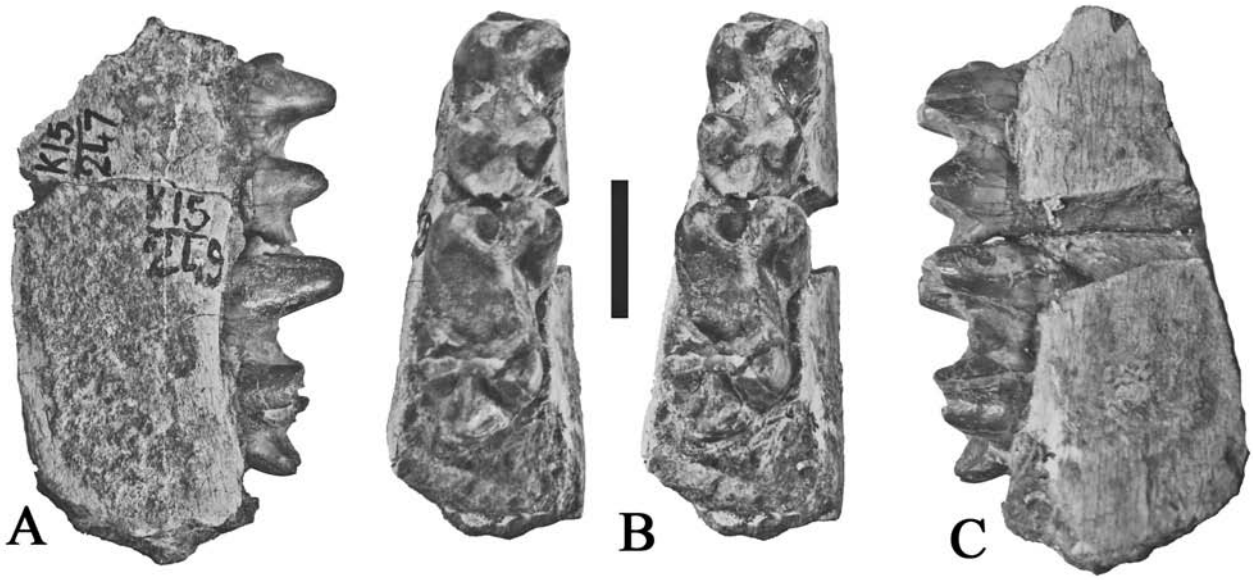

Fig. 18.—GSI K15/247+249, right mandible fragment of *Yunnanochoerus dangari* Prasad (1970) containing lightly worn m/1 and m/2, from Hari Talyangar, India. A) lingual, B) stereo occlusal and C) buccal views (scale bar: 10 mm).

ing, but it is complete in GSI K 15/247). The posterior cristids linking the front pair of cusps (postprotocristid and postmetacristid) dip cervically and are aligned at the rear of the cusps, closing off the rear of the mesial fovea. The prehypoconid cristid is strongly developed and forms a continuous crest between the hypoconid and the mesial pair of cuspids meeting the distal wall of the mesial fovea in the midline of the tooth. The posthypoconid cristid is oriented transversely and reaches towards the postentocristid but there is a cleft between them. The centrally positioned hypoconulid is well formed but low and it sends a cristid obliquely towards the hypoconid. The lingual and buccal notches are mesio-distally elongated and are deep. The mesial cingulum is weak.

The m/2s are basically enlarged versions of the m/1, the main difference being that the hypoconulid sends a cristid directly mesially, and not as obliquely as in the m/1. The front two lophids of m/3 are similar to the m/2.

Measurements of lower molars are provided in Table 4.

Discussion: Prasad (1970) created the genus and species *Anthraconema dangari* in the belief that it was an anthracothere. The illustration provided by Prasad (1970, pl. XV, fig. 3) although of poor quality and taken in an oblique orientation, is that of a lophodont suiform with pointed cusp apices. His description of the holotype (GSI 18078) provides a succinct résumé of the main points of the morphology, including the molars with cusps more pointed than bunodont, with well marked ridges connecting the protoconid-metaconid and protoconid-hypoconid, and a minor ridge connecting hypoconid and entoconid, with an anteriorly extending cingulum. Examination of the specimen in the GSI, Calcutta, confirms its identification as a lophodont palaeochoerid and not an anthracothere. The discovery of two additional mandibular specimens in the cabinets of the GSI, described herein, removes any residual doubt that there might have been about the identification of this species (Pickford, 1988).

Species *Yunnanochoerus gandakasensis* (Pickford, 1977)

Material: PDYV 31, left m/1; PDYV 21, right m/2; PDYV 20, right m/3; PDYV 0232, right m/3, all from Yuanmou, housed in the Yunnan Institute of Archaeology, China.

Description: The lower left m/1 (PDYV 31) from Yuanmou, Yunnan, China, has four main cusps and a prominent median accessory cusp at the mesial end of the prehypocristid. The mesial cingulum is bucco-lingually broad but mesio-distally narrow. The preprotocristid curves lingually and ends in the midline of the crown. The premetacristid descends towards the mesial cingulum slightly obliquely. The postprotocristid and postmetacristid form the rear wall of the mesial fovea which lies between the protoconid and metaconid. Descending the rear of the protoconid and metaconid are "zygodont" cristids bordered by shallow grooves. This morphology superficially resembles the "M" morphology of the lower molars of tragulids. The buccal and lingual notches are broad and deep, meaning that apices of the mesial pair of cusps are far from those of the distal pair. The median transverse valley is blocked in its centre by the median accessory cusplet, which is strongly joined to the prehypocristid. The latter cristid descends from the apex of the hypoconid towards the centre of the crown. The hypoconid has a small posthypocristid that descends towards the centreline of the tooth where it joins the hypoconulid. The entoconid is detached from the hypoconid at its apex, but it has a buccally directed cristid that links it to the hypoconid, forming the mesial wall of the distal fovea. The distal fovea is small and is located between the hypoconid and entoconid, its rear wall being formed by the hypoconulid, which is low and centrally positioned.

The right m/2 (PDYV 21) is a larger version of the m/1, and although it is basically an upscaled version of this tooth, it shows some differences in morphology from it. The most

Table 4.—**Measurements (in mm) of lower molars of *Yunnanochoerus dangari* Prasad (1970) from Hari Talyangar, Himachal Pradesh, India, other material of the genus and of *Pecarichoerus*, *Choeromorus* and *Schizoporcus* from Asia and Europe (e = estimated measurement)**

Catalogue N° Locality	Tooth	Mesio-distal length	Bucco-lingual breadth	Data source
NHM M 12028 Bugti	m/2 left m/3 left	8.5 13.5	6.0 7.0	Forster-Cooper, 1913
GSI K15/247+249 Haritalyangar	m/1 right m/2 right	15.8 19.6	9.5 11.0	Own, 2007
GSI Htu Haritalyangar	m/2 left m/3 left	19.5 —	11.3 12.1	Own, 2007
GSI 18078 Haritalyangar	m/1 right	16.5	8.0	Prasad, 1970
GSP 4192 Gandakas	m/1 left m/2 left m/3 left	12[e] 16.0 22[e]	10.0 10[e] —	Pickford, 1977
PDYV 31 Yuanmou	m/1 left	12.0	7.2	Own, 2010
PDYV 21 Yuanmou	m/2 right	15.4	10.1	Own, 2010
PDYV 20 Yuanmou	m/3 right	18.4	9.0	Own, 2010
PDYV 252 Yuanmou	m/3 right	19.6	9.6	Own, 2010
IVPP V 6891 Lufeng	m/2 left m/3 left	13.0 16.4	9.2 9.5	Van der Made & Han, 1994
IVPP Lufeng	m/2	14 .3	8.1	Van der Made & Han, 1994
IVPP Lufeng	m/2	13.7	9.0	Van der Made & Han, 1994
IVPP Lufeng	m/2	—	8.6	Van der Made & Han, 1994
IVPP Lufeng	m/3	17.1	9.6	Van der Made & Han, 1994
Sihong, China	m/1 or m/2	11.0	7.1	Own, 1999
MNHN Yas 27 Yassiören	m/1 right m/2 right	15.6 17.8e	10.3 12.0	Van der Made, 1997a, 2003b Own, 2011
MTA 1338 Çandir	m/2 left	15.3	10.1	Van der Made, 2003a
MTA 1339 Çandir	m/3 right	20.2	11.4	Van der Made, 2003a
MTA no n° Çandir	m/3 left	—	10.8	Van der Made, 2003a
Paşalar	m/1 m/1 m/2	10.7 11.2 12.2	6.8 7.0 8.5	Fortelius & Bernor, 1990
TGPI I-782-785, Kalfa, Moldova	m/1 m/2 m/3	18.0 22.0 31.0	12.0 15.0 16.0	Lungu, 1971, 1974
Nsebar, Bulgaria	m/1 m/2	19.0 —	12.8 16 ?	Nikolov & Thenius, 1967
Mala Miliva, Serbia	m/1 m/2 m/3	9.6 11.6 17.2	7 8.0 8.5	Petronijevic, 1967

Table 4 *(continuation)*.—**Measurements (in mm) of lower molars of *Yunnanochoerus dangari* Prasad (1970) from Hari Talyangar, Himachal Pradesh, India, other material of the genus and of *Pecarichoerus*, *Choeromorus* and *Schizoporcus* from Asia and Europe (e = estimated measurement)**

Catalogue N° Locality	Tooth	Mesio-distal length	Bucco-lingual breadth	Data source
IPS Viladecaballs (Can Purull, La Tarumba)	m/1	20	11.5	Crusafont & Lavocat, 1954
	m/2	24.4	14.7	
SLJG 56634 Münzenberg	m/1 left	10.9	7.6	Van der Made, 1998
	m/2 left	12.0	9.1	
	m/3 left	15.9	8.8	
SLJG 56697 Münzenberg	m/1 right	10.7	7.8	Van der Made, 1998 (Zdarsky, 1909 has slightly different measurements)
	m/2 right	12.0	8.9	
	m/3 right	16.0	8.7	
SLJG 56698 Münzenberg	m/2 left	13.5	9.0	Van der Made, 1998
	m/3 left	16.9	8.7	
SLJG 1880 Göriach	m/1 left	10.3	6.7	Van der Made, 1998
SLJG 58817 Göriach	m/2 right	11.9	7.8	Van der Made, 1998
BSPG 1959 II 8217 Sandelzhausen	m/1 right	12.3	7.9	Van der Made, 2010
	m/2 right	12e	—	
NHM M 5411	m/3 left	15.0	8.5	La Grive St-Alban Own, 2010
NHM M 5413 La Grive St-Alban	m/1 right	7.3	5.0	Own, 2010
SMNS 44311 Steinheim, Germany	m/1 left	10.0	6.0	Own, 2010
	m/2 left	10.6	6.5	
	m/3 left	15.3	7.1	
SMNS 20237 Steinheim, Germany	m/1 right	8.7	5.1	Own, 2010
	m/2 right	9.8	6.3	
	m/3 right	12.6	6.6	
	m/2 left	9.5	6.3	
SMNS 20236 Steinheim, Germany	m/2 right	11.9	7.2	Own, 2010
	m/3 right	16.0	8.1	
SMNS 44033 Steinheim, Germany	m/1 right	10.0	6.0	Own, 2010
SMNS 40408 Steinheim, Germany	m/1 left	9.7	5.6	Own, 2010
	m/2 left	10.2	6.7	
SMNS No N° Steinheim, Germany	m/1 left	9.7	6.0	Own, 2010
	m/2 left	—	—	
	m/3 left	13.5	7.2	
Béon, France	m/1	9.8	6.8	Orliac *et al*., 2006
	m/1	9.5	6.7	
	m/2	11.3	7.9	
	m/2	10.3	7.6	
	m/3	14.5	7.7	
	m/3	12.1	7.6	

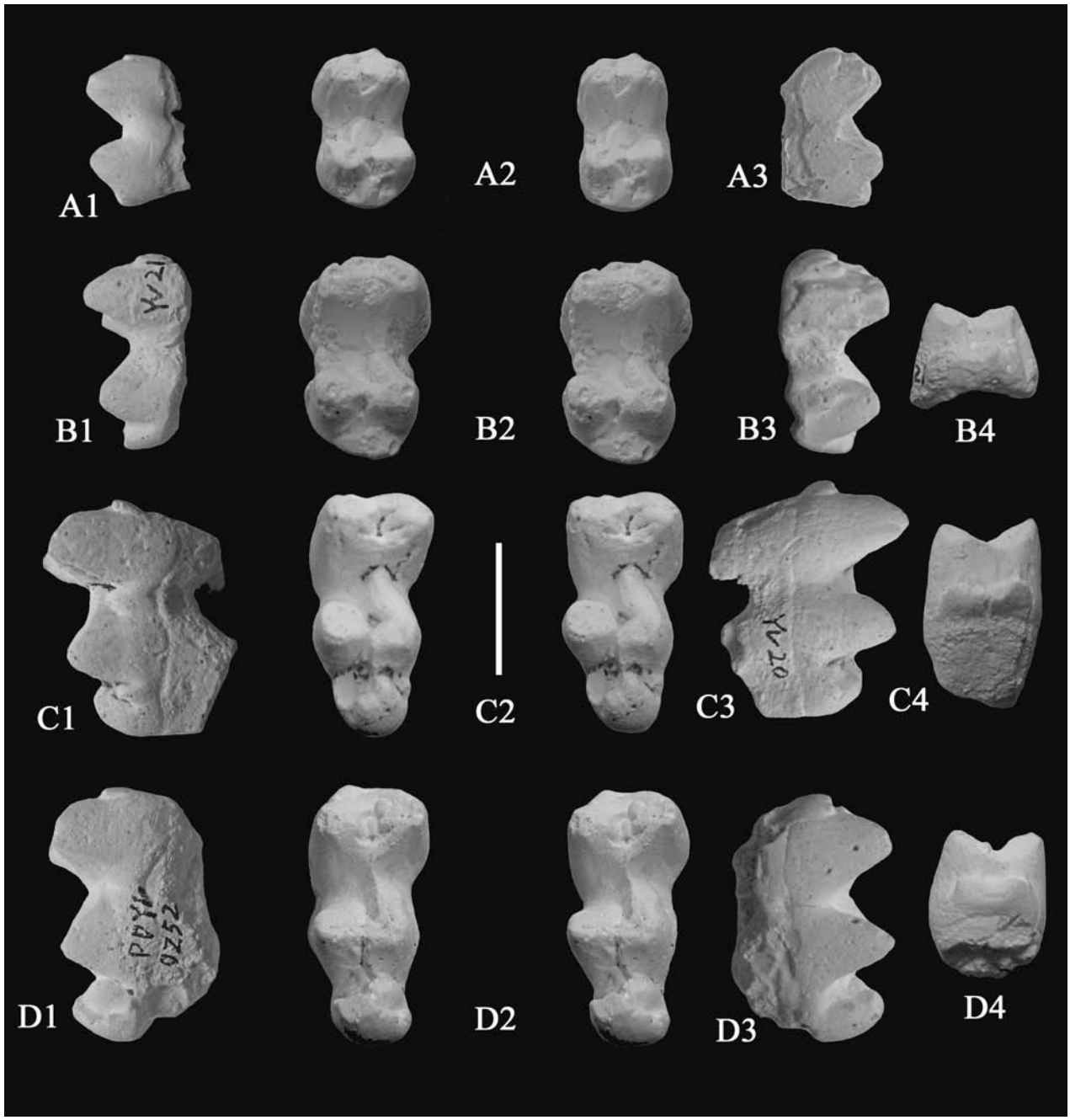

Fig. 19.—*Yunnanochoerus gandakasensis* casts of lower molars from Yuanmou, Yunnan, China, A) PDYV 31, left m/1, A1) lingual, A2) stereo occlusal and A3) buccal view; B) PDYV 21, right m/2, B1) buccal, B2) stereo occlusal, B3) lingual and B4) mesial view; C) PDYV 20, right m/3, C1) buccal, C2) stereo occlusal, C3) lingual and C4) mesial view; D) PDYV 0252, right m/3; D1) buccal, D2) stereo occlusal, D3) lingual and D4) mesial view (scale bar : 10 mm).

notable differences concern the lingual side of the tooth. The lingual surface of the metaconid is adorned with a tall cingular cusplet that tapers apically, almost reaching the apex of the cusp. Behind this structure, there are two lower cingular cusplets at the lingual end of the transverse valley, and there is a slightly taller cingular cusplet at the front of the entoconid.

The two right m/3s (PDYV 20 and PDYV 0252) are basically upscaled versions of the m/1 but with the addition of a well developed talonid behind the distal cusp pair. Unlike the m/2 described above, there is no sign of lingual cingular cusplets in either of the m/3s. The mesial fovea is prominent between the protoconid and metaconid, the "zygodont" cristids are present

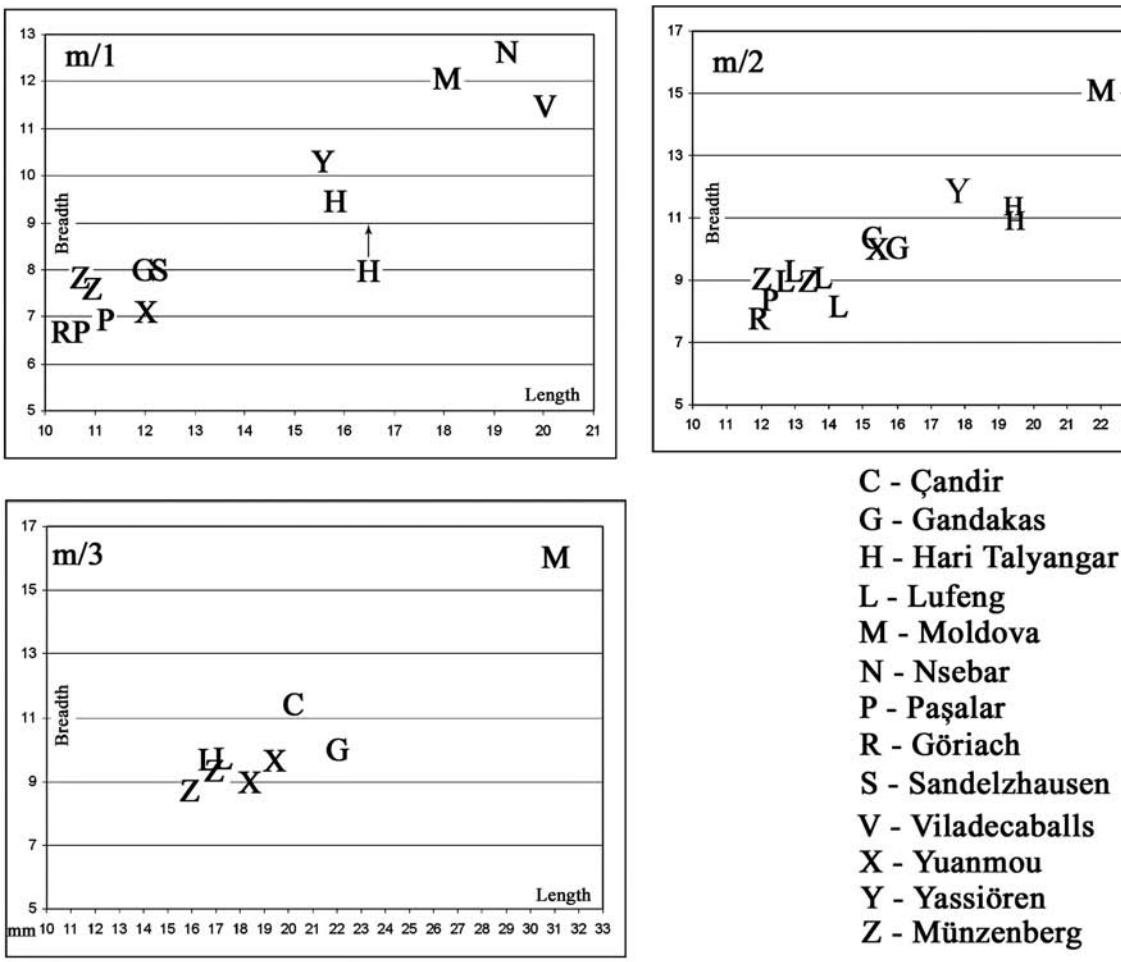

Fig. 20.—Length-breadth plots of the lower molars of lophodont Palaeochoeridae. The Paşalar specimens have until recently been attributed to *Choeromorus inonuensis* (ex *Taucanamo inonuensis*) but the cusps are rather lophodont, suggesting a possible transfer to *Pecarichoerus*, close to *Pecarichoerus orientalis*. Molars of *Yunnanochoerus* tend to be narrower than those of *Schizoporcus*. (N.B. the breadth measurement of Prasad's specimen from Hari Talyangar is probably too narrow – arrow in figure). Note also the relatively small dimensions of the specimen from Yassiören when compared with those of *Schizoporcus vallesensis*, which supports its identification as a distinct species, *Schizoporcus arambourgi* (Ozansoy, 1965).

but almost worn away, their position being shown by the grooves that parallel them. The distal fovea is poorly developed and open to the rear, being more like a groove than a basin. The talonid is comprised of a large hypoconulid about half the height of the crown, accompanied by a prehypoconulid cristid that descends towards a low lingual cusplet or basal pillar. In PDYV 20 the basal pillar is small, but in PDYV 0252 it is enlarged and almost as tall as the hypoconulid. The hypoconulid sends low but sharp cristids buccally and lingually.

Where preserved the roots of these teeth reveal that they are fused bucco-lingually, as is usual in palaeochoerids. In the m/3s the root beneath the hypoconulid slants distinctly towards the rear, but it is strongly fused to the root beneath the hypoconid and entoconid.

Discussion: The four lower molars from Yuanmou, Yunnan, China, are similar in dimensions and morphology to the holotype of *Yunnanochoerus gandakasensis* (Pickford, 1977). They are similar in morphology to the Lufeng fossils of *Yunnanochoerus lufengensis* (Han, 1983) but are appreciably larger than them (Fig. 20, Table 4).

Van der Made & Han (1994) separated the European and Asian palaeochoerids into two genera, *Schizochoerus* for Europe (now *Schizoporcus*), and *Yunnanochoerus* for Asia. The main differences between these genera concern the elongation of the premolars (longer in *Yunnanochoerus* than in *Schizoporcus*) and the number of cusps in the p/4 (double cusped in *Schizoporcus*: single cusp in *Yunnanochoerus*). The separation between the molar lophids appears to be greater in the Asian than in the European forms, but it is clear that the two genera are closely related. The Asian species also appears to have more developed mesial molar cingula than the European species.

There can be little doubt that Van der Made & Han (1994) are correct about the material from the Indian subcontinent

Table 5.—**Measurements (in mm) of molars of *Lophochoerus nagrii* from Chiang Muan, Thailand Hari Talyangar, India, Nagri, Pakistan and from Chinese Drug Stores in Hong Kong**

Catalogue N°/ Country	Tooth	Mesio-distal length	Bucco-lingual breadth	Data source
CMu 426 Thailand	m/1 left	9.9	6.85	Kunimatsu pers. comm. 2010
GSI B 692 India	m/1 left	9.2	7.0	Pickford, 1988 (estimated)
GSI B 693 India	m/1 right	9.4	7.4	Pickford, 1988 (estimated)
GSI B 693 India	m/2 right	10.6	8.4	Pickford, 1988 (estimated)
YPM 39223 Pakistan	m/3 right	16.7	9.7	Pickford, 1988
SMF 6499 China	m/3 left	20.5	9.7	Von Koenigswald, 1963 fig. 10
SMF 6503 China	M1/ left	9.8	9.5	Von Koenigswald, 1963 fig. 13
SMF 6501 China	M2/ right	12.0	11.4	Von Koenigswald, 1963 fig. 12
SMF 6134 Pakistan	M1/ left	11.0	11.0	Own, 2011
SMF 6134 Pakistan	M2/ left	13.2	12.6	Own, 2011
SMF 6134 Pakistan	M3/ left	14.7	12.7	Own, 2011

being congeneric with that from Yunnan (they classified the Potwar holotype as *Yunnanochoerus gandakasensis*).

Family Suidae Gray, 1821
Subfamily Tetraconodontinae Simpson, 1945
Genus *Lophochoerus* Pilgrim, 1926
Species *Lophochoerus nagrii* Pilgrim 1926

Material: CMu 426, left m/1 from Chiang Muan, Thailand, SMF 6134 (Ng 3), left maxilla containing M1/-M3/ from Nagri, Pakistan.

Description: The lower molar from Chiang Muan, Thailand, CMu 426, is a left m/1 lacking its roots. The cusp tips of the mesial cusp pair are lightly worn, exposing small dentine lakes. There is a bucco-lingually broad mesial cingulum which is narrow mesio-distally. The preprotocristid is well developed and descends mesio-centrally and links to the premetacristid forming a loop of enamel that slightly overhangs the mesial cingulum. The median transverse valley is moderately broad and is obstructed in its centre by the median accessory cusplet. At its buccal end, the median transverse valley has low basal pillar. The entoconid is isolated from the hypoconid except at its base. The hypoconulid is small and joined to the hypoconid by the posthypocristid (Fig. 21). The base of the tooth is deep, which distinguishes it from molars of lophodont palaeochoerids. The slight flattening of the lingual cusps agrees with Pilgrim's (1926) description of the molars of this genus.

Because the upper dentition of *Lophochoerus nagrii* is extremely poorly known, it is appropriate to provide measurements and illustrations of a maxilla from Nagri, Pakistan, collected by G.H.R. Von Koenigswald in 1954. The specimen (Fig. 21B, Table 5) is housed in the Senckenberg Museum, Frankfurt.

Discussion: In a previous paper on the biochronology of Chiang Muan this tooth was identified as a lower molar of *Pecarichoerus sminthos* (Pickford *et al*., 2004). However, the median transverse valley is considerably narrower than is usual in lophodont palaeochoerids, the cristids are not as well developed, the Fürchen are open and shallow, and the base of the tooth is deep, all of which are features that indicate that the specimen represents a suid rather than a lophodont palaeochoerid (Fig. 21). Comparisons with specimens from India (Pilgrim, 1926; Pickford, 1988) reveal that it is a left m/1 of *Lophochoerus nagrii*, a tiny tetraconodont suid.

Von Koenigswald (1963) described briefly and illustrated two upper molars that he obtained from Chinese Drug Stores in Hong Kong, designating the upper first or second molar (Von Koenigswald, 1963, fig. 12) as the holotype of *Lophochoerus pilgrimi* (the tooth is likely an M2/) and a first upper molar as *Lophochoerus* cf *pilgrimi* (Von Koenigswald, 1963, fig. 13). The specimens have the right dimensions and morphology to belong to *Lophochoerus nagrii* (Table 5). A third lower molar described in the same paper (Von Koenigswald, 1963, fig. 10) as the holotype of *Sus officinalis* is likely the same species. Its breadth is similar to that in a specimen of *Lophochoerus nagrii* from the Siwaliks (Table 5) housed in the Yale Peabody Museum (Pickford, 1988) but the Drug Store specimen is somewhat longer (20.5 mm versus 16.7 mm). These records extend the range of the genus to unknown localities in southern China where much of the fossil material in Chinese Drug Stores was obtained (Fig. 1).

Pickford (1988) estimated the age range of *Lophochoerus nagrii* to be 12-9 Ma. The species is exceedingly rare, so this age range is provisional, but it agrees with the age estimate of the Chiang Muan, Thailand, deposits made on the basis of the proboscideans and other mammals (Pickford *et al*., 2004). The Thai record extends the geographic range of the species 2,700 km to the southeast of its previously known distribution in the Indian Subcontinent (Fig. 1).

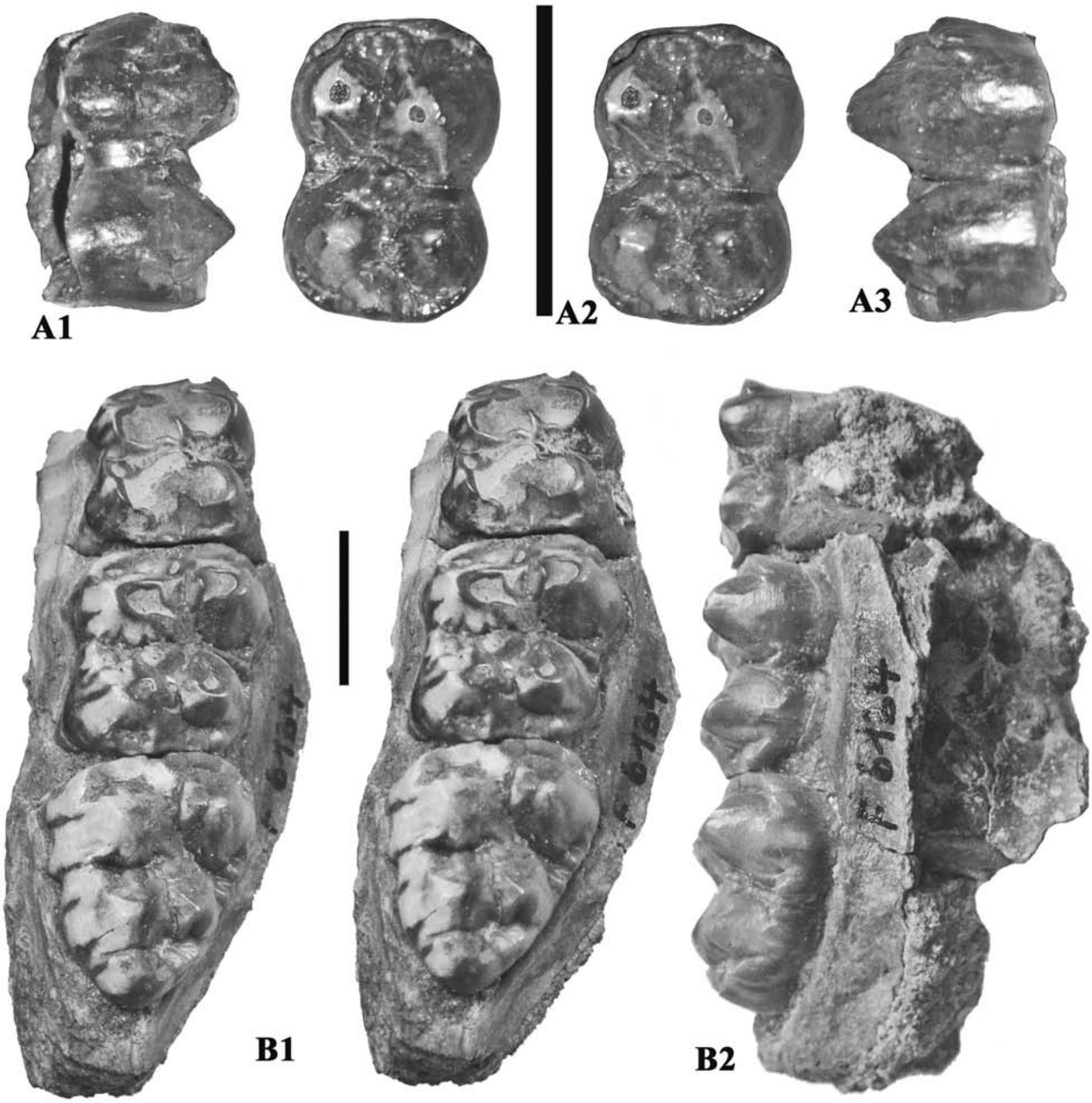

Fig. 21.—Dental elements of *Lophochoerus nagrii* A) CMu 426, left m/1, from Chiang Muan, Thailand; A1) buccal, A2) stereo occlusal, and A3) lingual views; B) SMF 6134, left maxilla with M1/-M3/ from Nagri, Pakistan, B1) stereo occlusal, and B2) lingual views (scale bars : 10 mm) (image of Cmu 426 courtesy of Y. Kunimatsu).

Genus *Albanohyus* Ginsburg, 1974
Species *Albanohyus pygmaeus* (Depéret, 1892)

Material: SMNS 42820, right mandible fragment containing m/3 from Przeworno, Poland; NHM M 13507, three isolated m/3s (two left, one right) from La Grive-St-Alban, France.

Description: The m/3 in the Przeworno mandible is in medium wear and measures 11.8 x 7.0 mm. The buccal and lingual roots are not fused to each other, the lophs are closer together than is the case in *Taucanamo*, and the precristid of the hypoconid is weaker than in palaeochoerids. The buccal and lingual notches are not deep and broad, but are about half the height of the crown and narrow.

The three lower third molars from La Grive-St-Alban are unworn, and none of them preserves the roots (Fig. 23). The lophs are close together, the buccal and lingual notches are narrow, and shallow, the bases of the teeth being relatively tall.

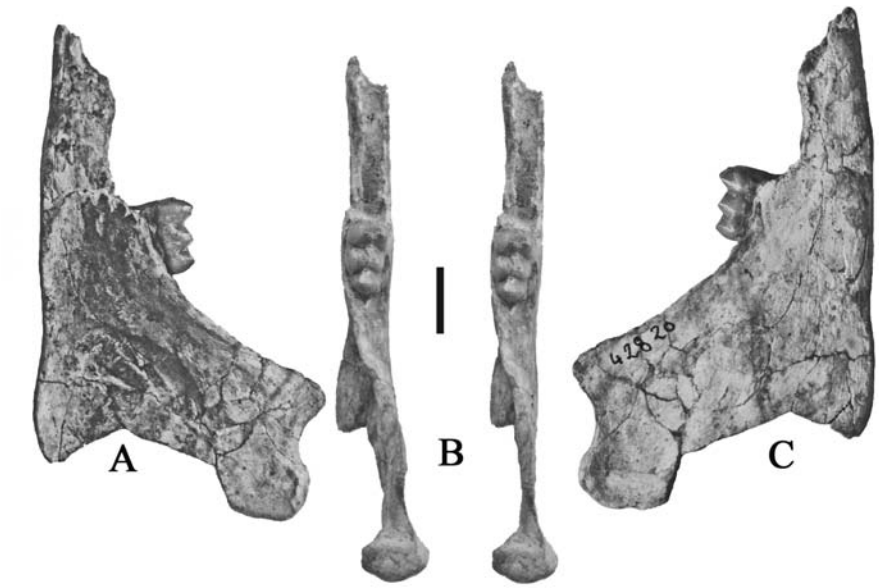

Fig. 22.—SMNS 42820, *Albanohyus pygmaeus*, right mandible with m/3 from Przeworno, Poland, A) lingual, B) stereo occlusal, and C) buccal views. Note the mandibular condyle located well above the occlusal surface of the cheek teeth, a character that separates suids from palaeochoerids (scale : 10 mm).

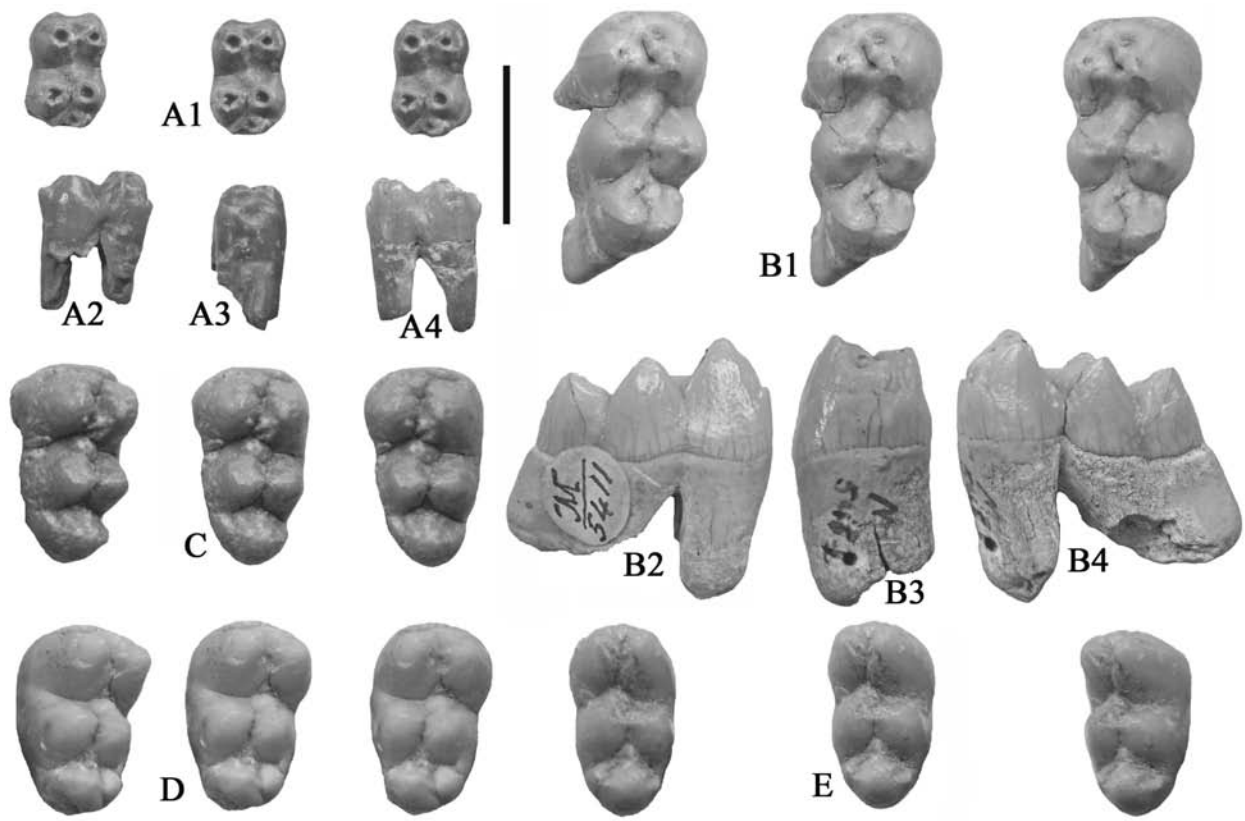

Fig. 23.—Lower molars of *Choeromorus grandaevus* (A-B) and *Albanohyus pygmaeus* (C-E) from La Grive-St-Alban, France. A) NHM M 5413, right m/1, stereo occlusal, buccal, mesial and lingual views, B) NHM M 5411, left m/3, stereo occlusal, lingual, mesial and buccal views, C) NHM M 13507, left m/3, stereo occlusal views, D) NHM M 13507, right m/3, stereo occlusal views, E) NHM M 13507, left m/3, stereo occlusal views (scale : 10 mm).

Table 6.—**Measurements (in mm) of lower third molars of *Albanohyus pygmaeus***

Catalogue N°	Locality	Tooth	Mesio-distal length	Bucco-lingual breadth
SMNS 42820	Przeworno	m/3 right	11.8	7.0
NHM M13507	La Grive	m/3 left	12.9	7.6
NHM M13507	La Grive	m/3 left	11.7	6.9
NHM M13507	La Grive	m/3 right	12.5	8.0

Discussion: The mandible fragment from Przeworno housed in the Stuttgart Museum was previously attributed to *Taucanamo* but it belongs to the small suid *Albanohyus* and not to a palaeochoerid. This is revealed not only by the morphology of the molar and its roots, but also by the high position of the mandibular condyle (Fig. 22). Previous authors (Kubiak 1981, 1982) attributed the small Przeworno suoids to *Taucanamo*, but Chen (1984) referred them to *Barberahyus* Golpe-Posse (1977) at the time thought to be a tayassuid, but now known to be a suid. *Barberahyus* is a junior synonym of *Albanohyus* Ginsburg (1974) according to Van der Made (1996). The latter author (Van der Made, 1996, 2010) considered that Przeworno has yielded two small suoids, the suid *Albanohyus* and the palaeochoerid *Taucanamo grandaevum*, the latter attributed in this paper to *Choeromorus grandaevus*. The same species occurs at Atzelsdorf, Austria (Daxner-Höck & Bernor, 2009).

Systematics

The following systematic arrangement and synonymy is proposed for Middle and Late Miocene Palaeochoeridae.

Family Palaeochoeridae Matthew, 1924
(For detailed synonymy lists of *Propalaeochoerus* and *Palaeochoerus* reference is made to Hellmund, 1992)
Subfamily Taucanaminae Van der Made, 1997a
Tribe *Schizoporcini* Van der Made, 2010
Genus *Pecarichoerus* Colbert, 1933
Type species *Pecarichoerus orientalis* Colbert, 1933
Species *Pecarichoerus orientalis* Colbert, 1933
Holotype AMNH 29955, three isolated upper teeth (Colbert, 1933, figs 1-2)
Synonymy

1909 *Choerotherium sansaniense* Lartet; Zdarsky, pp. 260-264, pl. 7, figs 12-14.
v*1933 *Pecarichoerus orientalis* gen. et sp. nov.; Colbert, pp. 1-7, figs 1-2, 3a, 4d, table.
1934 *Choerotherium sansaniense* Lartet; Pia & Sickenberg, pp. 183 (n° 1585), 187 (n° 1616, 1618).
v1935 *Pecarichoerus orientalis* Colbert; Colbert, pp. 214-216, fig. 98.
1956 *Taucanamo sansaniense* (Lartet); Thenius, pp. 366-369, fig. 27-28, not n° 56633.
1967 *Taucanamo sansaniense* (Lartet); Petronijevic, pp. 77-78, 144, pl. 13, figs 2-5.
1969 *Taucanamo sansaniense* (Lartet); Pavlovic, pp. 333-338 (Prebreza), 382, pls 12-13.
1970 *Taucanamo sansaniense* (Lartet); Mottl, p. 26.
1983 *Taucanamo sansaniense* (Lartet); Weber & Weiss, p. 122.
1983 *Palaeochoerus* (*Aureliachoerus*) *aurelianensis* Stehlin; Zapfe, p. 175-180, figs 6-10.
1993 *Taucanamo sansaniensis* (sic) lineage (Lartet); Van der Made, p. 128.
1998 *Taucanamo*? *muenzenbergensis* sp. nov. Van der Made, pp. 234-239.
2003a *Schizochoerus muenzenbergensis* (Van der Made); Van der Made, 152-155.
v2010 *Schizoporcus muenzenbergensis* (Van der Made); Van der Made, pp. 46-53, figs 1-5, fig. 32.
v2010 *Pecarichoerus orientalis* Colbert; Van der Made p. 98, fig. 32.
2010b *Pecarichoerus orientalis* Colbert; Orliac *et al*., p. 1301.

Species *Pecarichoerus sminthos* (Forster-Cooper, 1913)
Holotype NHM M 12028, left mandible containing m/2-m/3.
Synonymy

v* 1913 *Microbunodon sminthos* sp. nov.; Forster-Cooper, p. 519, fig. 5.
v 1924 *Anthracotherium sminthos* (Forster-Cooper); Forster-Cooper, p. 21, fig. 19.
v 1926 *Lophochoerus exiguus* sp. nov.; Pilgrim, p. 29, pl. 10 fig. 6.
v *1935* *Lophochoerus exiguus* Pilgrim; Colbert, p. 237.
1980 *Macaca youngi* sp. nov. Gu Yumin, pp. 1-7, text-fig.
1984 *Anthracotherium sminthos* (Forster-Cooper): Raza & Meyer, p. 51.
1987 *Macaca youngi* Gu Yumin; Pickford, p. 297.
p1987 *Pecarichoerus sminthos* (Forster-Cooper); Pickford, p. 297.
v1987 *Pecarichoerus sminthos* (Forster-Cooper); Pickford, pp. 306-307.
2004 *Pecarichoerus sminthos* (Forster-Cooper); Pickford *et al*., pp. 66, 68.
2010b *Pecarichoerus* sp. Orliac *et al*., pp. 1300-1303, figs 2.2, 2.3.

Species *Pecarichoerus anatoliensis* (Van der Made, 1997a)
Holotype MTA AÇH 1339, right m/3 (Pickford & Ertürk, 1979, fig. 7, Pl. 3, fig. 5)
Synonymy

v1979 Gen. nov. cf *Taucanamo* Simpson, 1945 sp. nov. Pickford & Ertürk, pp. 148-150, figs 6-7, pl. 3, figs 2-5.

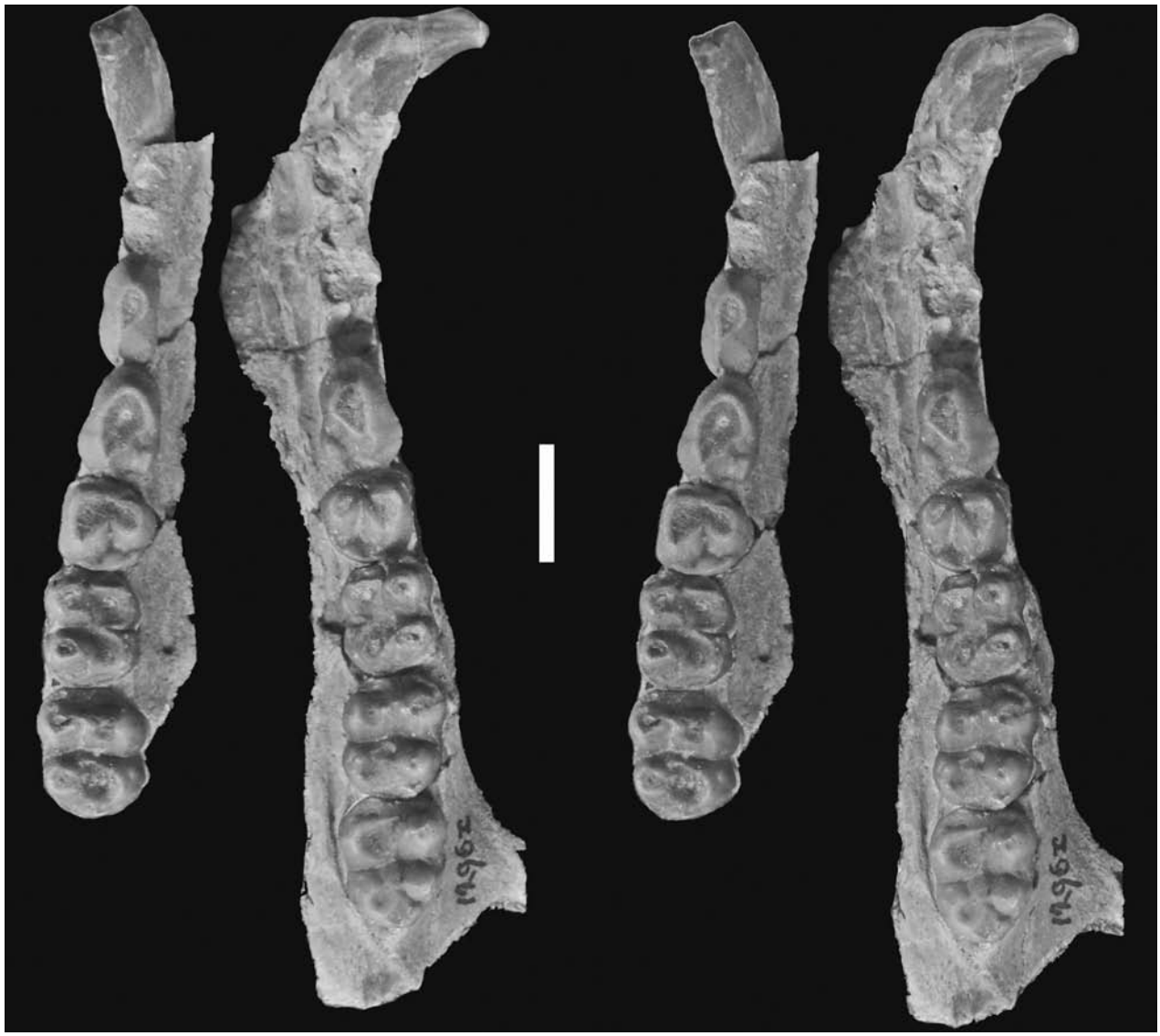

Fig. 24.—SMNS 12962, *Choeromorus grandaevus* (Fraas, 1870) stereo view of left and right maxillae from Steinheim, Germany (scale : 10 mm).

*1997a *Schizochoerus anatoliensis* sp. nov. Van der Made, p. 133.
2007 *Schizochoerus anatoliensis* Van der Made; Harris & Liu Liping, p. 146.
2010 *Schizoporcus anatoliensis* (Van der Made); Van der Made, p. 98, fig. 32.

Species *Pecarichoerus primus* (Van der Made, 1997a)
Holotype MNHN Ar 5, left mandible containing p/1-m/3 from Artenay.
Synonymy
1908 *Choerotherium pygmaeum* Depéret; Mayet, pp. 149-154, Pl. 5, figs 6-7 (specimen from Artenay)
1987 *Taucanamo sansaniense* (Lartet, 1851); Ginsburg & Bulot, pp. 461-462, Pl. 3, figs 10-11 (specimens from Bézian).
v1994 *Taucanamo pygmaeum* (Depéret, 1892); Pickford & Moyà-Solà, pp. 1569-1574, figs 1-6 (specimens from Els Cassots).
v*1997 *Taucanamo primum* nov. sp. Van der Made, pp. 132-133.
2006 *Taucanamo primum* Van der Made; Orliac, Antoine & Duranthon, fig. 11a, appendix 4, fig. 2b
2010 *T. primum* Van der Made; Orliac, Antoine, Roohi & Welcomme, p. 1303.
2010 *Taucanamo primum* Van der Made; Van der Made, p. 98.

Genus *Schizoporcus* Van der Made, 2010, replacement name for *Schizochoerus* Crusafont & Lavocat, 1954, junior homonym of *Schizochoerus* Poche, 1922.
Type species *Schizoporcus vallesensis* (Crusafont & Lavocat, 1954)

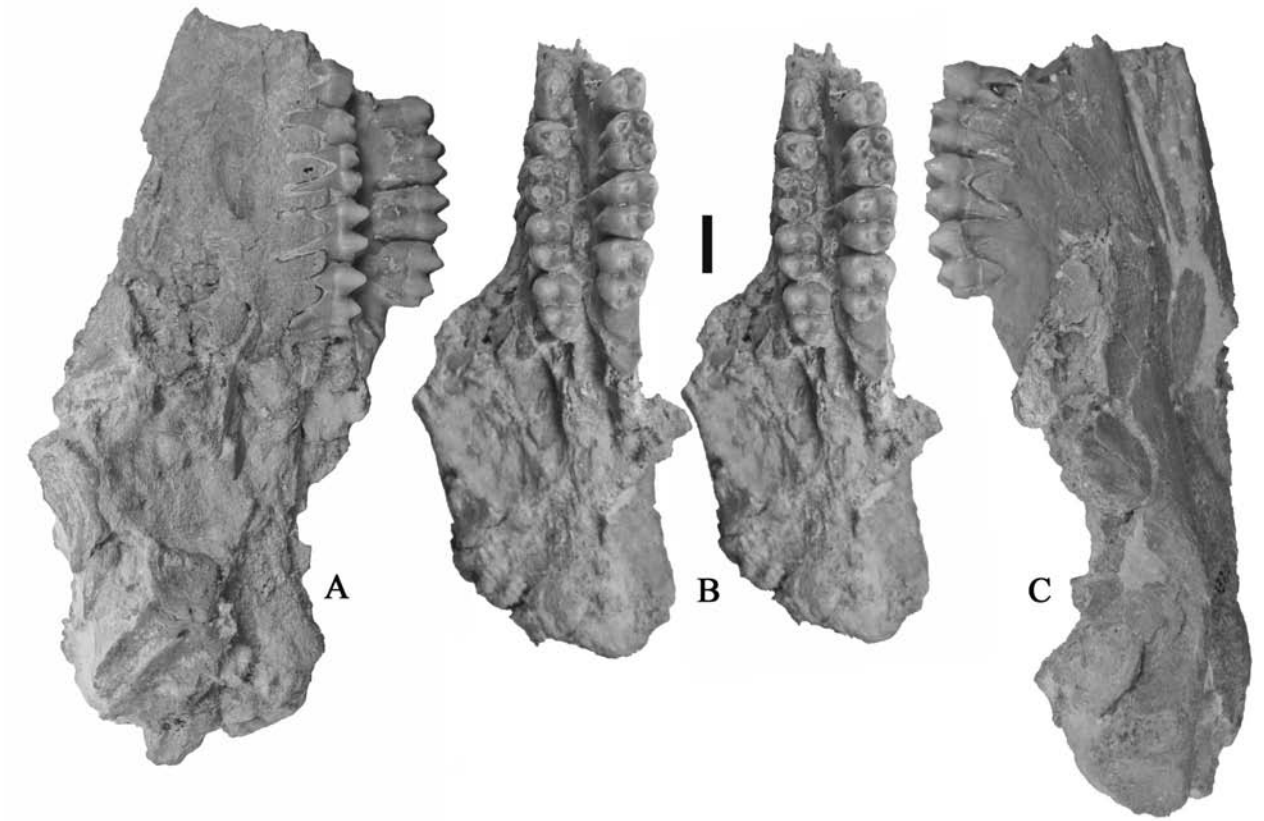

Fig. 25.—SMNS 13234, skull fragment of *Choeromorus grandaevus* (Fraas, 1870) from Steinheim, Germany, A) right lateral view, B) stereo occlusal view, C) left lateral view (scale : 10mm).

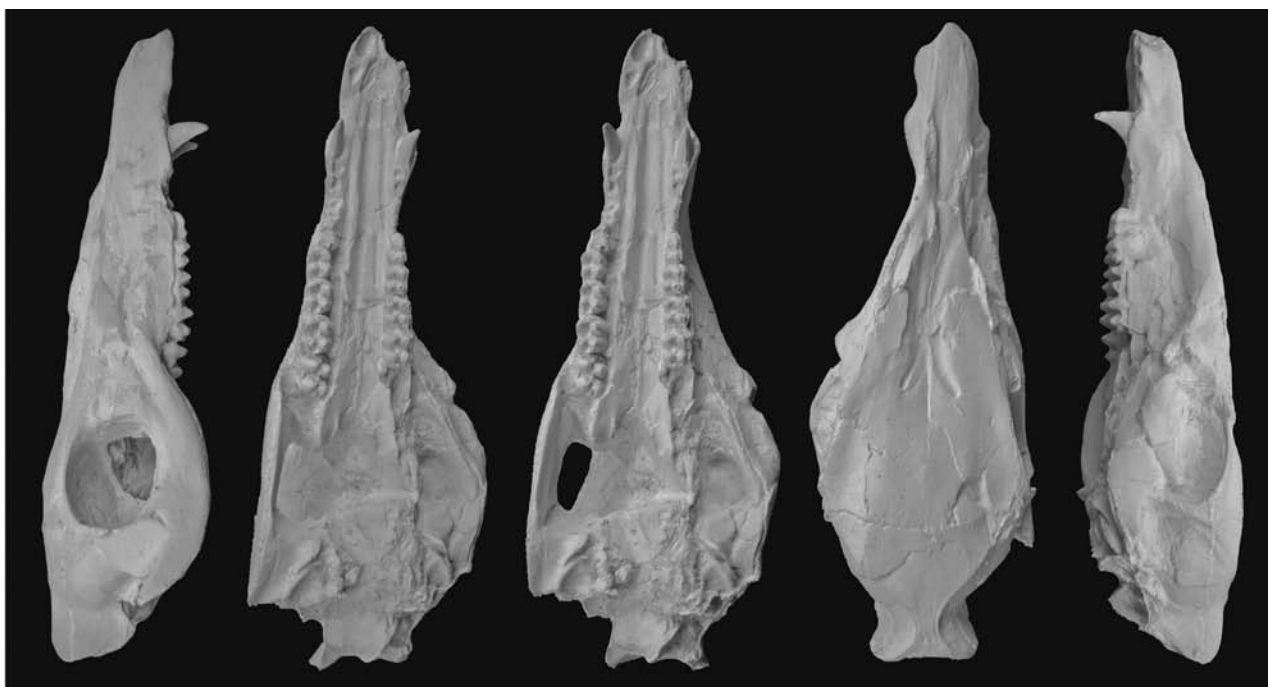

Fig. 26.—SMNS 9901, cast of a skull of *Choeromorus grandaevus* (Fraas, 1870), from Steinheim, Germany, right lateral, stereo occlusal, dorsal and left lateral views (scale : 10 mm).

Fig. 27.—SMNS 44311, left mandible of *Choeromorus grandaevus* (Fraas, 1870) from Steinheim, Germany, stereo occlusal views (scale : 10 mm).

Species *Schizoporcus vallesensis* (Crusafont & Lavocat, 1954)
Holotype Mandible fragments from Can Purull (Viladecaballs), near Sabadell, Catalunya, Spain.
Synonymy

v*1954 *Schizochoerus vallesensis* gen. et sp. nov. Crusafont & Lavocat, pp. 6-11, text-fig.1-2, table.
1957b *Schizochoerus pachecoi* nom. nud. Ozansoy, p. 23.
v1965 *Schizochoerus* cf *arambourgi* sp. nov. Ozansoy, p. 62-64, pl. 6, fig. 8.
v1967 *Schizochoerus vallesensis* Crusafont & Lavocat; Nikolov & Thenius, pp. 330-339, text-fig. 2-4, table.
v1970 *Schizochoerus vallesensis* Crusafont & Lavocat; Thenius, p. 335, text-fig. 5.
1971 *Schizochoerus vallesensis* Crusafont & Lavocat; Lungu, pp. 175-182, figs1-3.
1972a *Schizochoerus vallesiensis* (sic) Crusafont & Lavocat; Golpe-Posse, pp. 153-154.
1972b *Schizochoerus vallesensis* Crusafont & Lavocat; Golpe-Posse, p. 18.
1972 *Schizochoerus vallesensis* Crusafont & Lavocat; Thenius, p. 578, text-fig. 10.
1974 *Schizochoerus vallesensis* Crusafont & Lavocat; Lungu, pp. 60-65, figs 10 & 11, pl. 11, figs 1-3.
1974 *Schizochoerus vallesiensis* (sic) Crusafont & Lavocat; Ginsburg, p. 77.
1975 *Schizochoerus vallesensis* Crusafont & Lavocat; Golpe-Posse, pp. 36, 41, 51,
1975 *Schizochoerus* Crusafont & Lavocat; Becker-Platen, Sickenberg & Tobien, p. 91.
1976 *Schizochoerus* Crusafont & Lavocat; Wilkinson, p. 277.
v1979 *Schizochoerus vallesensis* Crusafont & Lavocat; Pickford & Ertürk, p. 150.
1990 *Schizochoerus vallesiensis* (sic) Crusafont & Lavocat; Van der Made, p. 85.
1994 *Schizochoerus vallesiensis* (sic) Crusafont & Lavocat; Van der Made & Han, p. 56 pl. 3, figs1-3.
1996 *Schizochoerus vallesiensis* (sic) Crusafont & Lavocat; Fortelius, Van der Made & Bernor, pp. 352-353, 374.
1997a *Schizochoerus vallesiensis* (sic) Crusafont & Lavocat; Van der Made, p. 134.
2003b *Schizochoerus vallesiensis* (sic) Crusafont & Lavocat; Van der Made, p. 310.
2003 *Schizochoerus vallesensis* Crusafont & Lavocat; Liu Liping, pp. 15, 20-24.
2007 *Schizochoerus vallesiensis* (sic) Crusafont & Lavocat; Harris & Liu Liping, p. 146.
2010a *Schizochoerus* Crusafont & Lavocat; Orliac *et al*., pp. 318-328.
2010 *Schizoporcus vallesiensis* (sic) (Crusafont & Lavocat); Van der Made, p. 98, fig. 32.

Species *Schizoporcus arambourgi* (Ozansoy, 1965)
Holotype MNHN Yas 27 TRQ 1010, juvenile mandible with mixed dentition.
Synonymy

1957a *Schizochoerus arambourgi* nom. nud. Ozansoy, pp. 33, 43, pl. 1, fig. 3.
1957b *Schizochoerus arambourgi* nom. nud. Ozansoy, pp. 21, 23.
v*1965 *Schizochoerus arambourgi* sp. nov. Ozansoy, pp. 61-62, pl. 6, figs 1, 1a.
v1978 *Schizochoerus* cf *gandakasensis* (Pickford); Pickford, pp. 32-33, text-fig. 4.
v1979 *Schizochoerus* cf *gandakasensis* (Pickford); Pickford & Ertürk, pp. 150-152, text-figs 8-11, pl. 3, fig. 6.
1994 *Schizochoerus* cf *gandakasensis* (Pickford); Van der Made & Han, pp. 42-43, fig. 6.
v1996 *Schizochoerus* sp. Fortelius, Van der Made & Bernor, pp. 352-353, fig. 6.
1997a *Schizochoerus sinapensis* sp. nov. Van der Made, p. 134.
2003b *Schizochoerus sinapensis* Van der Made; Van der Made, pp.309-310, table 13.1.
2007 *Schizochoerus sinapensis* Van der Made; Harris & Liu Liping, p. 146.
2010 *Schizoporcus sinapensis* (Van der Made); Van der Made, p. 98, fig. 32.

Tribe Taucanamini Van der Made, 1997a
Genus *Choeromorus* Gervais, 1850
Type species *Choeromorus mamillatus* Gervais, 1850
Species *Choeromorus mamillatus* Gervais, 1850
Holotype MNHN Sa 4580, right mandible with p3-p4 and m2-m3 (originally with all three molars) (Gervais, 1850, pl. 33, fig. 4).
Synonymy of the Sansan material

1847 *Sus choerotherium* Blainville, p. 231, pl. IX.
1847 *Sus lemuroides* Blainville, p. 231, pl. IX.
v*1850 *Choeromorus mamillatus* gen. and sp. nov. Gervais, p. 7, pl. 33, fig. 4.
v1850 *Choeromorus simplex* sp. nov. Gervais, p. 7, pl. 33, fig. 5.

v1851 *Choerotherium sansaniense* sp. nov. Lartet, p. 33.
1859 *Sus choerotherium* Blainville; Gervais, 1859, p. 170.
1859 *Sus*? *lemuroides* Blainville; Gervais, 1859, p. 179.
v1859 *Choeromorus mamillatus* Gervais; Gervais, p. 185, pl. 33, fig. 4.
v1859 *Choeromorus simplex* Gervais; Gervais, p. 186, pl. 33, fig. 5.
1859 *Choerotherium sansaniense* Lartet; Gervais, p. 187.
1873 *Choerotherium* Lartet; Kowalesky, pp. 201, 261-263, pl. 7, fig. 6; pl. 8, fig. 77, table opposite p. 152.
v1882 Palaeocherus (sic) Filhol, p. 1259
v1890 *Choeromorus sansaniense* (Lartet); Filhol, p. 219, pl. XIX, figs 1-9; pl. XX; pl. XLIV, figs 1-4.
v1890 *Choerotherium mamillatum* (Gervais); Filhol, p. 228, pl. XIX, figs 10-11.
v1892 *Choeromorus sansaniensis* (Lartet); Depéret, pp. 87-88.
v1899-1900 *Choerotherium sansaniense* Lartet; Stehlin, pl. 1, figs 18, 23; pl. 3, figs 26, 27; pl. 5, figs 4, 11; pl. 9, fig. 2.
v1908 *Choerotherium sansaniensis* Lartet; Mayet, p. 152.
1927 *Sansaniense* (sic) Lartet; Pearson, p. 407, figs 15-17.
1945 *Choerotherium sansaniense* Lartet; Simpson, 1945, p. 146, foot note.
1963 *Taucanamo sansaniense* (Lartet); Ginsburg, pp. 3-15.
v1967 *Taucanamo sansaniense* (Lartet); Bergounioux & Crouzel, p. 4, figs 1-11.
1997a *Taucanamo sansaniense* (Lartet); Van der Made, p. 134.
2004 *Taucanamo sansaniense* (Lartet, 1851); Stefanovic, p. 80.
2006 *Taucanamo sansaniense* (Lartet); Orliac, Antoine & Duranthon, appendix 4, figs 1c, 1d, 3b, 4b.

Species *Choeromorus inonuensis* (Pickford & Ertürk, 1979)
Holotype MTA AKI 3.4, palate with canine and right cheek dentition.
Synonymy
v*1979 *Taucanamo inonuensis* sp. nov. Pickford & Ertürk, pp. 147-148, fig. 5, table 3.
1990 *Taucanamo inonuensis* Pickford & Ertürk; Fortelius & Bernor, pp. 521, 523-524, figs 7-8, table 3.
1997a *Taucanamo inonuensis* Pickford & Ertürk; Van der Made, p. 134.
1998 *Taucanamo inonuensis* Pickford & Ertürk; Van der Made, p. 236.
2007 *Taucanamo inonuensis* Pickford & Ertürk; Harris & Liu Liping, p. 146.
2010 *Taucanamo inonuensis* Pickford & Ertürk; Van der Made, p. 98, fig. 32.

Species *Choeromorus grandaevus* (Fraas, 1870)
Synonymy
v*1870 *Colobus grandaevus* sp. nov. Fraas, p. 3-4, pl. 1, fig. 1.
1885 *Cebochoerus suillus* sp. nov. Fraas, p. 324-325, pl. 5, fig. 2, 3a, 3b.
1892 *Choeromorus pygmaeus* Depéret, p. 87-90.
1899-1900 *Choerotherium pygmaeum* Depéret; Stehlin, pp. 77-80, 129, 273-276, 421-422, pl. 1 fig. 24.
1927 *Choerotherium pygmaeum* (Depéret); Pearson, pp. 405-409, text-fig. 14.
1945 *Taucanamo pygmaeum* (Depéret); Simpson, p. 143.
1973 *Taucanamo pygmaeum* (Depéret); Heizmann, p. 86.
1984 *Taucanamo pygmaeum* (Depéret); Chen Guanfang, pp. 88-91, table, pl. 2, figs 4-6, pl. 3, figs 1-8.
1997a *Taucanamo grandaevum* (Depéret); Van der Made, p. 134.

Fig. 28.—Cast of left maxillary teeth (P4/-M3/) of *Choeromorus grandaevus* from Anwil, Switzerland, stereo occlusal views. Original fossil is in Basel (scale : 10 mm).

2006 *Taucanamo grandaevum* (Depéret); Orliac, Antoine & Duranthon, pp. 705-707, table 1, figs 8.5-8.10, 9.1, 11b, appendix 5, fig. 2c, 2f

Tribe Yunnanochoerini nov.
Definition
Taucanaminae with elongated molars and premolars, tall cusps in molars, larger body size than in Taucanamini.
Type genus *Yunnanochoerus* Van der Made & Han, 1994
Genus *Yunnanochoerus* Van der Made & Han, 1994
Type species *Yunnanochoerus lufengensis* (Han, 1983).
Synonymy
*1970 *Anthraconema* nov. gen. Prasad, p. 37.
1977 *Taucanamo* partim (*T. gandakasense* Pickford, pp. 13-17, text-fig. 1, table 1)
1978 *Schizochoerus* partim (*S. gandakasensis* Pickford, p. 36, text-fig. 2).
1994 *Yunnanochoerus* gen. nov. Van der Made & Han, pp. 33-44.

Species *Yunnanochoerus lufengensis* (Han, 1983)
Holotype IVPP V 6891, left mandible fragments containing p/2-p/4, m/2-m/3 (Han, 1983, pl. 1, fig. 4, pl 2, fig. 3, text figs 1 and 2).
Synonymy
*1983 *Lophochoerus lufengensis* sp. nov. Han, pp 22-26, figs 1 & 2, not fig. 3, table.
1985 *Lophochoerus lufengensis* Han; Han, p. 45.
1994 *Yunnanochoerus lufengensis* (Han); Van der Made & Han, pp. 34-44, table 1, pls 1-2, pl. 4, figs 1-2.
2003 *Yunnanochoerus lufengensis* (Han); Liu Liping, pp. 11, 15, 20-24.
2007 *Yunnanochoerus lufengensis* (Han); Liu & Pickford, pp. 45, 67, table 2, 3.

2007 *Yunnanochoerus lufengensis* (Han); Harris & Liu Liping, p. 146.
2010a *Yunnanochoerus* Van der Made & Han; Orliac *et al*., pp. 318-328.
2010 *Yunnanochoerus lufengensis* (Han); Van der Made, p. 98, fig. 32.

Species *Yunnanochoerus dangari* (Prasad, 1970)
Holotype GSI 18078, isolated molar (Prasad, 1970, pl. XV, fig. 3).
Synonymy
v*1970 *Anthraconema dangari* gen. et sp. nov. Prasad, p. 37, pl. XV, fig. 3.
v1978 *Schizochoerus dangari* (Prasad); Pickford, p. 36.

Species *Yunnanochoerus gandakasensis* (Pickford, 1977)
Holotype GSP 4192, left mandible with cheek teeth (Pickford, 1977, fig. 1)
Synonymy
v*1977 *Taucanamo gandakasense* sp. nov. Pickford, pp. 13-17, fig. 1, table 1.
v1978 *Schizochoerus gandakasensis* (Pickford); Pickford, p. 36, text-fig. 2.
1997a *Yunnanochoerus gandakasensis* (Pickford); Van der Made, p. 134.
2003 *Schizochoerus gandakasensis* Pickford; Liu Liping, p. 15.
2006 *Yunnanochoerus* sp.; Qi *et al*., p. 709.
2007 *Yunnanochoerus gandakasensis* (Pickford); Harris & Liu Liping, p. 146.
2010 *Yunnanochoerus gandakasensis* (Pickford); Van der Made, p. 98, fig. 32.

Phylogenetic considerations

Some authors (Pickford, 1988; Van der Made, 1997a) have considered that lophodont palaeochoerids evolved from bunodont ancestors. The transition from bunodont to lophodont morphology has caused debate in the literature, with some forms originally classified in *Taucanamo* by various authors (see synonymy lists) being transferred to *Schizochoerus* by Van der Made (1997a) (now *Schizoporcus*) and *Pecarichoerus*. The relationships between the end products of the lophodont trends (*Schizoporcus*, *Yunnanochoerus*) initially proved to be difficult to disentangle because of the high degree of convergence and the relatively poor fossil record. Historically, this has meant that many of the lophodont palaeochoerid fossils were originally thought to represent suids related to *Listriodon* or even to be anthracotheres, perissodactyls or monkeys. Once better material was found, it became clear that the lophodonty in palaeochoerids was derived independently from that in lophodont suids such as Listriodontinae and Namachoerinae (Pickford, 1995).

Van der Made (2010) classified some middle Miocene species in *Schizoporcus* (replacement name for *Schizochoerus* Crusafont & Lavocat, 1954) that had hitherto been classified in *Taucanamo*, including *Schizoporcus muenzenbergensis* (Van der Made, 1998) here considered to be a junior synonym of *Pecarichoerus orientalis* Colbert, 1933, and *Schizoporcus anatoliensis* (Van der Made, 1997a) which are here referred to the genus *Pecarichoerus*. He also classified two Late Miocene species in the same genus *Schizoporcus* (*S. sinapensis* (Van der Made, 1997a) and *S. vallesensis* (Crusafont & Lavocat, 1954)). The former is a junior synonym of *Schizoporcus arambourgi* (Ozansoy, 1965).

I consider that the Middle Miocene European species, *S. muenzenbergensis* and *S. anatoliensis* have closer morphological and metric affinities to *Pecarichoerus orientalis* than they do to *Schizoporcus arambourgi* (Ozansoy, 1965; Van der Made, 1997a) and *Schizoporcus vallesensis* (Crusafont & Lavocat, 1954) (this proximity of relationship is implied by Van der Made (2010, fig. 32)) and I therefore transfer them to this genus as *Pecarichoerus orientalis* (Colbert, 1933) and the new combination *Pecarichoerus anatoliensis* (Van der Made, 1997a) and I leave the two Late Miocene species in the genus *Schizoporcus* (*S. arambourgi* (Ozansoy, 1965) = *S. sinapensis* (Van der Made, 1997a) and *S. vallesensis* (Crusafont & Lavocat, 1954). If not, then *Schizoporcus* Van der Made (2010) would become a junior synonym of *Pecarichoerus* Colbert (1933).

Van der Made (2010, fig. 32) recognised a deep split between the *Schizoporcus* and *Yunnanochoerus* lineages, dating back to the middle of MN 5 (ca 15 Ma), and he recognised *Pecarichoerus orientalis* as an offshoot of the *Schizoporcus* lineage. Among the important features differentiating these lineages are the molar and premolar proportions (Van der Made, 1997a, 2010; Van der Made & Han, 1994). Another is the morphology of the P4/ which in the *Choeromorus* group has an anteriorly positioned protocone in line with the paracone, with the lingual sinus oriented obliquely forwards, whereas in the *Pecarichoerus* group the protocone is posteriorly positioned and the lingual sinus is oriented obliquely posteriorly (Fig. 9) (Colbert, 1933; Van der Made, 2010). Orliac *et al*., (2010b) reached much the same conclusion, highlighting the "sharp oblique ridge running between the anterior and posterior pairs of cusps of the upper molars" that occurs in *Pecarichoerus ori-*

entalis and "*Taucanamo*" *primum* from the Early Miocene, but not in species of *Taucanamo* (i.e. *Choeromorus sansaniensis* and *Choeromorus grandaevus*). As these authors pointed out, this ridge is comprised of the premetacristule and the centroconule.

Conclusions

My assessment of the relationships and taxonomy of Miocene Palaeochoeridae taking into account the information yielded by the newly available fossils from the Late Miocene of India and China, is that Van der Made's (2010) scheme has much to recommend it, but it is evident that some changes of nomenclature are needed. Early members of the schizoporcine group are here attributed to *Pecarichoerus* rather than to *Schizoporcus*. If these two should eventually prove to be congeneric when their fossil record improves, then *Pecarichoerus* would prevail as the valid name. I also include *Pecarichoerus primus* in the genus on account of its shared derived molar morphology with other species of the genus (Orliac *et al*., 2010b), different from the morphology found in species of *Choeromorus*. *Schizoporcus sinapensis* is here considered to be a junior synonym of *Schizoporcus arambourgi*.

The systematic arrangement adopted in this paper is shown in Table 7, subject to change when poorly understood taxa become better known. Subfamily and tribe names are omitted on account of uncertainty about the utility of some recently proposed subfamily and tribe names (Van der Made, 1997a, 2010) and of doubts about their contents. Van der Made (2010) subdivided the Palaeochoeridae into three subfamilies (Unknown, Taucanaminae Van der Made, 1997a, and Palaeochoerinae Matthew, 1924) the two named subfamilies being further subdivided into two tribes each (Schizoporcini Van der Made, 2010, and Taucanamini Van der Made, 1997a, for the former and Doliochoerini Simpson, 1945, and Palaeochoerini Matthew, 1924, for the latter). There is a slight possibility, evoked by Van der Made (1997a) and explained in detail by Orliac *et al*., (2010) that *Taucanamo* and *Pecarichoerus* could be synonyms, in which case *Pecarichoerus* would be the valid name.

This uncertainty impinges on the nomenclature of the Sansan palaeochoerids, Van der Made (1997a) having proposed that, in the interests of stability, *Taucanamo* Simpson, 1945, should be retained (instead of *Choeromorus* Gervais, 1850). Given the possible synonymy between *Taucanamo* and *Pecarichoerus* (Orliac *et al*., 2010) then the most stable solution is to recognise *Choeromorus* Gervais 1850, as the valid genus name for the Sansan palaeochoerids.

Choeromorus Gervais (1850) (type species *Choeromorus mamillatus* Gervais, 1850) has priority over *Taucanamo* Simpson (1945). Simpson (1945) recognised the validity of *Choeromorus*, but erroneously classed it in the Cebochoeridae, and erected the genus *Taucanamo* to replace *Choerotherium* (type species *Choerotherium sansaniense* Lartet, 1851) in ignorance of the fact that *Choerotherium sansaniense* was a junior synonym of *Choeromorus mamillatus*, thereby creating a homonym. Van der Made (1997a) wondered whether *Pecarichoerus*

Table 7.—**Systematic arrangement of Palaeochoeridae Matthew, 1924**

Family Palaeochoeridae Matthew, 1924
- *Pecarichoerus* Colbert, 1933
  - *P. sminthos* (Forster-Cooper, 1913)
  - *P. orientalis* Colbert, 1933
  - *P. primus* (Van der Made, 1997a)
  - *P. anatoliensis* (Van der Made, 1997a)
- *Schizoporcus* Van der Made, 2010
  - *S. vallesensis* (Crusafont & Lavocat, 1954)
  - *S. arambourgi* (Ozansoy, 1965)
- *Choeromorus* Gervais, 1850
  - *C. mamillatus* Gervais, 1850
  - *C. grandaevus* (Fraas, 1870)
  - *C. inonuensis* (Pickford & Ertürk, 1979)
- *Yunnanochoerus* Van der Made & Han, 1994
  - *Y. dangari* (Prasad, 1970)
  - *Y. gandakasensis* (Pickford, 1977)
  - *Y. lufengensis* (Han, 1983)
- *Doliochoerus* Filhol, 1882
  - *D. quercyi* (Filhol, 1882)
- *Propalaeochoerus* Stehlin, 1899
  - *P. gergovianus* (Croizet *in* de Blainville, 1847)
  - *P. leptodon* (Pomel, 1848)
  - *P. elaverensis* (Viret, 1929)
  - *P. paronae* (Dal Piaz, 1930)
  - *P. pusillus* (Ginsburg, 1974)
- *Lorancahyus* Pickford & Morales, 1998
  - *L. hypsorhizus* Pickford & Morales, 1998
  - *L. daamsi* Pickford & Morales, 1998
  - Unnamed species, Corcoles, Spain
- *Palaeochoerus* Pomel, 1847
  - *P. typus* Pomel, 1847
  - *P. aquensis* (Repelin, 1930)

?Palaeochoeridae Matthew, 1924
- *Odoichoerus* Tong & Zhao, 1986
  - *O. uniconus* Tong & Zhao, 1986
- *Huaxiachoerus* Liu, 2001
  - *H. guanxiensis* Liu, 2001
- *Eocenchoerus* Liu, 2001
  - *E. savagei* Liu, 2001

and *Taucanamo* were synonyms, and suggested that the Chinji palaeochoerid should be classified in *Taucanamo*, but since *Pecarichoerus* Colbert (1933) was erected before *Taucanamo* Simpson (1945) then, if he is right, it ought to be called *Pecarichoerus*. He also made a plea, in the interests of stability, to suppress *Choeromorus* Gervais (1850) in preference to *Taucanamo* Simpson (1945) but given the possibility that *Taucanamo* and *Pecarichoerus* may be synonyms (as recognised by Van der Made (1997a) and as discussed by Orliac *et al*., 2010b) then it is preferable, in the interests of stability, to recognise that the most stable nomenclature flows from using Gervais' (1850) name for these suoids (*Choeromorus*: type species *Choeromorus mamillatus*, type locality, Sansan, France).

Among the Suoidea, analyses that are based exclusively or mainly on dental comparisons tend to produce weak scenarios of relationship. Liu (2003) considered the genus *Schizochoerus* to be closely related to *Taucanamo* and *Yunnanochoerus* a finding with which I agree, but she grouped the ensemble into an enlarged family Suidae, a suggestion not retained by Orliac *et al*., (2010a) who concluded that *Schizochoerus* is part of the Suidae *sensu stricto* (including some cranial characters) while the other two genera are not (Palaeochoeridae), in contrast to the position demonstrated by Pickford (1988) and supported by Van der Made (1997a). The new material of *Yunnanochoerus dangari* from Hari Talyangar and *Yunnanochoerus gandakasensis* from Yuanmou, China, adds support to the views of the latter two authors, as it is clear that, even though fragmentary, the remains belong in the same subfamily as *Schizoporcus* and *Pecarichoerus*. In addition, the mandibles from Nsebar, Bulgaria (Nikolov & Thenius, 1967) and Kalfa, Moldova (Lungu, 1971, 1974) show marked differences from Suidae, and, apart from size, exhibit closer similarities to Palaeochoeridae such as *Choeromorus mamillatus* Gervais (1850) from Sansan.

The species *Schizoporcus arambourgi* (Ozansoy, 1965) is considered to be the same as *Schizoporcus sinapensis* (Van der Made, 1997a). The holotypes of both species are from the Sinap area, Turkey, which evidently contains two species of *Schizoporcus*, a small one, *S. arambourgi*, in the Middle Miocene beds, and a large one, *S. vallesensis*, in the Late Miocene strata. Some individuals of the younger of the two species, *S. vallesensis,* possess five upper premolars, an unusual trait among artiodactyls, but known to occur in the anthracothere genus *Libycosaurus* (Pickford, 1991).

The relatively common European species previously classified in *Taucanamo muenzenbergensis* (or *Schizoporcus muenzenbergensis*) (Van der Made, 1998) is transferred to the genus *Pecarichoerus*, and because the dimensions and morphology of its teeth are similar to those of the type species from Chinji, it is considered to be synonymous with *Pecarichoerus orientalis* Colbert (1933) at the species level as well.

The hitherto poorly known taxon *Yunnanochoerus dangari* (Prasad, 1970) from India is now better represented by two mandible fragments from the type locality, Hari Talyangar. The species *Yunnanochoerus lufengensis* (Han, 1983) is smaller than *Y. dangari* and *Y. gandakasensis*, and is therefore valid.

New fossils attributed to *Lorancahyus daamsi* and *Lorancahyus hypsorhizus* from St Gérand-le-Puy, France, extend the geographic ranges of these species and suggest a possible ancestor in *Propalaeochoerus pusillus*. The humerus and talus of *L. hypsorhizus* reveal its appurtenance to Palaeochoeridae, and indicate that its post-cranial articulations were stabilised in the parasagittal plane. The two species of *Lorancahyus* are possibly ancestral to a tubulident palaeochoerid from Corcoles, Spain (Alferez *et al*., 1988).

The origin of the family Hippopotamidae is still the subject of debate (Pickford, 2008). The earliest described members of the family occur in the Middle Miocene of Kenya (Pickford, 2007) represented by *Palaeopotamus ternani*, which gave rise to *Kenyapotamus* Pickford, 1983. All the Neogene Eurasian palaeochoerids are too specialised to represent hippopotamid ancestors although they retains several characters such as extremely short neurocranium compared to the splanchnocranium that are also found in hippos.. This indicates that the origin of hippos needs to be sought among the Oligocene palaeochoerids; lineages such as *Propalaeochoerus* and its relatives holding some potential in this respect.

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