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SUOIDEA FROM THE LOWER MIOCENE OF CETINA DE ARAGÓN (SPAIN)

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ABSTRACT

The Suoidea (Mammalia) of the Lower Miocene (Agenian, MN 2a) locality Cetina de Aragón (Spain) are *Hyotherium meisneri, Hyotherium major* (Suidae) and *Propalaeochoerus* sp. A (Tayassuidae).

Most of the fossils belong to *Hyotherium meisneri;* all permanent teeth are represented. Up to now this species was known by few material. Currently, *H. meisneri* and *H. major* were considered to be either regional subspecies or synonyms. *H. meisneri* from Cetina is compared to *H. major* from its type locality St.-Gérand-le-Puy. The morphology does not differ much, but there is an average size difference of 15 %. Size differences of 15 % are common in sympatric species of suoids and tragulids. As the ranges of *H. major* and *H. meisneri* overlap in time and space the two taxa are different species, in stead of subspecies.

Hyotherium meisneri is one of the oldest known suids, but shows already the outward flare in the upper canines of the males, which is typical for the Suidae. Within the Hyotheriinae the genus *Hyotherium* is characterized by elongated premolars.

Propalaeochoerus sp. A from Cetina and Montaigu is similar in size to *Propalaeochoerus* sp. B from Tomerdingen, but differs in having larger posterior molars and smaller premolars, it might be a direct descendant. These tayassuids and *Propalaeochoeruss elaverensis* differ from all other *Palaeochoerus*-like tayassuids, including *Palaeochoerus? pusillus*, in the elongated last upper molar.

Keywords: ***Hyotherium, Palaeochoerus,*** **Suoidea, Suidae, Tayassuidae, Cetina de Aragón.**

RESUMEN

Los Suoidea (Mammalia) del yacimiento del Mioceno Inferior (Ageniense, MN 2a) de Cetina de Aragón son *Hyotherium meisneri, Hyotherium major* (Suidae) y *Propalaeochoerus* sp. A (Tayassuidae).

La mayor parte de los fósiles pertenecen a *Hyotherium meisneri;* todos los dientes permanentes están representados. Esta especie estaba representada por escaso material y *H. meisneri* y *H. major* eran consideradas como subespecies geográficas o como sinónimas. En el trabajo se compara *H. meisneri,* de Cetina, con *H. major* del yacimiento tipo St.-Gérand-le-Puy. La morfología no difiere mucho, pero hay una diferencia en la talla media del 15 %. Diferencias del tamaño del 15 % son comunes en especies simpátridas de Suoidea y Tragulidae. Dado que hay un solapamiento de las distribuciones temporales y geográficas, *H. major* y *H. meisneri* deben considerarse como dos especies distintas y no como dos subespecies.

Hyotherium meisneri es uno de los suidos más antiguos, no obstante los caninos superiores de los machos ya están orientados hacia fuera, lo que es típico de los Suidae. Dentro de los Hyotheriinae, el género *Hyotherium* se caracteriza por premolares alargados.

Propalaeochoerus sp. A, de Cetina y Montaigu, es similar en tamaño a *Propalaeochoerus* sp. B de Tomerdingen, pero difiere en sus molares posteriores más largos y sus premolares más pequeños y podría ser un descendiente directo. Estos tayassuidos y *Propalaeochoerus elaverensis* difieren de todos los demás tayassuidos semejantes a *Palaeochoerus,* incluso *Palaeochoerus? pusillus*, en el alargamiento del último molar superior.

Palabras clave: ***Hyotherium, Palaeochoerus,*** **Suoidea, Suidae, Tayassuidae, Cetina de Aragón.**

INTRODUCTION

The locality and excavation

The locality of Cetina de Aragón was known already in the twenties of this century (Villalta & Crusafont, 1945). It is Lower Miocene (Agenian) locality where both large and small mammals (Daams, 1976) have been collected.

The fossils described in this paper were excavated in 1983 and are stored in the Museo Nacional de Ciencias Naturales (MNCN) in Madrid. There are some smaller collections in other institutes, to which reference is made. An older collection is stored in the Institut Palaeontologic Dr. M. Crusafont in Sabadell (IPS). This collection was described by Truyols (1962), but the description was not published. A copy of this description is present in the IPS. Some more fossils were collected in 1987 and are stored in the Museo Paleontológico de la Universidad de Zaragoza (MPZ). Some fossils of larger mammals were collected along with the micromammalia described by Daams (1976) and are stored in the Instituut voor Aardwetenschappen, Utrecht (IVAU).

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In Cetina there are two fossiliferous peat beds. Between them there is about one meter of limestone. The lower peat bed was excavated in 1983. The provenance of the IPS and IVAU collections is unknown to me and the MPZ collection comes from both beds (B. Azanza, pers. comm.).

Methods and abbreviations

Measurements of the cheek teeth were taken as indicated by Van der Made (1991). Measurements of all teeth studied (including those in the IPS, IVAU and MPZ) are given in the tables. If a measurement could not be taken because of damage this is indicated by "–", if it was not taken for another reason this is indicated by "..". Of all teeth an example is figured. If there are more types of one element these are figured too and in some cases also different degrees of wear are illustrated.

The abbreviations are:

Cf	Upper and/or lower canine(s) of a female, C^f and C_f indicate upper and lower canines respectively.
Cm	Canine(s) of male(s); C^m and C_m upper and lower canine(s).
Cx	Canines of both sexes or of unknown sex.
DAP	Maximum length of the tooth in mm in meso-distal direction. DAP, DAPp, DAPd in bones gives the maximum, proximal or distal antero-posterior diameter.
DAP'	Length of a tooth as a percentage of the length of the first molar (using complete tooth rows or means of populations).
DT	Maximum width of a tooth in mm. DTa, DTm, DTp and DTpp are the width of the first lobe, middle lobe (in D_4), posterior lobe and third lobe (in M3).
DT'	Width of a tooth expressed as a percentage of the width of the first molar.
DLL	Linguo-labial diameter in incisors in mm.
DLL'	Linguo-labial diameter in incisors expressed as a percentage of the DT of the first molar.
DMD	Meso-distal diameter in incisors in mm.
DMD'	Meso-distal diameter in incisors expressed as a percentage of the DT of the first molar.
H	Height of the crown (mm). In lower molars it is measured from the base of the crown to the tip of the metaconid and in upper molars to the tip of the paracone. In upper premolars it is taken buccally and is the distance between the highest point of the tooth and the line through the two lowest points of the crown. In lower premolars H is measured in the same way on the lingual side.
Hla	Height of the crown of an incisor measured in the middle of the labial side (mm).
Hli	Height of the crown of an incisor measured in the middle of the lingual side (mm).
Ha	The height of a bone measured at the anterior side (mm).
L	Length of a bone (mm).

Comparative material

The material stored in the MNCN is described in this paper, but reference is made also to material in the IPS, IVAU and MPUZ. Comparisons were made with the following collections/specimens.

Hyotherium meisneri: Aarberg – Rappenfluh, a cast of the holotype in the Naturhistorisches Museum, Basel (NMB); Tudela (IPS); Horta das Tripas (Natural history museum in Lisbon).

Hyotherium major from type locality St.-Gérand-le-Puy in the Muséum national d'Histoire naturelle in Paris (MNHN), in the Muséum Guimet in Lyon (MGL), in the Muséum d'Histoire Naturelle de Toulouse (MHNT), casts from St.-Gérand in the Staatliches Museum für Naturkunde in Stuttgart (SMNS), from Ulm-Westtangente (SMNS), Gibel (cast in MNHN) and from Weissenau in the Forschungs-Institut Senckenberg, Frankfurt (FISF).

Hyotherium soemmeringi from Georgensgmünd (type material in FISF; NMB), Baigneaux-en-Beauce (NMB, MGL), Sandelzhausen in the Bayerische Staatssammlung für Paläontolgie und historische Geologie in München (BSPHGM).

Aureliachoerus aurelianensis from Artenay (MNHN).

Palaeochoerus typus from St.-Gérand-le-Puy (casts MNHN & SMNS and originals MGL; including type material), La Milloque (NMB).

Palaeochoerus? paronae types from Monteviale in the Istituto e Museo di Geologia della R. Università di Padova (IMGURP).

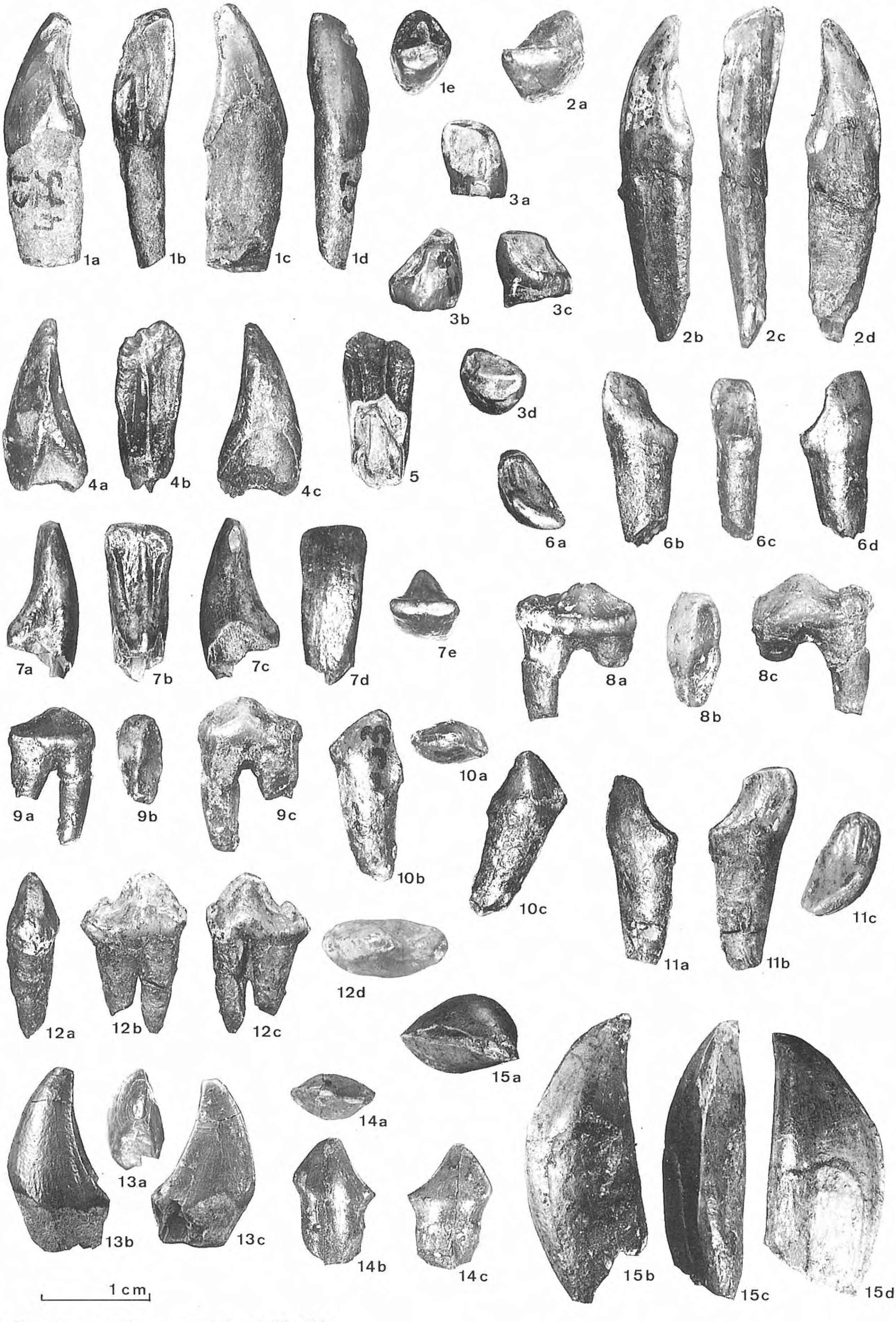
Palaeochoerus leptodon from Cadibona in the Dipartimento di Scienze della Terra, Università degli Studi di Torino (DSTT), including type.

Palaeochoerus aquensis from Pérignat/La Sauvetat (cast in SMNS), St. André (UCBL, MGL, casts in

Plate I *Hyotherium meisneri* from Cetina de Aragón. All pieces are stored in the Museo Nacional de Ciencias Naturales, Madrid. There may be minor deviations from the scale in individual pieces.

1 CT 475, left I_2, a) distal view, b) lingual view, c) mesial view, d) labial view, e) apical view.
2 CT 469, left I_2, a) apical view, b) distal view, c) lingual view, d) mesial view.
3 CT 11, right I_3, a) lingual view, b) distal view, c) mesial view, d) occlusal view.
4 Left I_2, a) distal view, b) lingual view, c) mesial view.
5 Right I_2, lingual view.
6 CT 469, right I_3, a) apical view, b) mesial view, c) lingual view, d) distal view.
7 Right I_1, a) distal view, b) lingual view, c) mesial view, d) labial view, e) apical view.
8 CT 469, right P^2, a) lingual view, b) occlusal view, buccal view.
9 CT 469, right P^1, a) lingual view, b) occlusal view, c) buccal view.
10 CT 533, right I^3, a) lingual view, b) apical view, c) labial view.
11 CT 469, left I_3, a) distal view, b) mesial view, c) apical view.
12 CT 469, left P_2, a) anterior view, b) lingual view, c) labial view, d) occlusal view.
13 Left C_f, a) apical view, b) labial view, c) lingual view.
14 CT 469, right I^3, a) apical view, b) labial view, c) lingual view.
15 CT 469, right C^m, a) apical view, b) labial view, c) anterior view, d) lingual view.

Plate I


1a
1b
1c
1d
1e
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3d
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12a
12b
12c
12d
15a
13a
13b
13c
14a
14b
14c
15b
15c
15d
1 cm

BSPHGM), St. Henri (UCBL), "Bouches du Rhone" (UCBL) and Les Milles (type material in Laboratoire de Sédimentologie et Paléontologie, Université de Provence, Marseille – UPM and UCBL), La Bénissons Dieu (UCBL), Pech Crabit (Laboratoire de Paléontologie, Université de Montpellier II – UM) and Pech Desse (UM), Aarwangen (cast in NMB), Wischberg (NMB), Quercy (cast of the skull described by Dechaseaux, 1959 in MNCN), Binisalem (cast in IPS).

P. elaverensis from Coderet (NMB; type material in UCBL).

Propalaeochoerus sp. B from Tomerdingen (SMNS).

Propalaeochoerus sp. A from Montaigu (NMB).

Recent suoids in the Zoological Museum of Amsterdam (ZMA).

Earlier literature on *Hyotherium* and *Palaeochoerus* -like Suoids and aim of this study

For material of *Palaeochoerus*-like suoids and *Hyotherium* many names have been proposed, of which a large part are synonyms. Remains of *Hyotherium meisneri* have been assigned to the smaller *Aureliachoerus aurelianensis* and the larger *Hyotherium major* and *H. meisneri* has even been synonymized with the latter species as late as in 1992 (Hellmund). All these species are Hyotheriinae, Suidae. All of these species have been placed in *Palaeochoerus,* Palaeochoerinae, Tayassuidae and fossils of these species have been assigned to species of *Palaeochoerus* and *Propalaeochoerus* and even were considered to be synonymous with such species as late as in the nineteenseventies (probably by Wilkinson, 1976 and certainly by Golpe, 1972) and a species of *Palaeochoerus* was recently placed in the Suidae (Hellmund, 1992). In addition, there are a number of technical nomenclatorial problems. Since there is such a chaos, a review of the literature is necessary, highlighting the most accepted taxonomical and nomenclatorial decisions, before the material is described. The taxonomy used in this paper is given in this section, so that the content of taxa used in the discussions in the systematical section will be clear.

Meisner (1818, as cited by Hellmund, 1991) described a part of a mandible of a suid from the Rappenfluh near Aarberg and two years later he described and figured it (Meisner, 1820). He noted that the morphology of the teeth resembled that of *Babyrousa,* but he did not name the animal. More recently, the holotype was figured by Studer (1896, pl. III, figs. 3 & 4). H. von Meyer (1829) described a larger suid from Georgensgmünd which has almost the same morphology. The type material is in the FISF and is not lost as supposed by Hellmund (1991, p. 8). Meyer named the species *Chaeropotamus Meissneri* for the mandible from Aarberg and *Chaeropotamus Soemmeringii* for the material from Georgensgmünd after Meisner and Soemmering. Obviously, Meyer made an error in Meisner's name and should be corrected (Ride *et al.,* 1985). Consequently the correct spelling is *H. meisneri* and *H. soemmeringi.* Meyer (1834) realized that *"Ch." soemmeringi* is not related to *Choeropotamus* (which is a Paleogene artiodactyle) and made the genus *Hyotherium* with *H. soemmeringi* as type species. In this paper Meyer is not quite clear on *H. meisneri,* later (Meyer, 1841) he placed it in *Hyotherium.*

Hyotherium medium Meyer, 1841 is a problematical species; in the original concept it was based on size and reference was made to material from Mösskirch that probably belongs to small individuals of *H. soemmeringi* and to material from Weissenau of the species that will be named here *Hyotherium major.* No holotype was indicated. The taxon was used at the subspecies level as late as 1970 (Mottl). However, since the content of the taxon is not clear, it seems best not to use this name.

Meyer (1850) described and figured a skull and other material of *H. meisneri* from Wiesbaden. Ginsburg (1974) and possibly also Stehlin (1899/1900) took this description as the first valid publication of *H. meisneri.* As *H. meisneri* was named before 1931 and as reference was made to a description and figure by Meisner, the name is valid from 1829 on (Ride *et al.,* 1985) and the holotype is the mandible from Aarberg and not the better material from Wiesbaden.

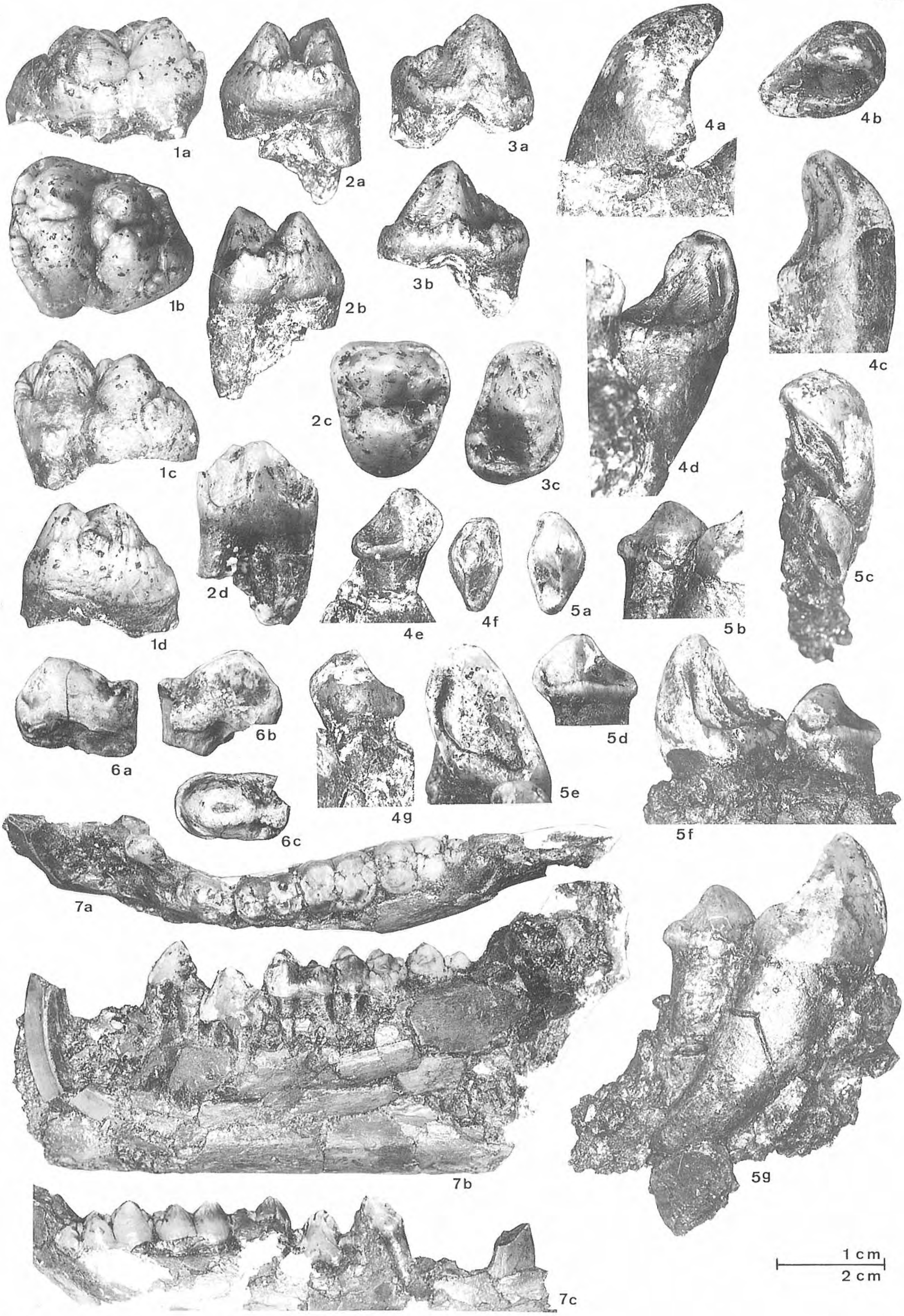
Pomel (1847) made the genus and the two species *Palaeochoerus typus* and *P. major* on the basis of fossils from St.-Gérand-le-Puy. Stehlin (1900) made the species *Palaeochoerus aurelianensis.* He figured an M^3 from Artenay and P_3 and P_4 from the "Sanden des Orléanais". Ginsburg (1974) created a genus for this species: *Aureliachoerus aurelianensis* and placed *P. major* in the genus *Hyotherium.*

Often species are classified as *Hyotherium* because they lack any important or striking specialization. The original description of *Hyotherium major* as a *Palaeochoerus* and the idea that *Hyotherium* evolved from *Palaeochoerus* gave rise to the custom of placing smaller Suidae like *H. major, H. meisneri* and *Aureliachoerus aurelianensis* in the genus *Palaeochoerus.* Stehlin (1899/1900) used names like *major, soemmeringi, typus* and *meisneri* for size classes. This becomes apparent

Plate II *Hyotherium meisneri* from Cetina de Aragón. All pieces are stored in the Museo Nacional de Ciencias Naturales, Madrid. For figures 1-6, the bar represents 1 cm, for figure 7, the bar represents 2 cm. There may be minor deviations from the scale in individual pieces.

1 CT 469, left M^3, a) buccal view, b) occlusal view, lingual view, d) anterior view.
2 CT 469, left P^4, a) anterior view, b) posterior view, c) occlusal view, d) buccal view.
3 CT 469, left P^3, a) buccal view, b) lingual view, c) occlusal view.
4 CT 469, right I^1, a) labial view, b) apical view, c) mesial view, d) lingual view and right I^2, e) lingual view, f) apical view, g) labial view.
5 CT 469, left I^1 and I^2, a) apical view I^2, b) labial view I^2, d) I^1 and I^2 apical view, d) I^2 lingual view, e) I^1 occlusal view, f) I^1 mesial view and I^2 lingual view, g) and I^2 labial view.
6 Right P_3, a) lingual view, b) buccal view, c) occlusal view.
7 CT 468, left mandible with C_f, P_3, P_4, M_1, M_2 and M_3, a) occlusal view, b) buccal view, c) lingual view.

Plate II


1a
2a
3a
4a
4b
1b
2b
3b
4c
2c
1c
3c
4d
1d
2d
4e
4f
5a
5b
5c
6a
6b
6c
4g
5e
5d
5f
7a
7b
5g
7c
1 cm
2 cm

from his synonymy list of *"Palaeochoerus cfr. typus et Meisneri"*. He believed that local populations of a line *Palaeochoerus – Hyotherium* could have a different size as result of local circumstances and/or local evolution. This doubtless was the result of the belief that there were many isolated regions in Europe. Ginsburg (1974) considered *H. meisneri* valid from 1850 (when Meyer figured the material from Wiesbaden) and he divided *H. major* into two subspecies: *H. major major* for the French population and *H. major meisneri* for the German population. Hellmund (1991) considered the type of *H. major* as a large individual of *H. meisneri* and stressed that *H. meisneri* has priority over *H. major*.

The taxonomy of the *Palaeochoerus*-like tayassuids is confused. A number of species have been described, which conveniently are grouped to size here. The smallest is *Palaeochoerus paronae* Dal Piaz, 1930 from Monteviale. *Palaeochoerus pusillus* Ginsburg, 1974 of the old collections from the Quercy is the next smallest. *Anthacotherium gergovianus* De Blainville, 1846 from Ivoine near Gergovie, *Palaeochoerus typus* Pomel, 1847 from St.-Gérand-le-Puy, *Sus leptodon* Pomel, 1848 from Cadibona and *Doliochoerus quercyi* Filhol, 1882 from the Quercy are of similar size and it is very likely that some of these are synonymous. (De Blainville published the species after a manuscript by Croizet. As far as I understand articles 10 and 50 by Ride *et al.*, 1985, this makes De Blainville the author and not Croizet –Hellmund, 1992–, nor Croizet *et*-Blainville – Ginsburg, 1974.) *Palaeocherus meissneri* mut. *elaverensis* Viret, 1929 from Coderet is larger. *Palaeochoerus Waterhousii* Pomel, 1853 from Pérignat, *Palaeochoerus massiliensis* Viret, 1929 from St. Henri and *Doliochoerus aquensis* Repelin, 1930 from Les Milles are of the same size and same morphology and very likely are one species (Ginsburg, 1974).

Besides *Palaeochoerus* Pomel, 1847 has, as its name indicates, type species *P. typus*. Those who recently studied *P. typus*, agree that it is a tayassuid (Ginsburg, 1974; Hellmund, 1992). Three other genus names have been proposed for the *Palaeochoerus*-like tayassuids.

Propaleochoerus Stehlin, 1899 was made for suoids from the Quercy that have upper molars with fused, but divergent lingual roots (Stehlin, 1899, p. 107), although it is not clear which material exactly was studied by Stehlin. He compared those suoids with *Palaeochoerus,* which in his opinion included a number of species that are now placed in *Hyotherium*, which has very well separated lingual roots in the upper molars. He did not indicate a type species for *Propalaeochoerus*, nor included any nominal species, however he indicated that *P. leptodon* from Cadibona might belong to the genus (p. 108). Stehlin (1929) assigned *P. elaverensis* from Coderet to *Propalaeochoerus*, which became in this way the type species (Hellmund, 1992). Although this changes the content of the genus (see discussion on *Propalaeochoerus* sp. A), the procedure seems to be valid.

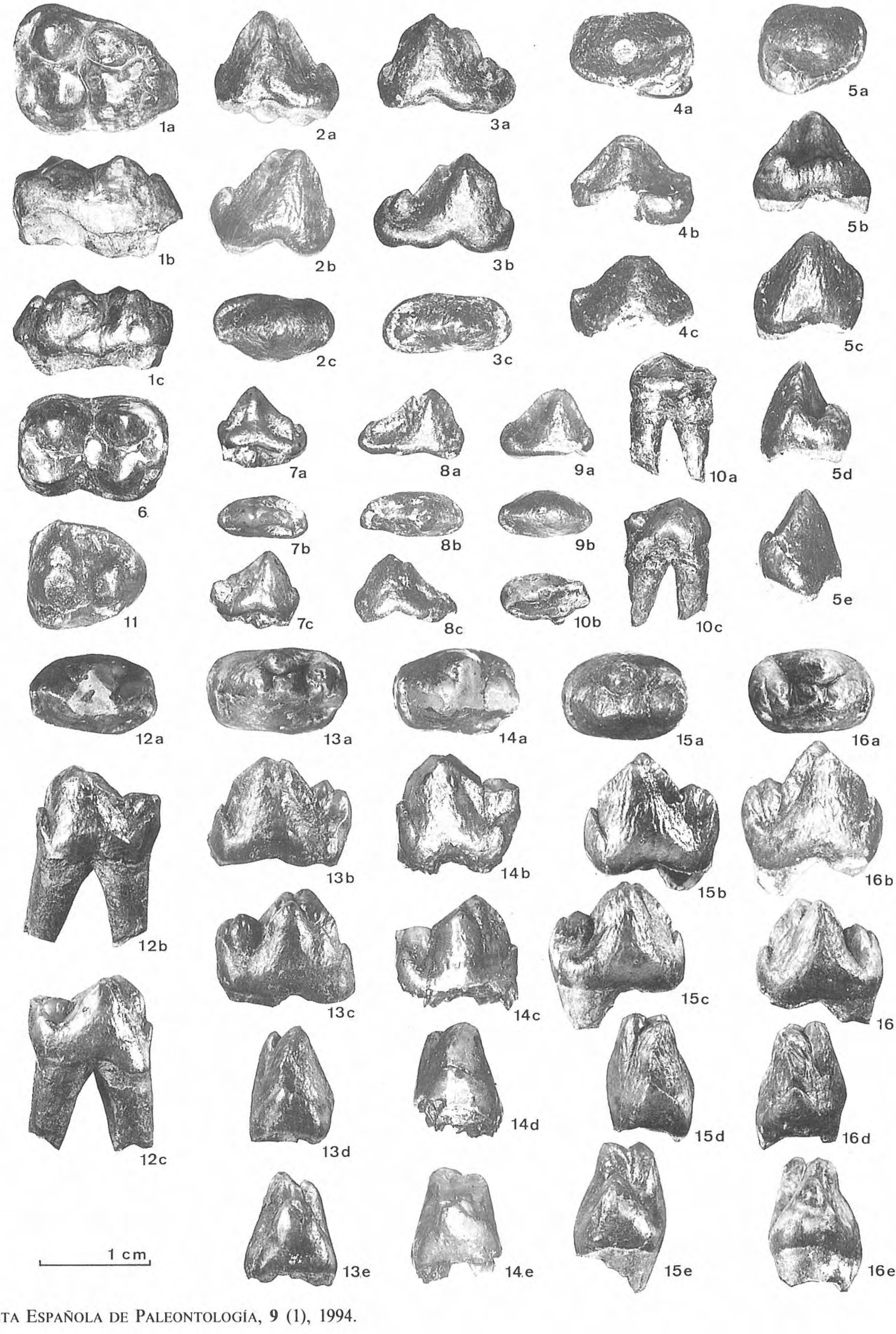
Doliochoerus Filhol, 1882 is based on *D. quercyi*. The differences between *Doliochoerus* Filhol, 1882 and *Palaeochoerus* cited by Ginsburg (1974) are skull characters and the elongation of the upper molars. A skull from the Quercy, the type of *D. quercyi*, and a skull from Coderet were compared. The supposed differences between *Palaeochoerus* and *Doliochoerus* are differences between *Propalaeochoerus* (Coderet) and *Doliochoerus/Palaeochoerus* (Quercy). Also the elongation between the upper molars are differences between *Propalaeochoerus* and *Doliochoerus/Palaeochoerus*, as we will see in the discussion on *Propalaeochoerus* from Cetina. The differences in skull characters between *Doliochoerus* and *Palaeochoerus* listed by Pearson (1927) are differences between the type skull of *D. quercyi* and material of *Hyotherium* (including *"Palaeochoerus waterhousi"* from St. Gérand).

Dubiotherium Hellmund, 1992 is based on the species *Palaeochoerus waterhousi* Pomel, 1853. It is not known for sure whether mandible BMNH 27789 (which is supposed to be from La Sauvetat) is really the type which Pomel indicated to be from Pérignat. Lavocat (1951) thought this likely, but indicated the specimen as neotype. Ginsburg (1974, p. 62) had serious doubts about this and even advised not to use the name *waterhousi;* the species occurs with a question mark in his synonymy of *Doliochoerus quercyi*. Hellmund (1992) considered BMNH 27789 to be the real holotype of *P. waterhousi* and indicated material from St. André to belong to the same species. A maxilla from St. André was figured by Dechaseaux (1959, fig. 2) as *Doliochoerus quercyi*. The suoid from St. André is identical to that from St. Henri and Les Milles (all three localities are near Marseille) and all were assigned to *Doliochoerus quercyi aquensis* by Ginsburg (1974). There is general consensus that the species from Marseille is tayassuid (Dechaseaux, 1959; Ginsburg, 1974). Hellmund (1992) considered *Dubiotherium waterhousi* to be a suid, but did not discuss possible links with *Doliochoerus* nor with *Palaeochoerus aquensis*.

Plate III *Hyotherium meisneri* from Cetina de Aragón. All pieces are stored in the Museo Nacional de Ciencias Naturales, Madrid. There may be minor deviations from the scale in individual pieces.

1 CT 7, left M^3, a) occlusal view, b) lingual view, c) buccal view.
2 Left P^3, a) lingual view, b) labial view, c) occlusal view.
3 Left P^3, a) lingual view, b) labial view, c) occlusal view.
4 CT 112, left P^3, a) occlusal view, b) lingual view, c) buccal view.
5 Right P^3, a) occlusal view, b) lingual view, c) buccal view.
6 CT 90, left M_2, occlusal view.
7 Right P_1, a) lingual view, b) occlusal view, c) buccal view.
8 Left P_2, a) labial view, b) occlusal view, c) buccal view.
9 Left P_1, a) labial view, b) occlusal view.
10 CT 469, left P^1, a) lingual view, b) occlusal view, c) buccal view.
11 CT 112, left P^4, occlusal view.
12 Left P_4 a) occlusal view, b) buccal view, c) lingual view.
13 Left P_4 a) occlusal view, b) buccal view, c) lingual view, d) anterior view, e) posterior view.
14 CT 483, left P_4 a) occlusal view, b) buccal view, c) lingual view, d) anterior view, e) posterior view.
15 Left P_4 a) occlusal view, b) buccal view, c) lingual view, d) anterior view, e) posterior view.
16 Right P_4 a) occlusal view, b) buccal view, c) lingual view, d) anterior view, e) posterior view.

Plate III


1a
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4a
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1c
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3c
4c
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7a
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15a
16a
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16b
13c
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15c
16c
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13d
14d
15d
16d
13e
14.e
15e
16e
1 cm

One of the most persistent confusions between *Palaeochoerus* and *Hyotherium* started when Filhol (1880) described and figured two skulls of *Hyotherium major* from St. Gérand as *Hyotherium waterhousi.* Since that time, it became custom to use the name *waterhousi* for material of *H. major*, despite the fact that the other name is older and should have priority if they were synonymous (Viret, 1929, p. 243). As late as 1972 (or even 1976?) material of *H. major* was assigned to *P. waterhousi*, leading to errors at all levels of taxonomy. In an important study, Pearson (1927) gave differences between the tayassuid and suid basicranium, but she followed Filhol (1880) in assigning the skulls of *H. major* from St.-Gérand to *Palaeochoerus waterhousi.* Although Pearson's observations on suids and tayassuids remain valid, *Palaeochoerus* should not be placed in the Suidae as was done by Pickford (1988), who placed the Palaeochoerinae in the Suidae and Simpson (1945) who synonymized Hyotheriinae and Palaeochoerinae.

The name *waterhousi* has probably been applied more often to remains of *H. major* than to remains which belong to the same species as its possible holotype (compare the synonymy *H. major* in this paper with the one of *D. waterhousi* by Hellmund, 1992), which moreover is of disputed provenance and unknown age. Besides the species is in the center of a historical misunderstanding of long duration. *Palaeochoerus aquensis* has two cotypes, which have been figured in the first publication, their origin is known and more material of the same locality is available, besides the age of the locality is known. The name *P. massiliensis* has probably never been used after Viret (1929). Keeping stability in mind, it seems best to follow Ginsburg's (1974) suggestion and to forget about *waterhousi* and use *aquensis* in stead.

The most recent overviews of the *Palaeochoerus*-like tayassuids are given by Ginsburg (1974) and Hellmund (1992). Ginsburg recognised three parallel lineages: *Palaeochoerus paronae – P. pusillus – P. typus, Palaeochoerus (Propaleochoerus) gergovianus gergovianus – P. (P.) g. elaverensis* and *Doliochoerus quercyi quercyi – D. q. aquensis.* Hellmund considered *Propalaeochoerus paronae* the stemform of the two lineages *Propalaeochoerus pusillus* and *Propaleochoerus gergovianus – Palaeochoerus typus* and the considered *Dubiotherium waterhousi* to be a suid. In this paper still another classification is used, which, this should be stressed especially for the tayassuids, is tentative.

- Suoidea Cope, 1887
- Tayassuidae Palmer, 1897
  - Palaeochoerinae Matthew, 1924 (=Doliochoerinae, Simpson, 1945)
    - *Palaeochoerus* Pomel, 1847 (=? *Doliochoerus* Filhol, 1882; = *Dubiotherium* Hellmund, 1992)
      - *Palaeochoerus gergovianus* (De Blainville, 1846) Lavocat, 1951
      - *Palaeochoerus typus* Pomel, 1847 (=? *P. gergovianus)*
      - *Palaeochoerus leptodon* (Pomel, 1848) Stehlin, 1899 (=? P. *gergovianus)*
      - *Palaeochoerus quercyi* (Filhol, 1882) Van der Made (=? P. *gergovianus)*
      - *Palaeochoerus paronae* (Dal Piaz, 1930) Ginsburg, 1974
      - *Palaeochoerus aquensis* (Repelin, 1930) Van der Made (= *Palaeochoerus massiliensis* Viret, 1929; = *Palaeochoerus waterhousi* Pomel, 1853)
      - *Palaeochoerus? pusillus* Ginsburg, 1974
    - *Propalaeochoerus* Stehlin, 1899
      - *Propalaeochoerus elaverensis* (Viret, 1929) Stehlin, 1929
      - *Propalaeochoerus* sp. B
      - *Propalaeochoerus* sp. A

- Suidae Gray, 1827
  - Hyotheriinae Cope, 1888
    - *Hyotherium* Meyer, 1834
      - *Hyotherium soemmeringi* (Meyer, 1829) Meyer, 1834
      - *Hyotherium major* (Pomel, 1847) Filhol, 1880
      - *Hyotherium meisneri* (Meyer, 1829) Meyer, 1841
    - *Aureliachoerus* Ginsburg, 1974
      - *Aureliachoerus aurelianensis* (Stehlin, 1899/1900) Ginsburg, 1974
      - *Aureliachoerus minus* (Golpe, 1972) Van der Made, 1990
    - *Xenohyus* Ginsburg, 1980
      - *Xenohyus venitor* Ginsburg, 1980 (=? "*Conohyus*" *betpakdalensis* Trofimov, 1949)
      - *Xenohyus* sp.

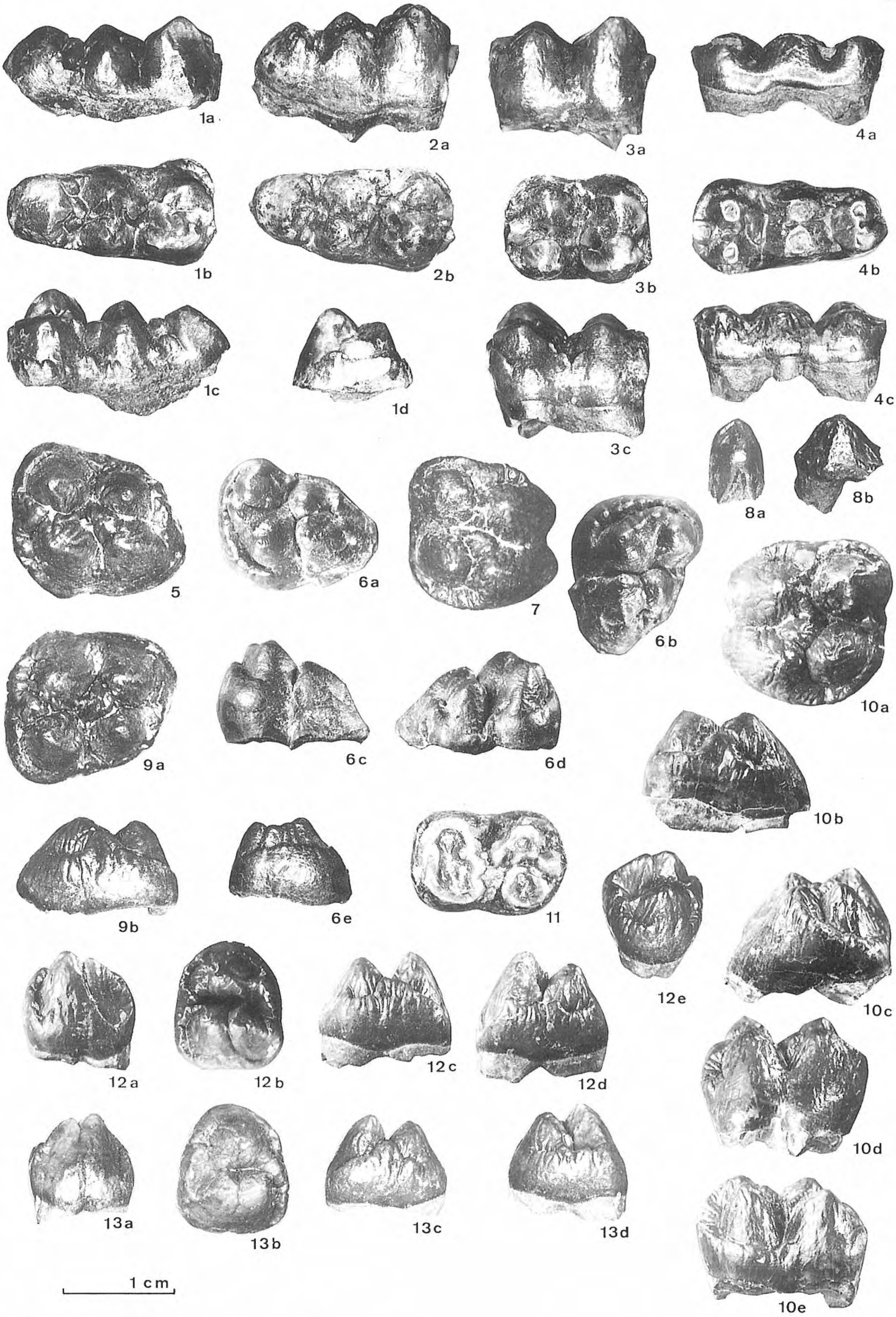
It is the aim of this paper:

1. To describe the suid fossils from Cetina and assign them to a taxon.
2. To characterize well the species *Hyotherium meisneri* biometrically and morphologically, to show that *H. meisneri* really is different from *H. major* and from *A. aurelianensis* and to give the synonymies of *H. major* and *H. meisneri,* species that where often lumped together.
3. To assign the tayassuid from Cetina to a taxon. In order to do this tayassuid evolution has to be discussed.

Plate IV *Hyotherium meisneri* (figures 1-5, 7-13) and *Propalaeochoerus* sp. A (figure 6) from Cetina de Aragón. All pieces are stored in the Museo Nacional de Ciencias Naturales, Madrid. There may be minor deviations from the scale in individual pieces.

1 CT 90, left M_3, a) lingual view, b) occlusal view, c) buccal view, d) anterior view.
2 Left M_3, a) lingual view, b) occlusal view.
3 Left M_2, a) lingual view, b) occlusal view, c) buccal view.
4 Left D_4, a) lingual view, b) occlusal view, c) buccal view.
5 Left M_3, occlusal view.
6 CT 410, *Propalaeochoerus* sp. A left M^3, a) occlusal view, b) occlusal view, c) lingual view, d) labial view, e) anterior view.
7 Right M^2, occlusal view.
8 Right D_3, a) occlusal view, b) labial view.
9 Right M_3, a) occlusal view, b) anterior view.
10 Left M^2, a) occlusal view, b) anterior view, c) posterior view, d) lingual view, e) labial view.
11 Right M_1, a) occlusal view.
12 Right P^4, a) buccal view, b) occlusal view, c) anterior view, d) posterior view, e) linguo-occlusal view.
13 Left P^4, a) buccal view, b) occlusal view, c) anterior view, d) posterior view.

Plate IV


1a
2a
3a
4a
1b
2b
3b
4b
1c
1d
3c
4c
8a
8b
5
6a
7
6b
10a
9a
6c
6d
10b
9b
6e
11
12e
10c
12a
12b
12c
12d
10d
13a
13b
13c
13d
10e
1 cm

4. Since Hellmund (1991, 1992) and to a lesser extent Ginsburg (1974) presented different views on the taxonomy of *Hyotherium* and the Palaeochoerinae, the main differences will be discussed. And in addition:

5. Some attention will be paid to the ecological phenomenon of related sympatric species, such as the different European Hyotheriinae.

SYSTEMATICS

Order ARTIODACTYLA Owen, 1849
Superfamily **SUOIDEA** Cope, 1887
Family **Tayassuidae** Palmer, 1897
Subfamily **Palaeochoerinae** Matthew, 1924
(= Doliochoerinae Simpson, 1945)
Genus *Propalaeochoerus* Stehlin, 1899.

Generic diagnosis: Tayassuidae with M_1 and M_2 with the hypoconulid close to the hypoconid, M^1 and M^2 with the lingual roots fused and convergent and with a tendency to enlarge M3; the M^3 may be elongated.

Propalaeochoerus sp. A
Pl. IV, Fig. 6

1972 *Palaeochoerus typus* Pomel, 1847; Golpe, 115, partially.
1990 *Palaeochoerus typus* Pomel, 1847; Van der Made (a), 84, Fig. 3.
1990 *Palaeochoerus typus*; Van der Made (b), 99 & 104, partially.

Material: CT 410 left M^3 (Pl. IV, Fig. 6).

Description and comparison: The M^3 is smaller than the molars which are attributed to *H. meisneri* (DAP 12.7, DTa 11.6, DTp 9.2, compare with Table 4). The cusps are rounded and the enamel does not have folds (Pl. IV, fig. 6a). There is no trace of a central cusp (Pl. IV, fig. 6ab). From the protocone a high ridge (Pl. IV, fig. 6e) runs antero-buccally, ending very near the tip of the paracone (Pl. IV, fig. 6b). This must be the paraconule (=protoconule) or preprotocrista (terminology of Coombs & Coomb, 1977). The paraconule is not connected to the cingulum (Pl. IV, fig. 6b).

The posterior cusps are very small (Pl. IV, fig. 6ab) and low (Pl. IV, fig. 6cd) and the talon is nothing more than a cingulum, which however at the lingual side extends much distally. This morphology is very similar to that of an M^3 from Montaigu (NMB). Both teeth are elongate like those from Coderet and Tomerdingen; those of other tayassuids are wider (Fig. 1) and the posterior cingulum of their M^3 is not extended distally, but resembles much more the cingulum of an M^1 or M^2.

Golpe (1972) attributed five teeth in the IPS to *P. typus*. Four of them belong certainly to *H. meisneri* and one, a P^4, is similar in morphology to a not numbered P^4 which is very small, but resembles in its protoconule morphology *Hyotherium*, rather than *Palaeochoerus*, these teeth might also belong to *H. meisneri*. A not numbered right P^1 in the IVAU collection, may belong to the same species as CT 410 because of its size (DAP 4.9, DTa 2.9, DTp 2.8) and simple morphology.

Discussion: The determination of this single suoid tooth is difficult and is done in three steps: determination to family, to genus and to species.

The paraconule morphology is of importance for the determination to family. Up to now the character is not well studied in a systematic way. The paraconule (or protoconule) is connected to the protocone and separate from the cingu-

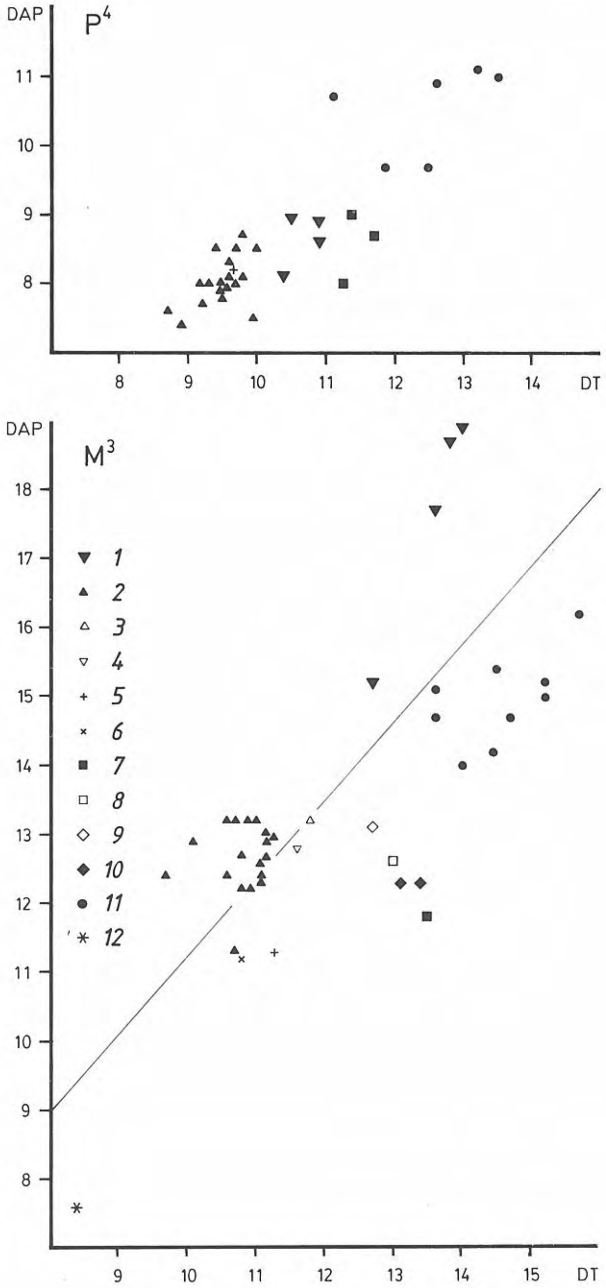


Figure 1. Length (DAP)-width (DT) bivariate plot of the P^4 and M^3 of *Palaeochoerus* and *Propalaeochoerus*. Legend: 1) *Propalaeochoerus elaverensis* from Coderet (NMB, material published by Viret, 1929 in UCBL); 2) *Propalaeochoerus* sp. B from Tomerdingen (SMNS); 3) *Propalaeochoerus* sp. A from Montaigu (NMB); 4) *Propalaeochoerus* sp. A from Cetina (MNCN); 5) *Palaeochoerus? pusillus* holotype from the Quercy (data from Ginsburg, 1974); 6) *Palaeochoerus? pusillus* from Montalban (data from Golpe, 1971); 7) *Palaeochoerus typus* from St.-Gérand-le-Puy (casts in SMNS); 8) *Palaeochoerus typus* from Rickenbach (NMB); 9) *Palaeochoerus typus* from La Milloque (NMB); 10) lectotype of *Doliochoerus quercyi* from the Quercy (data from Ginsburg, 1974); 11) *Palaeochoerus aquensis* from the area of Marseille (Les Milles, St. André, St. Henri, "Bouches du Rhône" - UCBL, UPM, MGL, cast BSPHGM); 12) *Palaeochoerus paronae* from Monteviale (MIGURP). The line indicates index I = 100 DAP/DT = 112.5.

lum in the *P. typus* holotype, in other *Palaeochoerus* species, *Taucanamo, Sanitherium* and probably in *Perchoerus* and *Helohyus* (Pearson 1932, plate 15, the paraconule is sometimes drawn as if connected to the cingulum and sometimes as if isolated; it is always connected to the protocone). The upper molars of *H. meisneri* and many other suidae (including *Aureliachoerus*) have a large cusp in the middle of the cingulum projecting backwards between the anterior parts of the paracone and protocone, but it is not connected to them. This cusp is also thought to be the paraconule. In the most primitive suids the paraconule may be connected to the protocone (as in *Xenohyus*, Ginsburg, Huin & Locher, 1988, plate 1, figs. 13, 14) or to both cingulum and protocone, as is occasionally the case in *Hyotherium soemmeringi* from Sandelzhausen and *Xenohyus* (Ginsburg & Huin & Locher, 1988, plate 1, fig. 15). The suid *Listriodon* has lophodont molars and the first lophe of the upper molars is formed by the preprotocrista or paraconule fusing with both protocone and paracone and being isolated from the cingulum. In *Bunolistriodon* the paraconule may be fused to the cingulum or to the protocone and both morphologies may be observed in one tooth row. *Listriodon* is supposed to have evolved from one of the species of *Bunolistriodon* and it is possible that this lineage reversed the evolution of the paraconule morphology. In recent peccaries the paraconule is not connected to the cingulum, nor to the protocone. A paraconule connected to the protocone and not to the cingulum probably is a primitive character. It may be useful in determination of primitive suids: if in a sample specimens are found with the paraconule connected to the cingulum, the species is more likely a suid than a tayassuid. This corroborates the finding of Ginsburg (1974) that *Aureliachoerus* is a suid and no tayassuid, it indicates that *Xenohyus* is more likely a suid than a tayassuid (contrary to Pickford and Morales, 1990) and it indicates that CT 410 is a tayassuid and no suid. The European Tayassuids include *Palaeochoerus*-like tayassuids and the group *Taucanamo* - *Schizochoerus*. The latter tayassuids have a tendency towards lophodonty, besides they enter later in Europe. *Albanohyus* has the paraconule fused to the cingulum and might represent a suid and no tayassuid.

In order to determine the tooth from Cetina to genus level, it first has to be clear which genera are around. Three characters are compared in the various species, leading to a probably more natural grouping of the species into genera than in the present taxonomies. Fig. 2 will be help the reader keeping a clear view of the (tentative) taxa, their localities and stratigraphic positions.

In the *Palaeochoerus*-like tayassuids, there are two types of M^3: elongate ones and wide ones (Fig. 1), the species with elongate M^3 tend to have larger M_3, but there is no difference in the DAP/DT index. Elongate M^3: *Propalaeochoerus elaverensis* (Coderet - Viret, 1929, plate 31, Fig. 11) and Tomerdingen (Hellmund, 1992, Pl. 6, Fig. 8), Cetina (Pl. IV, Fig. 6), Montaigu; all others have wide M^3: *Palaeochoerus aquensis* (St. Henri; St. André - Dechaseaux, 1959, Fig. 2; Les Milles; Marseille; Quercy - Dechaseaux, 1959, fig. 1), *Palaeochoerus typus* (St.-Gérand - Hellmund, 1992, Pl. 2, Fig. 1; Rickenbach; La Milloque), *Doliochoerus quercyi* (holotype), *P.? pusillus* (holotype from the Quercy — Hellmund, 1992, Pl. 12, Fig. 1; Montalban) and *P. paronae* (Monteviale — Dal Piaz, 1930, Pl. 1, Fig. 6). It should be noted that Hellmund (1992) described the material from Tomerdingen as *P. pusillus*, yet the holoty-

MN / MP	*Palaeochoerus*			*Palaeochoerus?*	*Propalaeochoerus*		*Hyotherium*			*Aureliachoerus*
	aquensis	*typus* *gergovianus* *leptodon* *quercyi*	*paronae*	*pusillus*	sp. B - sp. A	*elaverensis*	*meisneri*	*major*	*soemmeringi*	
5								Vieux Collognes?	Seegraben	Köflach
4									Baigneaux	Artenay
3							Horta das Tripas?		Chilleurs?	Agreda Wintershof West
2		St. Gérand			Cetina Montaigu		Eselsberg Cetina ?Wiesbaden ?Tudela	Gibel Westtangente St. Gérand		
1	Wischberg	La Milloque			Tomerdingen		Aarberg	Weissenau		
30						Coderet				
29		Rickenbach ?Cadibona								
28	Pech Desse	Gaimersheim Pech du Fraysse								
27	Aarwangen									
26	St. André St. Henri Les Milles "Marseille"									
25										
24		Etamps								
23	Pech Crabit			Montalban						
22		Möhren 13								
21		Dvérce	Monteviale							

Figure 2. The stratigraphic distribution of the species of *Palaeochoerus, Propalaeochoerus, Hyotherium* and the genus *Aureliachoerus. Palaeochoerus typus/gergovianus/leptodon/quercyi* indicates animals with similar size; the fossils may belong to different taxa. A question mark in front of a locality means that the exact stratigraphic position is unknown and a question mark behind a locality means that it is not sure the species occurs in that locality.

pe of this species is far outside the range of the Tomerdingen sample.

There are two hypoconulid morphologies. In the first type, the hypoconulid may be close to hypoconid so that it fuses with that cusp after little wear and there is labially a piece of posterior cingulum, lingually there is no space for it: *P. elaverensis* (Coderet; Romagnat – Hellmund, 1992, Pl. 2, Fig. 2) and in Tomerdingen (Hellmund, 1992, Pl. 10, Figs. 1a, 2a, 4; Pl. 4, Fig. 1a) and Montaigu. In the second type, the hypoconulid is on the axis of the tooth and with wear it remains a long time an isolated dentine "island": *P. aquensis* (St. André – Hellmund, 1992, Pl. 3, Fig. 2; St. Henri; Les Milles – Repelin, 1930, Pl. 14, Figs. 5 & 6; Quercy-Dechaseaux, 1959, Fig. 5 and the mandible from La Sauvetat/Pérignat – Hellmund, 1992, Pl. 3, Fig. 1a), *P. typus* (St.-Gérand - Viret, 1929, Pl. 18, Fig. 3b), *P. gergovianus* (holotype - Hellmund, 1992, Pl. 12, Fig. 2), *P. leptodon* (Cadibona - Dal Piaz, 1930, Pl. 1, Figs. 15 & 16) and *P. paronae* (Monteviale - Dal Piaz, 1930, Pl. 1, Fig. 14).

The lingual roots of the upper molars are fused and convergent in: *P. elaverensis* (Coderet) and Tomerdingen (Hellmund, 1992, pl. 7, fig. 16) and Montaigu. The roots are divergent and connected with a thin lamina of bone, like a webbed foot, and sometimes the roots are even separated to some extend, in: *P. typus* (St.-Gérand-Hellmund, 1992, Pl. 1, Fig. 1b; foot note p. 7), *P. aquensis* (St. Henri) and *P. paronae* (Monteviale - Dal Piaz, Pl. 1, Fig. 6). The roots of the M^3 of *P.? pusillus* (Hellmund, pl. 12, fig. lb) might be more divergent than those of the first two molars and might not be reliable.

These three characters divide the tayassuids into two groups, which are interpreted here as genera, *Propalaeochoerus,* which includes the material from Coderet, Tomerdingen Montaigu and Cetina and *Palaeochoerus,* which includes most of the remaining material; *P. pusillus* and *P. paronae* cannot yet be assigned to one of the groups.

In *Propalaeochoerus, P. elaverensis* is clearly larger. *Propalaeochoerus* from Tomerdingen, Cetina and Montaigu, is smaller, but it is apparent that the M^3 of Cetina and Montaigu are larger than those of Tomerdingen and their second lobes seem more reduced, yet the teeth are still of the long type. The M_2 and M_3 from Montaigu are also larger than the material from Tomerdingen (M_2 DAP 11.8 versus a maximum 12.6, DT 8.8 versus a maximum 8.6; M_3 DAP 16.1 versus 14.2-16.4, DT 9.1 versus 7.8-8.8), but the P_4 smaller (DAP 7.8 versus 8.9-10.1, DT 5.5 versus 4.9-6.2). The M_3 is large but has a reduced third lobe. The differences seem great enough for recognizing the two forms as species: "species B" from Tomerdingen (MN 1) and "species A" from Cetina and Montaigu (MN 2). It seems that overall size is similar, as well as the typically smooth enamel, but that species A has larger M3 and smaller premolars than species B. The apparent reduction of the posterior half of the last molars is a strange trend, which seems to be a reversal of the tendency for these teeth to become more elongate. However, enlargement of the last molar and reduction of the anterior dentition is a common trend in suoid evolution and *Propalaeochoerus* sp. B - sp. A may well present a lineage.

Propalaeochoerus has elongated M^3, which seems to be a progressive feature and the hypoconulid morphology and morphology of the lingual roots of the upper molars, which seem to be conservative features. This combination of characters precludes any derivation of *Propalaeochoerus* from *P. aquensis, P. paronae, P. typus, P. gergovianus* or *P. leptodon.* It might have evolved from an early member of the *P. typus* size group and from *P.? pusillus.* Of *P.? pusillus* very little is known and the stratigraphic position was not known, but it seems to occur in Montalban (MP 23), whereas a citation from Möhren (Hellmund, 1992) might be based on small material of a *P. typus* sized animal. *P.? pusillus* has the same size as the species from Tomerdingen and it is possible that this species just elongated the M^3 between MP 23 and MP 30 and that the larger *P. elaverensis* branched off after the trend of elongation of the M^3 started and before MP 30 (it should be noted that some short M^3 are still present in both large Tomerdingen and Coderet samples). However, more work has to be done to test such an hypothesis. The species might prove to be of stratigraphical interest, especially the evolution of the species of Tomerdingen to the species of Cetina might be indicative of the transition from MN 1 to MN 2.

Family **Suidae** Gray, 1821
Subfamily **Hyotheriinae** Cope, 1888
Genus *Hyotherium* Meyer, 1834

Type species: *Hyotherium soemmeringi* (Meyer, 1829) Meyer, 1834

		I_1 DMD	DLL	Hli	Hla	I_2 DMD	DLL	Hli	Hla	I_3 DMD	DLL	Hli	Hla
CT 11	r									7.0	5.3		
CT 469	l					5.7	7.6	14.2	16.7	7.5	4.7	6.2	7.0
	r					5.7	7.7	±14.2	15.7	7.7	5.0	±5.7	8.1
CT 475	l					5.7	7.7	>12.9	>14.4				
CT --	l					6.1	7.7	14.0	15.5				
	r					6.3	--	--	15.2				
CT --	r	6.3	6.7	12.3	13.9	6.3	--	--	>14.0				
CT --	l	--	6.8	--	--	5.4	≥7.8	--	--	6.4	6.2	--	--
	r	--	--	--	--					>5.1	>5.0	--	--
IPS 1401	l	5.8	>5.9	--	13.6								
IPS 1443	l	6.0	7.6	--	>15								
		I^1 DMD	DLL	Hli	Hla	I^2 DMD	DLL	Hli	Hla	I^3 DMD	DLL	Hli	Hla
CT 469	l	11.8	7.8	..	13.4	8.8	5.0	5.8	6.3	7.9	--	6.5	--
	r	11.3	7.7	11.5	±12.6	8.9	4.9	6.2	6.4	6.9	3.7	5.8	5.7
CT 533	r									7.2	2.4	6.5	7.2
IPS 1424	l	11.2	7.6	12.1	14.9								
IPS 1430	l	12.3	7.4	10.8	12.2								
IVAU --	r	10.9	7.6	..	..								

Table 1. Measurements of the incisors of *Hyotherium meisneri* from Cetina de Aragón.

Generic diagnosis: Suid: 1) in which the males have canines that do not flare out much, 2) with ovoid bullae with antero-posterior directed long axis, 3) with no, or small diastemas, 4) with elongated premolars, 5) with P_4 with two large cusps on the trigonid.

Hyotherium meisneri (Meyer, 1829) Meyer, 1841

Pl. I, Figs. 1-15; Pl. II, Figs. 1-7; Pl. III, Figs. 1-16; Pl. IV, Figs. 1-5, 7-13

1820	"... dieses fossile Thier dem Babirussa nahe verwandt ..."; Meisner, 71-72, Fig. 2.
1829	*Chaeropotamus Meissneri;* Meyer, 151.
1834	*Chaeropotamus Meissneri;* Meyer, 51.
1841	*Hyotherium Meissneri;* Meyer, 104.
1844	*Chaeropotamus Meissneri* H. v. Meyer; Pictet, 257.
1850	*Hyotherium meissneri* H. v. Meyer; Meyer, 116-126, Pl. IV, Figs. 1-7.
1853	*Hyotherium Meissneri* H. de Meyer; Pictet, 330.
1859	*Sus meissneri* H. v. Meyer; Kaup, 13-15, Pl. V, Figs. 6 & 7.
1859	*Palaeochoerus major* Pomel; Gervais, 183-184.
1896	*Palaeochoerus (Hyotherium) Meissneri* Meyer; Studer, 11-18, Pl. III, Figs. 3 & 4.
1899/ 1900	*Palaeochoerus*; Stehlin, 237, Pl. VII, Fig. 22.
?1907	*Palaeochoerus aurelianensis* Stehlin; Roman, 50-51, Pl. II, Figs. 4-6.
1911	*Palaeochoerus Meissneri* Meyer; Zittel, Broili, Koken & Schlosser, 473 partially, not Fig. 656.
1923	*Palaeochoerus Meissneri* v. Meyer; Zittel, Broili & Schlosser, 561 partially, probably not Fig. 695.
1962	*Palaeochoerus meissneri;* Truyols.
1972	*Palaeochoerus typus* Pomel, 1857; Golpe, 115, partially.
1972	*Palaeochoerus meissneri* Meyer, 1850; Golpe, 115-116.
1974	*Hyotherium major meissneri;* Meyer, 1850; Ginsburg, 76-77.
1990	*Hyotherium meissneri* Von Meyer, 1829; Van der Made (a), 87, Fig. 3.
1990	*Hyotherium meissneri;* Van der Made, 100 & 104.
1992	*Hyotherium meissneri* (H. v. Meyer 1829); Hellmund, Pl. 6, Fig. 1; partially: 1-36; not: textfig. 3, textfig. 4, Fig. 1, 3, 4, 8, Pl. 1-5, Pl. 6 Fig. 2, Pl. 7-11.

Diagnosis: *Hyotherium* with cheek teeth that measure on average 80 % the cheek teeth of *H. soemmeringi,* the I^1 does not have a distal cusp.

Material: CT 7 left and right M^3 (Pl. III, Fig. 1); CT 11 right I_3 (Pl. I, Fig. 3); CT 17 right M^3; CT 61 right M^2; CT 90 left M_2 - M_3 (Pl. III, Fig. 6; Pl. IV, Fig. 1); CT 99 left mandible with M_{2-3} and roots of M_1; CT 112 left P^3 - M^3 (Pl. III, Figs. 4 & 11), right M^1 - M^3; CT 208 right M_1; CT 386 fragments of incisors; CT 392 left navicular; CT 468 left mandible C_m, P_3 - M_3 (Pl. II, Fig. 7); CT 469 mandible with right M_{1-3} and remains of P_{2-3}, right and left I^1 - I^2 (Pl. II, Figs. 4 & 5) in connection and isolated teeth: right and left I^3 (Pl. I, Fig. 14), left P_2 (Pl. I, Fig. 12), right (Pl. I, Fig. 15) and left C^m, left P^1 - P^4 (Pl. I, Fig. 8; Pl. II, Figs. 2 & 3; Pl. III, Fig. 10) right P^1 (Pl. I, Fig. 9) and P^3, right and left M^1, left M^{2-3} (Pl. II, Fig. 1), right and left I_2 - I_3 (Pl. I, Figs. 2, 6 & 11), probably from one individual; CT 475 left I_2 (Pl. I, Fig. 1); CT 481 left M^2; CT 483 left P_4 (Pl. III, Fig. 14); CT 523 right M^2 - M^3; CT 533 right I^3 (Pl. I, Fig. 10); CT 774 left M_2; CT – associated teeth: left P^3 - M^3 (Pl. IV, Figs. 5, 10 & 13) and right P^3 - M^3 (Pl. III, Fig. 5; Pl. IV, Figs. 9 & 12); CT – apical fragment of a left I^1; CT – right mandible with P_4 – M_2 (P_4 still in alveolus), associated left P_2 - M_2 (Pl. III, Figs. 3, 8 & 13) and remains of left M_3, left D_4 (Pl. IV, Fig. 4) and part of left D_3 (Pl. IV, Fig. 8), left C_f (Pl. I, Fig. 13), left and right I_2 (Pl. I, Figs. 4 & 5), right I_1 (Pl. I, Fig. 7); probably all from the same individual; CT – left mandible with P_{2-4}; CT – right mandible with P_1 (Pl. III, Fig. 7) and roots of P_{2-3}; CT – right P_4 - M_3 (Pl. III, Fig. 16; Pl. IV, Fig. 11) and left M_2 - M_3 (Pl. IV, Fig. 2); CT – right P_3 (Pl. III, Fig. 2); CT – left P_4 (Pl. III, Fig. 15); CT – left P_1 (Pl. III, Fig. 9); CT – left P_2 - M_3 (Pl. III, Fig. 12; Pl. IV, Fig. 3); CT – left I_2; CT – right I_1; CT – left P3 (Pl. II, Fig. 6); CT – remains of a mandible with remains of left I_{1-3}, P_{3-3} and the root of a C_f and remains of right I_1, I_3 and P_3 - M_3.

Description and comparison: The measurements of the incisors are given in Table 1 and in Fig. 3, the sizes are compared with the sizes of the incisors of other taxa.

The $\mathbf{I_1}$ (Pl. I, Fig. 7) have relatively low crowns. The lower border of the crown is well defined: the enamel does not become thin over a long distance but ends abruptly.

The $\mathbf{I_2}$ (Pl. I, Fig. 1; Pl. I, Fig. 2; Pl. I, Fig. 4; Pl. I, Fig. 5; Fig. 3) differs from the I_1 in being less symmetrical, but also in having distally a large facet caused by wear by the I^2 (Pl. I, Fig. 1b).

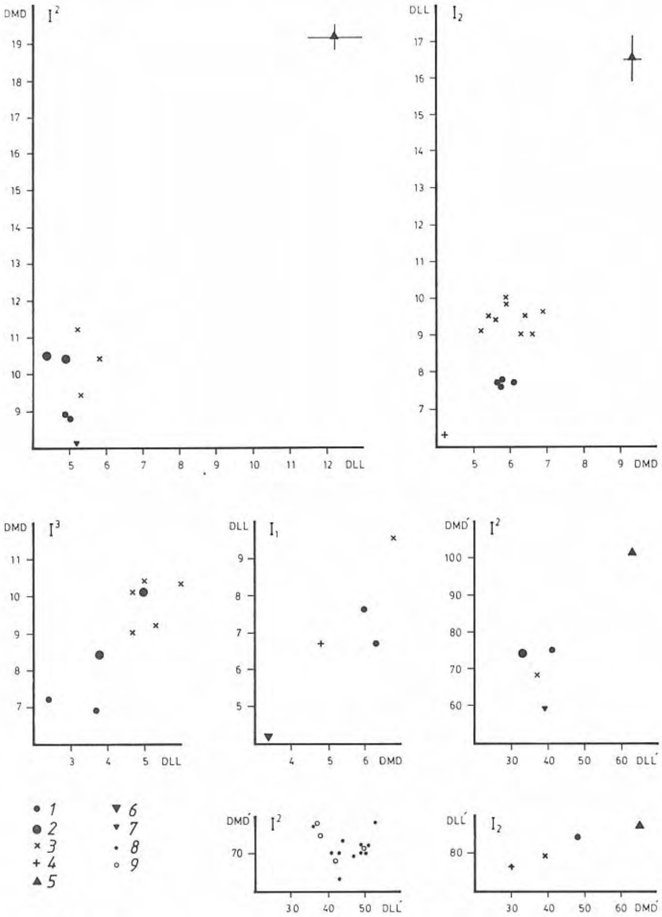


Figure 3. Scatter diagrams of the incisors of Hyotheriinae and *Palaeochoerus.* Legend: 1) *Hyotherium meisneri* from Cetina de Aragón (MNCN, IPS); 2) *Hyotherium major* from St.-Gérand-le-Puy (MNHN); 3) *Hyotherium soemmeringi* from Sandelzhausen (BSPHGM); 4) *Aureliachoerus aurelianensis* from Artenay (MNHN); 5) *Xenohyus venitor* from Les Beilleaux à Savigné-sur-Lathan (average and range; data from Ginsburg, Huin & Locher, 1988); 6) *Palaeochoerus typus* from St.-Gérand-le-Puy (MGL); 7) *Palaeochoerus aquensis* from the Quercy (cast in MNCN); 8) recent *Tayassu pecari*-(ZMA); 9) recent *Tayassu tayacu* (ZMA). The recent peccaries have been added to show the variability in DMD' and DDL' values.

		Li	La	Po
C_m				
CT 468	l	8.3	5.1	6.4
		DAP	DT	
c^m				
CT 469	l	--	--	
	r	10.8	7.7	
C_f				
CT --	l	9.2	4.3	
CT --	l	--	--	
IPS 1426	r	8.4	6.3	
c^f				
IPS 1434	l	7.4	4.6	

Table 2. Measurements of the canines of *Hyotherium meisneri* from Cetina de Aragón.

The **I$_3$** (Pl. I, Fig. 3; Pl. I, Fig. 6; Pl. I, Fig. 11) has the same structure as the I$_1$ and I$_2$, but is even more asymmetrical and has a lower crown. The tooth may be more (Pl. I, Fig. 6ac; Pl. I, Fig. 11c) or less laterally compressed (Pl. I, Fig. 3ad).

The **I^1** are of the primitive type (sensu, Van der Made, 1990d). The crown is low (Pl. II, Fig. 4a; Pl. II, Fig. 5g), labially the crown height is 13.5 mm. At the lingual side (Pl. II, Fig. 4d; Pl. II, Fig. 5e) there is a mesial ridge, a wider medial elevation ("medial ridge") and a distal ridge. In both specimens of the MNCN collection the lingual cingulum is continuous and is connected to the distal ridge (Pl. II, Fig. 4b; Pl. II, Fig. 5ce), but in other specimens the cingulum and distal ridge are not connected.

The **I^2** are larger and more elongate than the I^3. The crown is low (Pl. II, Fig. 4g; Pl. II, Fig. 5b; Table 1). There is a lingual cingulum, but it is not very pronounced (Pl. II, Fig. 4ef; Pl. II, Fig. 5ad).

The **I^3** has the same structure as the I^2, but is less elongate (Pl. I, Fig. 10a; Pl. I, Fig. 14a), has a relatively higher crown (Pl. I, Fig. 10b; Pl. I, Fig. 14b; Table 1) and there is no clear lingual cingulum (Pl. I, Fig. 10c; Pl. I, Fig. 14c). The homologies in *H. soemmeringi* and *H. major* have a small distal talon and anteriorly a crest running up to

		P_1			P_2			P_3			P_4			M_1			M_2			M_3			
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
CT 90	l																15.5	10.2	10.5	20.1	10.9	11.1	7.3
CT 99	l													--	--	--	13.2	10.4	10.5	20.0	10.0	9.1	7.1
CT 208	r													12.8	>8.6	--							
CT 468	l							≤13.1	5.2	--	≥12.3	7.0	7.9	11.8	8.6	9.0	14.4	10.7	10.8	>18.6	10.6	10.0	--
CT 469	l				8.7	3.8	4.0																
	r				--	--	--	--	--	--	--	--	--	12.2	8.7	≥8.6	13.9	10.8	10.8	21.0	10.7	9.8	8.5
CT 483	l										11.6	>7.1	≥8.1										
CT 494	l																--	10.2	--				
CT 774	l																--	--	10.2				
CT --	r	8.0	3.6	3.8	--	--	--	--	--	--													
CT --	l				7.9	--	--	10.6	5.3	5.6	--	7.3	--										
CT --	l							10.3	5.8	6.1													
CT --	l	8.5	3.9	4.4																			
CT --	r							11.0	5.2	6.0													
CT --	l										11.4	7.7	7.6										
CT --	l				8.5	..	5.2	--	4.9	--	11.3	6.7	7.2	12.1	8.5	8.9	13.6	10.3	10.0	19.0	10.3	9.1	7.0
CT --	l																14.8	11.1	10.9	19.0	11.0	9.4	6.9
	r										11.7	7.5	7.8	12.6	8.7	9.3	14.7	11.2	10.8	18.6	11.0	9.3	6.7
CT --	l				9.4	3.9	4.1	12.3	5.5	5.9	12.4	7.4	7.9	13.2	9.2	9.6	14.9	11.0	10.7	--	10.4	9.2	--
	r										11.7	7.3	--	13.0	9.0	9.3	14.8	10.9	11.0				
CT --	l							--	5.1	--	12.1	6.8	7.8										
	r							--	--	--	±10.5	--	--	11.3	..	..	13.2	--	10.6	--	--	9.1	7.3
IPS 1301	r										11.1	..	8.0										
IPS 1371	l																14.1	11.2	11.0				
IPS 1385	r										12.4	..	8.2										
IPS 1387	l										11.9	..	8.5										
IPS 1389	r										12.0	..	7.5										
IPS 1397	r																14.3	10.9	10.7				
IPS 1399	r																15.2	11.2	11.0				
IPS 1401	l							--	..	--													
IPS 1409	r				9.3	..	4.1																
IPS 1427	r													--	--	9.2							
IPS 1428	r													12.9	9.1	9.3							
IPS 1429	l													12.8	9.1	9.1							
IPS 1432	l																14.1	≥9.9	≥9.8				
IPS 1435	l													12.3	8.2	8.6							
IPS 1437	l													--	≥8.4	--							
IPS 1439	l													12.7	8.6	8.9							
IPS 1440	r																			19.9	11.8	10.1	8.3
IPS 1442	l																			19.2	11.8	10.3	8.0
IPS 1444	r							11.4	..	6.7													
IPS 1445	l										11.9	..	8.5	12.1	--	--	14.0	11.1	11.0				
	r																			19.8	11.5	10.0	8.2
IVAU --	r										10.6	7.0	≥6.7										

Table 3. Measurements of the lower cheek teeth of *Hyotherium meisneri* from Cetina de Aragón.

the tip that stands out from the lingual surface. In these species the anterior edge of the tooth (in side view) is convex. In *H. meisneri* it is nearly straight. The I^3 of *H. major* and *H. soemmeringi* are clearly longer (Fig. 3).

The measurements of the canines are given in table 2.

The C_m is a very hypsodont tooth and does not show any sign of the formation of a root (Pl. II, Fig. 7b). What remains of it is approximately the fifth of a circle. The section is scrofic (Pl. II, Fig. 7a; Table 2): the labial side is shorter than the posterior side.

The C_f has a lower crown than its male equivalent and has a root (Pl. I, Fig. 13bc). The crown has enamel all around (Pl. II, Fig. 13a).

Anteriorly the C^m is sharp, posteriorly it is round (not well seen in Pl. I, Fig. 15a, as the tip protrudes over the contour of the lower part of the tooth). The tip of the tooth curves backward (Pl. I, Fig. 15bd) and outward (Pl. I, Fig. 15c). At the sharp anterior end the lower border of the crown curves down and runs parallel to this anterior end (Pl. I, Fig. 15bcd), there it is about a centimeter lower than on the

		P^1			P^2			P^3			P^4		M^1			M^2			M^3			
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DT	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
CT 7	l																		15.6	13.2	11.9	..
	r																		15.9	13.2	11.5	..
CT 17	r																		--	13.1	--	--
CT 61	r															--	14.1	--				
CT 112	l							11.2	..	7.7	9.7	11.0	>11.5	--	--	13.1	13.8	13.2	15.9	13.4	11.5	6.4
	r												>11.8	<11.9	12.1	13.1	13.7	13.3	16.3	13.5	11.4	5.5
CT 469	l	7.4	4.0	3.7				11.2	6.4	8.3	10.0	11.6	11.7	11.4	11.9	14.1	13.4	13.7				
	r	7.3	4.0	3.8	9.0	4.3	4.3	11.2	6.7	8.1			11.8	..	12.0							
CT 481	l															13.5	--	--				
CT 523	r															14.3	13.4	13.8	16.2	13.8	12.0	5.5
CT --	l							11.5	..	8.7	9.2	10.6	12.2	12.1	12.1	13.6	13.8	14.0	14.4	13.2	11.6	..
	r							10.7	7.0	8.8	9.0	10.7	12.2	12.1	11.9	13.6	13.7	13.6	14.6	13.2	11.6	..
CT --	l																		16.5	13.6	11.6	6.1
CT --	l															14.4	13.6	13.5				
IPS 1373	r																		16.0	13.5	11.4	..
IPS 1379	l																		16.0	--	--	--
IPS 1383	l																		16.1	13.3	10.7	5.8
IPS 1385	r																		16.8	--	12.5	--
IPS 1392	l																		15.2	13.2	11.2	..
IPS 1402	l															>13.6	13.4	10.9				
IPS 1405	r															13.4	13.4	12.0				
IPS 1438	l										8.8	10.3										
IPS 1439	r										9.4	11.7	11.8	11.8	11.6	13.5	13.0	12.6	16.1	12.4	10.5	..
IPS 1501	l															12.8	12.6	12.6				
IPS 1795	l															13.2	13.4	12.0				
IPS 1895	l												12.0	11.7	12.1							
IPS --	l										7.9	9.9										
IPS --	l							11.4	..	7.7												
IVAU --	r																		14.3	12.5	10.9	..
IVAU --	l															--	14.2	--				

Table 4. Measurements of the upper cheek teeth of *Hyotherium meisneri* from Cetina de Aragón.

	P_3			P_4			M_1			M_2			M_3			
	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
mean	11.1	5.3	5.9	11.7	7.2	7.7	12.4	8.8	9.2	14.3	10.7	10.6	19.6	10.6	9.6	7.3
n	4	7	4	7	8	6	8	7	5	10	10	11	6	8	9	7
SD	0.9	0.3	0.2	0.4	0.3	0.3	0.6	0.2	0.3	0.8	0.4	0.3	0.9	0.4	0.7	0.6
V	8.0	5.5	3.7	3.3	4.8	3.5	5.2	2.8	3.0	5.5	3.6	2.9	4.6	3.4	6.9	8.1
V'	18	17	9	9	14	9	16	8	8	16	9	10	12	7	20	24

	P^3			P^4		M^1			M^2			M^3			
	DAP	DTa	DTp	DAP	DT	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
mean	11.2	6.7	8.3	9.5	11.0	12.0	11.9	12.0	13.7	13.7	13.6	15.7	13.4	11.6	5.9
n	5	3	5	4	4	4	3	5	8	8	7	8	9	8	4
SD	0.3	0.3	0.4	0.5	0.5	0.3	0.4	0.9	0.5	0.2	0.3	0.8	0.2	0.3	0.5
V	2.6	0.4	5.4	4.8	4.1	2.2	3.4	0.8	3.7	1.7	1.9	5.0	1.8	2.3	7.7
V'	7	9	13	11	9	4	6	2	9	5	6	14	5	5	2

Table 5. Means, numbers of specimens, standard deviations, coefficients of variation and V' (Freudenthal & Cuenca, 1984) of the cheek teeth of *Hyotherium meisneri* from the lower bed at Cetina de Aragón collected in the 1983 excavation.

lateral and distal sides of the tooth. The crown height varies between 14 and 25 mm. The section differs from that of the canines of *H. major* and *H. soemmeringi* which are sharp anteriorly and posteriorly. There is no trace of cementum at the base of the tooth or bands of cementum covering the enamel.

The measurements of molars and premolars are given in Tables 3 and 4 and means, standard deviation, coefficient of variation and V' (Freudenthal & Cuenca, 1984) for the MNCN sample are given in Table 5. In Fig. 4 & 5, the sizes of the cheek teeth of *H. meisneri* are compared to those of other taxa.

The **P_1** (Pl. III, Fig. 7; Pl. III, Fig. 9) are smaller and less elongate than the P_2.

There are two types of **P_2**: one type with a small cusp on the talonid (Pl. I, Fig. 12) and one type without such a cusp (Pl. III, Fig. 8). In *Hyotherium*, the P_2 is more elongate and not so high as in *Palaeochoerus.*

The **P_3** may be more (Pl. III, Fig. 3) or less (Pl. III, Fig. 2; Pl. II, Fig. 6) elongate. The P3 is less hypsodont in *Hyotherium* than in Palaeochoerinae like *Palaeochoerus typus* (Table 6).

What Ginsburg (1974) called a paraconid in the **P_4** in tayassuids probably is analogous to the anterior end of the ridge that runs down from the buccal main cusp (protoconid). This ridge is very short and a cusp is not differentiated or forms part of the anterior cingulum. The anterior part of the P_4 of the holotype of *Hyotherium meisneri* has the same morphology (Studer, 1896, Pl. III, Fig. 4) as in Cetina. In *Palaeochoerus typus* and other *Palaeochoerus* and *Propalaeochoerus,* a large cusp is formed on the cingulum. This cusp may be high or low and may protrude much forward and between this cusp and the lingual main cusp a wide valley is formed. In Cetina, there are two types of P_4. The common type has a trigonid consisting of three cusps (Pl. III, Fig. 13; Pl. III, Fig. 15; Pl. III, Fig. 16). The biggest cusp (protoconid) is placed anteriorly in the middle or a little buccally of the medial plane. It has a ridge running down to the middle of the anterior cingulum. Directly behind the biggest is the smallest of the three cusps; it disappears with only a little wear and a large backward dipping facet is formed on the three cusps (Pl. III, Fig. 12; Pl. III, Fig. 14). This small cusp can be observed in 3 specimens. In the others it has been worn away. This cusplet is probably a remnant of a ridge connecting the protoconid and the talonid. The third cusp (metaconid) is placed lingually. The second type of P_4 (CT 468 (Pl. II, Fig. 7) and the specimen in the IVAU) has only

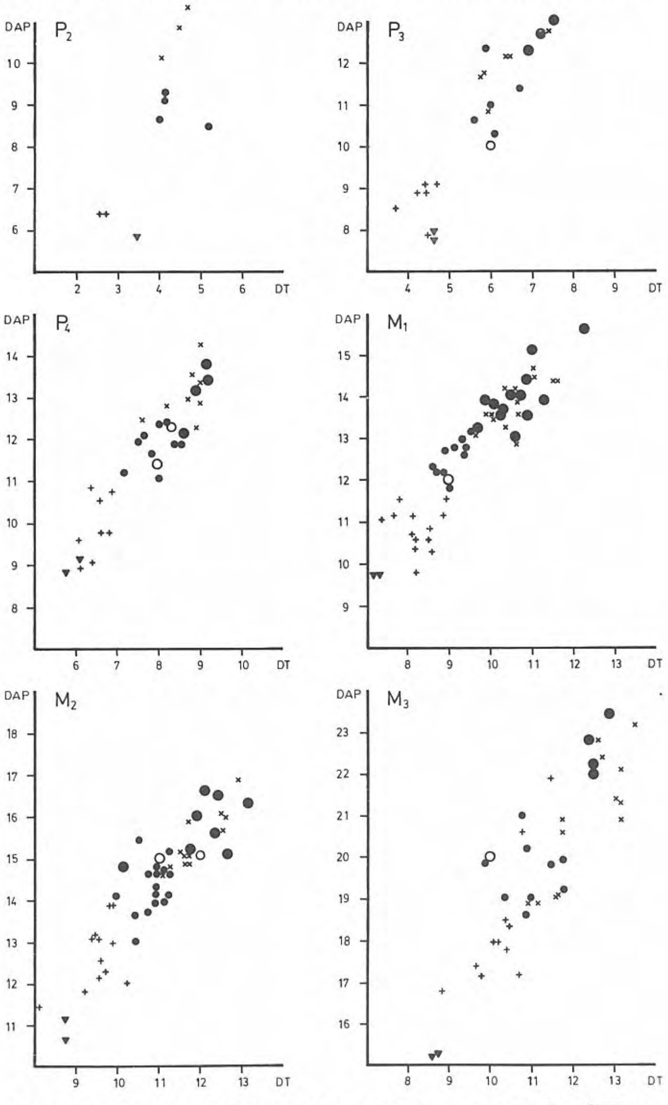


Figure 4. Scatter diagrams of the lower cheek teeth of Hyotheriinae and *Palaeochoerus.* Legend as in figure 5.

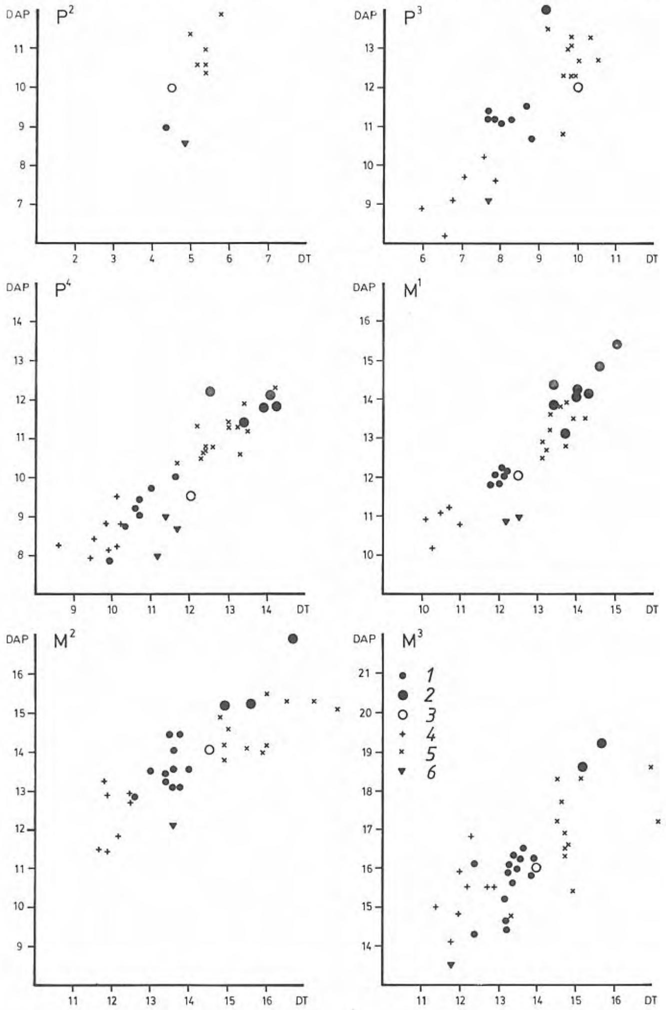


Figure 5. Scatter diagrams of the upper cheek teeth of Hyotheriinae and *Palaeochoerus.* Legend for figures 4 & 5: 1) *Hyotherium meisneri* from Aarberg and Wiesbaden; 2) *Hyotherium meisneri* from Cetina de Aragón (MNCN, IPS & IVAU); 3) *Hyotherium major* from St.-Gérand-le-Puy (MNHN); 4) *Aureliachoerus aurelianensis* from Artenay (MNHN: MGL; MHNT, casts SMNS), 5) *Hyotherium* cf. *major* from Ulm-Westtangente (SMNS); 6) *Palaeochoerus typus* from St.-Gérand-le-Puy (MGL; casts in SMNS).

	P_1		P_2		P_3		P^1		P^2		P^3	
	Hli/DAP	Hli/DT	Hli/DAP	Hli/DT	Hli/DAP	Hli/DT	Hla/DAP	Hla/DT	Hla/DAP	Hla/DT	Hla/DAP	Hla/DT
H. meisneri	0.7	1.4	0.6	1.5	0.8	1.5	0.6	1.1	0.5	1.1	0.9	1.1
	0.7	1.5	0.6	1.4	0.7	1.4	0.6	1.1				
H. soemmeringi	0.7	1.3	0.5	1.4			0.5	--	0.6	1.3		
	0.7	1.3	0.5	1.3			0.5	1.0	0.5	1.1		
	0.7	1.6	0.7	1.7			6.1	1.3	0.5	1.1		
			0.6	1.6			0.7	1.3	0.4	1.0		
									0.6	1.2		
P. aquensis			0.9	1.7	1.0	1.9	0.8-1.0	1.6-1.9	0.7	1.3	0.8	1.3
P. typus					1.0	1.7			0.9	1.6		

Table 6. Hypsodonty of *Hyotherium meisneri* from Cetina, *Hyotherium soemmeringi* from Sandelzhausen, *Palaeochoerus aquensis* from France and *Palaeochoerus typus* from St.-Gérand-le- Puy, expressed as a ratio of the height of the crown and the length or width. For the upper premolars the crown height was taken at the labial side, for the lower premolars at the lingual side.

		DAP	DTa	DTm	DTp
D_3					
CT --	l	--	4.7		--
D_4					
CT --	l	15.9	6.2	7.2	8.2
D^4					
IPS 1388	l	11.9	9.8		11.1
IPS 1436	l	11.4	10.7		10.9
IPS --	r	12.8	11.7		12.0

Table 7. Measurements of the deciduous teeth of *Hyotherium meisneri* from Cetina de Aragón.

navicular	DAP	DT	Ha		
CT 392 r	17.1	9.4	6.9		
MC III	DAPp	DTp	L	DAPd	DTd
IPS 1441 l	12.8	11.6	--	--	--

Table 8. Measurements of the foot bones of *Hyotherium meisneri* from Cetina de Aragón.

one main cusp, or the three cusps are not well separated. Also in *H. major* from St.-Gérand-le-Puy there is one P_4 with only one cusp (SG 3598). Stehlin (1899/1900) mentioned another case in *Hyotherium* and the holotype of *"Conohyus" betpakdalensis* Trofimov, 1949 (= *Xenohyus venitor*?) may be another example.

The **P^1** has two divergent roots (Pl. I, Fig. 9; Pl. III, Fig. 10). The P1 of Palaeochoerinae tend to be more pointed and the crown is higher (Table 6).

The **P^2** has a clear, but low metacone (Pl. I, Fig. 8). The low elongate shape and metacone is just like that of the P^2 depicted by Meyer (1850). The P^2 of *H. soemmeringi* has a wider postero-lingual cingulum. The premolars of the Palaeochoerinae tend to be more hypsodont (Table 6).

The **P^3** has either a high conical main cusp (Pl. III, Fig. 5) or a high laterally compressed cusp (Pl. II, Fig. 3) or a low cusp (Pl. III, Fig. 4). The tooth has a continuous lingual cingulum that is wide posteriorly. In the posterior half of the tooth, this cingulum is a low ridge enclosing a basin. There is no cusplet on the cingulum, nor in this basin. However there may be a small widening of the ridge in the postero-lingual corner of the tooth.

The **P^4** (Pl. II, Fig. 2; Pl. III, Fig. 11; Pl. IV, Fig. 12; Pl. IV, Fig. 13) has a large elongate labial cusp, but, in its upper part, it may be divided into two cusps. The labial wall of the tooth is flat and shows no sign of a bipartition (Pl. II, Fig. 2d), or shows only a slight sign near the tip (Pl. IV, Fig. 12; Pl. IV, Fig. 13a). On the lingual side of this ridge the partition is clear (Pl. IV, Fig. 12e). There is no "sagittal cusp" (sensu Pickford, 1988).

The **M_1** (Pl. IV, Fig. 11) and **M_2** (Pl. III, Fig. 6; Pl. IV, Fig. 3) have the same structure. Most of the teeth have been found in connection and their position is known. Size overlap occurs between first and second molars, but it is minimal.

In the **M_3** there is some variation in the length of the talonid. This is due to the varying slope of the posterior wall of the tooth (compare Pl. IV, Fig. la and Pl. IV, Fig. 2a).

The **M^1** and **M^2** (Pl. IV, Fig. 7; Pl. IV, Fig. 10) have the same structure. The paraconule is fused to the cingulum (Pl. IV, Fig. 7; Pl. IV, Fig. 10ab) (see description and discussion of *Propalaeochoerus*).

The talon of the **M^3** may be a cingulum which is a little wider on the lingual side. Two shorter M^3 (Pl. IV, Fig. 5; Pl. IV, Fig. 9a, Fig. 5) have this morphology, but more common is a small cusplet slightly lingually of the middle (Pl. II, Fig. 1; Pl. III, Fig. 1). The protoconule is fused to the cingulum (Pl. IV, Fig. 9b).

A fragment of the **D_3** (Pl. IV, Fig. 8; Table 7) can be recognised because of the triangular posterior facet (a premolar would have a ridge or develop separate cusps, D_3 in unworn state may have several posterior ridges).

The **D_4** (Pl. IV, Fig. 4; Table 7) is only slightly smaller than three specimens of *H. major* from St.-Gérand-le-Puy (DAP 16.5-16.7 versus 16.0 and DT 8.6-9.0 versus 8.4).

The **navicular** (Table 8) has a small facet for the cuneiform II (it measures 1.5 mm × 1.7 mm). This facet is not horizontal but dips away from the middle of the bone, if seen from the distal side. It has the shape of a crescent with the concave side bordering the facets for the cuneiforms I and III. The latter facets meet each other.

Discussion: The measurements of the cheek teeth from Cetina are close to those of the holotype of *H. meisneri* from Aarberg and the teeth of the skull and mandible from Wiesbaden (Figs. 4 & 5; Tables 2-4; Table 9). No significant differences in morphology can be detected. There is a size difference of about 15 % with both the larger *H. major* from St.-Gérand-le-Puy and the smaller *A. aurelianensis* from Artenay (Table 10). Size differences of approximately 15 % seem to be common between sympatric species (see section on palaeoecology).

The large collection from Ulm-Westtangente has for most of the teeth a wider size range than the collections from Cetina or St.- Gérand. It is common for larger samples to have larger size ranges (Freudenthal & Cuenca, 1984). Most, but not all teeth from St.-Gérand are within the Westtangente ranges and most teeth from Cetina are outside these ranges. The teeth from Wiesbaden and Aarberg are often, but not always smaller than those from the Westtangente, but close to Cetina. It seems justified to assign the material from Cetina, Wiesbaden and also Aarberg to one species, *Hyotherium meisneri*. The material from Ulm-Westtangente is close to, but not identical to that from St.-Gérand-le-Puy and is assigned to *Hyotherium* aff. *major*.

As *H. meisneri* has been found in several places in western Europe which are of different ages. This species must have existed in the same area and in the same time as *H. major*. For that reason it is not likely that these two taxa are subspecies, as has been supposed (Ginsburg, 1974). Also the idea of Hellmund (1991) that the holotype of *H. major* represents just a large individual is difficult to defend, since all individuals from St.-Gérand are large and there is nearly no size overlap with Cetina (Fig. 3; Fig. 4).

H. meisneri has been described from various localities, but the determinations are in some cases questionable. In another case possible *H. meisneri* teeth have been described as another species.

The teeth attributed to *"Palaeochoerus" aurelianensis* by Roman (1907) might belong to *H. meisneri* as morphology and measurements are closer to the Aarberg, Wiesbaden and Cetina material than to *A. aurelianensis* from Artenay. However, the material is few and some teeth which are important for the determination are not represented.

Stehlin (1899/1900) used the species names of *Palaeochoerus* and *Hyotherium* to indicate size (see pages 38 and 39). His determinations have to be used with care since there are tayassuids that are close in size to *H. meisneri*.

The maxilla from Aarwangen (MP 27) that was attributed by Studer 1896 to *H. meisneri* has the antero-buccally directed ridge that originated from the protocone (preprotocrista) that

	C^m		P^2		P^3		P^4		M^1		M^2		M^3		
	DAP	DT	DAP	DT	DAP	DT	DAP	DT	DAP	DT	DAP	DT	DAP	DT	
Wiesbaden	13	9	10	4.5	12	10	9.5	12	12	12.5	14	14.5	16	14	
	C_m		P_3		P_4			M_1			M_2			M_3	
	DAP	DT	DAP	DT	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DT
Aarberg					12.4	7.8	8.2	>11.8	--	--	15.1	12.0	11.9		
Wiesbaden	11.5	7	10	6	11.5		8	12		9	15		11	20	10

Table 9. Measurements of teeth of *Hyotherium meisneri* from the Rappenfluh near Aarberg (holotype) and from Wiesbaden. Measurements for the holotype from a cast in the NMB and for the Wiesbaden material from Meyer (1850).

	P_1			P_2			P_3			P_4			M_1			M_2			M_3			
	$\overline{\text{DAP}}$	%	n	$\overline{\text{DAP}}$	%	n	$\overline{\text{DAP}}$	%	n	$\overline{\text{DAP}}$	%	n	$\overline{\text{DAP}}$	%	n	$\overline{\text{DAP}}$	%	n	$\overline{\text{DAP}}$	%	n	
A. aurelianensis			0	6.4	73	2	9.1	82	2	9.4	80	4	10.4	84	6	12.0	84	3	17.8	91	3	
H. meisneri	8.3	105	2	8.8		5	11.1	86	5	11.7	87	13	12.4	92	13	14.3	90	15	19.6	87	9	
H. major	7.9	75	1			0	12.9	86	2	13.5	89	3	13.7	91	10	15.9	90	7	22.6	92	4	
H. soemmeringi	11.7	103	5	13.7	129	8	15.0	94	12	15.2	92	16	15.3	81	14	17.6	81	18	24.6	80	10	
X. venitor	11.4		2	10.6		2	15.9		7	16.4		8	18.9		3	21.9		12	30.7		11	
	P_1			P_2			P_3			P_4			M_1			M_2			M_3			
	$\overline{\text{DT}}$	%	n	$\overline{\text{DT}}$	%	n	$\overline{\text{DT}}$	%	n	$\overline{\text{DT}}$	%	n	$\overline{\text{DT}}$	%	n	$\overline{\text{DT}}$	%	n	$\overline{\text{DT}}$	%	n	
A. aurelianensis			0	2.7	61	2	4.5	74	2	6.5	82	4	8.3	91	6	9.7	90	3	10.1	93	3	
H. meisneri	4.1	114	2	4.4		4	6.1	82	5	7.9	87	11	9.1	87	10	10.8	88	13	10.9	87	11	
H. major	3.6	68	1			0	7.4	109	2	9.1	101	3	10.5	88	10	12.3	90	7	12.6	92	4	
H. soemmeringi	5.3	88	4	5.5	74	8	6.8	68	12	9.0	78	16	11.9	83	14	13.7	83	18	13.7	78	10	
X. venitor	6.1		2	7.4		2	10.0		7	11.5		9	14.4		3	16.4		12	17.5		11	
	p1			p^2			p^3			p^4			M^1			M^2			M^3			
	$\overline{\text{DAP}}$	%	n	$\overline{\text{DAP}}$	%	n	$\overline{\text{DAP}}$	%	n	$\overline{\text{DAP}}$	%	n	$\overline{\text{DAP}}$	%	n	$\overline{\text{DAP}}$	%	n	$\overline{\text{DAP}}$	%	n	
A. aurelianensis			0			0	9.3	83	6	8.4	88	7	11.5	96	2	12.3	90	2	14.8	94	1	
H. meisneri	7.4	80	2	9.0		1	11.2		6	9.5	81	5	12.0	85	6	13.6	89	12	15.7	83	15	
H. major	9.2	87	2			0			0	11.8	95	3	14.1	93	7	15.2	86	1	18.9	94	2	
H. soemmeringi	11.7	87	5	14.2	105	10	14.4	91	14	12.4	88	21	15.1	79	24	17.7	84	22	20.2	83	23	
X. venitor	13.5		1	14.4		1	15.8		4	14.0		7	19.0		10	21.0		12	24.2		10	
	p1			p^2			p^3			p^4			M^1			M^2			M^3			mean
	$\overline{\text{DT}}$	%	n	$\overline{\text{DT}}$	%	n	$\overline{\text{DT}}$	%	n	$\overline{\text{DT}}$	%	n	$\overline{\text{DT}}$	%	n	$\overline{\text{DT}}$	%	n	$\overline{\text{DT}}$	%	n	%
A. aurelianensis			0			0	7.0	85	6	9.6	88	7	10.4	87	2	11.9	88	2	12.0	91	1	85
H. meisneri	4.0	98	2	4.3		1	8.2		5	11.1	82	5	12.0	86	7	13.6	87	13	13.2	85	14	89
H. major	4.1	73	2			0			0	13.4	101	3	13.9	95	7	15.6	92	1	15.5	96	2	90
H. soemmeringi	5.6	72	4	6.5	57	10	10.7	77	14	13.3	78	21	14.7	76	24	17.0	76	22	16.1	78	23	84
X. venitor	7.8		1	11.5		1	14.0		4	17.0		7	19.4		8	22.5		11	20.8		9	

Table 10. Average measurements of cheek teeth of samples of Hyotheriinae and the percentages the averages present of the next largest species. *Aureliachoerus aurelianensis* from Artenay (material in the MNHN), *Hyotherium meisneri* from Cetina (MNCN), *Hyotherium major* from St.-Gérand-le-Puy (MNHN), *Hyotherium soemmeringi* from Sandelzhausen (BSPHGM) and *Xenohyus venitor* from les Beilleaux à Savigné-sur-Lathan (Ginsburg, Huin & Locher, 1988).

is typical for *Palaeochoerus* as was pointed out above. *P. aquensis* occurs in Aarwangen (cast in NMB) and the maxilla figured by Studer may well represent this species. The *"Palaeochoerus Meisneri"* figured by Zittel 1891/93 (Fig. 278) from Eckingen is too large for *H. meisneri.*

The *"H. meissneri* mut. *elaverensis"* from Coderet (Viret, 1929 Pl. XXXI, Figs. 1-12) is a tayassuid. This is indicated by the paraconule and hypoconulid morphologies of the molars, the roots of upper and lower molars and canine shape. Viret (1929) derived *H. meisneri* from the suoid of Coderet. Ginsburg (1980) determined the suoid from Coderet as *Palaeochoerus gergovianus elaverensis* and he was more cautious about a possible descent of *Hyotherium* from the animal from Coderet. The large sample from Coderet shows morphological differences in nearly all teeth and bones between *P. elaverensis* and *Hyotherium* and a lineage is far from likely.

The European Hyotheriinae include three genera *Hyotherium, Aureliachoerus* and *Xenohyus.* It is difficult to separate *Hyotherium* from *Aureliachoerus.* The premolars of *Aureliachoerus* are often, but not always smaller, or just shorter (and thus relatively wider) than in *Hyotherium.* Differences with *Xenohyus* are clearer: *Xenohyus* has relatively smaller P1 and P2 (Table 10) and much enlarged incisors (Fig. 3). Within the Hyotheriinae, the species of *Hyotherium* are united by the synapomorphy of elongated premolars and *Xenohyus* is characterized by the apomorphy of enlarged incisors.

Hyotherium major (Pomel, 1847)

1841 *Hyotherium medium;* Meyer, 104, partially.
1847 *Palaeochoerus major;* Pomel, 381, Pl. IV, Fig. 2.
1853 *Palaeochoerus major* Pomel; Pictet, 327, Pl. XII, Fig. 5.
1853 *Hyotherium medium* H. de Meyer; Pictet, 330.
1859 *Hyotherium medium*; Gervais, 182.
1859 *Palaeochoerus major* Pomel; Gervais 183-184
1859 *Palaeochoerus typus*; Gervais, Pl. XXXIII, Fig. 3.
1880 *Hyotherium majus*; Filhol, 19-20.
1880 *Hyotherium Waterhousi*; Filhol, 20-40, Pl. 4-10.
1884 *Hyotherium Waterhousii*; Filhol, 30.
1885 *Hyotherium waterhousei* (Pomel); Lydekker, 256-257, no. M 2203.
1885 *Hyotherium soemmeringi* H. v. Meyer; Lydekker, 257-258.
1891/
1893 *Palaeochoerus major*; Zittel, p. 340.
1891/
1893 *Palaeochoerus Waterhousi*; Zittel, 340, Fig. 277.
?1891/
1893 *Palaeochoerus Meissneri* H. v. Meyer; Zittel, 341, Fig. 278.
1895 *Palaeochoerus Waterhousi* Pomel; Zittel, 888 partially, Fig. 1976, Fig. 1977?
1899/
1900 *Palaeochoerus Waterhousii*; Stehlin, 41 & 236, Pl. II, Fig. 18, Pl. V, Fig. 8.
1899/
1900 *Palaeochoerus*; Stehlin, 239, Pl. IV, Fig. 1.
1923 *Palaeochoerus Meissneri* v. Meyer; Zittel, Broili & Schlosser, 561 partially, Fig. 659?
?1926 *P. waterhousii*; Pilgrim, table 1.
1927 *Palaeochoerus*; Pearson, 392-400 (partially), text-figs. 6, 8.
1929 *Palaeochoerus waterhousi* Pomel; Viret, 242-244, Pl. 18, figs. 4-8, Pl. 19, figs. 1-3.
1935 *Palaeochoerus typus*; Boule & Piveteau, 678-679 partially, figs. 1097 & 1099.
?1958 *Palaeochoerus* aff. *waterhousi* Pomel; Mein 91.
1968 *Palaeochoerus waterhousi*; Hünermann, 33.
1968 *Palaeochoerus typus* Pomel; Godina, Gromova, Sokolov, Trofimov, Flerov & Khaveson, 484, Fig. 456.
1972 *Palaeochoerus waterhousi* Pomel; Golpe, 116 (Cetina, not Sineu).
1974 *Hyotherium major major* (Pomel, 1847); Ginsburg, 76-77.
?1976 *H. waterhousi*; Wilkinson, 214 (partially?).
1980 *Hyotherium major*; Ginsburg, partially 869.
1990 *Hyotherium major* (Pomel, 1847); Van der Made (a), 88, figure 3.
1990 *Hyotherium major*; Van der Made (b), 100 & 104.
1991 *Hyotherium meissneri* (H. v. Meyer, 1829); Hellmund, text Fig. 3, text Fig. 4, Fig. 1, 3, 4, 8, Pl. 1-5, Pl. 6, Fig. 2, Pl. 7-11, partially 1-36.

Diagnosis: *Hyotherium* with cheek teeth that measure on average 93 % the cheek teeth of *H. soemmeringi,* the I^1 does not have a distal cusp.

Description: There is no *H. major* in the collection of the Museo Nacional de Ciencias Naturales.

Two I^3 and a lower molar of this species from Cetina were described by Truyols. The molar has a robust appearance, thick enamel and is well worn, what made it shorter. It is the widest of the M_1 and M_2 from Cetina and despite the wear, one of the longer molars (Table 11). I have seen only one of the I^3. It is flatter than the I^2 of *H. meisneri* (Table 11) and resembles the I^3 of *H. major.* It is not clear from which bed these teeth come.

A maxilla in the MPUZ comes from the upper bed (Azanza, personal communication). All teeth are larger than the other teeth from Cetina (Table 11), but are small for *H. major.*

Discussion: The evidence for the presence of *H. major* in Cetina is not overwhelming, but considering the number of fossils which cannot easily be assigned to *H. meisneri,* the presence of *H. major* in Cetina may be assumed.

As can be seen from the synonymy, *P. major* was mixed up often with *P. waterhousi* (=*P. aquensis*). An evolution from

	P^4 DAP	DT	M^1 DAP	DTa	DTp	M^2 DAP	DTa	DTp	M^3 DAP	DTa	DTp	DTpp
ZMA --	≥10.3	--	--	--	--	--	15.8	15.6	16.6	±14.8	12.7	..
	I^3 DMD	DLL	M_2 DAP	DTa	DTp							
IPS 1425 l			14.7	11.5	11.6							
IPS 1510 r	7.8	3.7										

Table 11. Measurements of the teeth of from Cetina de Aragón that probably belong to *Hyotherium major.*

P. massiliensis (= *P. aquensis*) over *P. waterhousi* (considered identical with *H. major*) into *H. soemmeringi* has been proposed (Viret, 1929). Hellmund (1992) considered *"D." waterhousi* to be a suid, without suggesting an evolution to *Hyotherium*. In the discussion on *Propalaeochoerus* it is argued, that *P. waterhousi* (= *P. aquensis*) is a tayassuid and that it differs in a number of characters from *Hyotherium*, which is a suid. An evolution from *P. aquensis* to *H. major* and *H. soemmeringi* seems as unlikely as an evolution from *P. elaverensis* to *H. meisneri* and for similar reasons.

STRATIGRAPHY

The stratigraphic positions of the localities where *Palaeochoerus, Propalaeochoerus, Hyotherium* and *Aureliachoerus* were found are indicated in Fig. 2.

In the European Oligocene only Tayassuidae are found. *Palaeochoerus* is the dominant suoid throughout the Oligocene and is found in two sizes (= lineages?), the youngest record of both sizes is in the lowermost Miocene. *Propalaeochoerus* is first recorded without doubt from the upper Oligocene, but seems to be of early Oligocene origin. In both lineages, the elongated M^3 seems to be indicative for a latest Oligocene age, or younger. The smaller *Propalaeochoerus* seems to evolve rapidly from one species into another and may be a useful marker for the MN 1-MN 2 transition.

The very beginning of the Miocene is marked by the entry of the first Suoidea: *Hyotherium meisneri* and *Hyotherium major*. These species are common in MN 2, but later occurrences are rare and doubtful. It is not clear whether *H. major* evolves into *H. soemmeringi*, or is simply replaced by it and when (later part of MN 2, or during MN 3). Ginsburg (1980) supposed that *Aureliachoerus* replaced ecologically *Palaeochoerus typus* in MN 2b. Here two small tayassuids are recognized in the lowermost Miocene, but in any case *Aureliachoerus* became abundant in MN 3 to MN 5 and the tayassuids disappeared.

PALAEOECOLOGY

Table 10 gives the mean measurements of the dentition of the European Hyotheriinae mentioned in this paper, as well as the percentage of the size of the next larger hyotheriine. The size of *A. aurelianensis* is 85 % of that of *H. meisneri* and the latter is 89 % of the size of *H. major*. But if the very small P^1 and P_1 of *H. major* are omitted (one specimen each, both of the same individual), the percentage 86. This probably is a more representative value. These three species may have overlapping distributions in time and space, although it is rare to find two of them in one locality. Size differences of 15 % are common in related sympatric species (Van der Made, 1990c), such as the recent collared and white-lipped peccaries, *Bunolistriodon lockharti* and *B. latidens* (Van der Made & Alférez, 1988; Van der Made 1991) and *Sus scrofa vittatus* and *Sus barbatus*. In *Kubanochoerus* there are three sizes, differing by 15 %; two of the species may occur in one locality (Guan & Van der Made in press).

Four species of *Dorcatherium* occur in MN 5 localities in Steiermark and southern Germany (Mottl, 1961; Fahlbusch 1985). These species differ approximately by 15 % in size. Up to three species may be found in one locality. Usually one species is dominant. In the Fayum a series of similar anthracotheres is found, with a nearly continuous range from small to large. The series represents probably four species.

In Lufeng two species of *Propotamochoerus* occur together, one measures 73 % of the other (Van der Made & Han, submitted). As 0.85 × 0.85 = 0.72 this also seems to fit the pattern.

Size differences of the order of 15 % between sympatric suid species are probably common. Body weight is related to the surface of the M_1 (Legendre, 1986). Here, all teeth are used in the comparison, because there are no great differences in the relative sizes of the premolars and M3 (save for P1-2 in *Xenohyus*). This is to increase the number of measurements on which the comparison is based.

It is to be expected that a group of animals that is well adapted for a particular environment, is represented by more than one species in this environment. This in fact occurs in recent environments. In order to avoid competition, body sizes differ and determine in part the niche of the species. The major part of a population of suids or tragulids varies in size within a range of 15 %, in this way a continuous range of individuals of all sizes may use most effectively the habitat.

Such a model would explain well the apparently regular pattern in size distribution found in recent and fossil suoids, tragulids and anthracotheres. A series of well adapted species would maintain the same size as long as the environment remained stable. A larger species would prevent the smaller species to become larger by competition. The same would occur with a smaller species. A change in size would then indicate either 1) a change in the environment, 2) imperfectly adapted species (they are too close in size) or 3) a species is free to grow (or become smaller) as there is no larger (smaller) species with which it will start competition in doing so.

It should be noted that *H. major* and *H. soemmeringi* differ less in size (10 %; 7 % if the P1 are omitted). There is no indication of size change in *H. soemmeringi* between Baigneaux (MN 4) and Sandelzhausen (MN 6). (However, the size of the type material from Georgensgmünd is outside the range of these two large samples.) The size difference of *H. soemmeringi* and *Xenohyus venitor* is 16 %, but in *Xenohyus* the P1 and P2 are relatively small, if they are omitted, the size difference is 18 %, still close to 15 %. The question arises, whether the entry of *H. soemmeringi* and *X. venitor* and the disappearance of *H. major* and *H. meisneri* (in MN 3??) indicates a change in the ecology. Also the material from the Westtangente does not seem to fit well in the system.

The estimated body weights of the Hyotheriinae are: *A. aurelianensis* 28 kg, *H. meisneri* 43 kg, *H. major* 62 kg, *H. soemmeringi* 90 kg and *X. venitor* 169 kg (using the method of Legendre, 1986 and the data of table 11). For *P. typus* this is 24 kg. Whereas species of *Hyotherium* differ 15 % in linear size, they differ by 30-35 % in weight, this time including *H. soemmeringi*. But *H. soemmeringi* is supposed to have weighed only 53 % of *X. venitor*.

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BIBLIOGRAPHY

Blainville H. M. D. de 1846. *Ostéographie ou description iconographique comparée du squelette et du système dentaire de mammifères récents et fossiles pour servir de base à la zoologie et à la géologie.* Tome Quatrième, atlas. Bertrand, Paris.

Boule, M. et Piveteau, J. 1935. *Les Fossiles-Élements de Paléontologie.* Masson et cie., Paris, 899 pp.

Coombs, MC. and Coombs, W. P. 1977. Dentition of *Gobiohyus* and a reevaluation of the Helohyidae (Artiodactyla). *Journal of Mammalogy*, **58**, 291-308.

Daams, R. 1976. Miocene rodents (Mammalia) from Cetina de Aragón (prov. Zaragoza) and Buñol (prov. Valencia) Spain. *Proceedings of the Koninklijke Nederlandse akademie van Wetenschappen, Series B*, **79**, 152- 182.

Dal Piaz, G. 1930. I mammiferi dell'Oligocene Veneto. *Propalaeochoerus paronae* n. sp. *Memorie dell'Istituto geologica della Reale Università di Padova*, **8 (9)**, 1-14, 1 Pl.

Dechaseaux, C. 1959. Le genre *Doliochoerus. Annales de Paléontologie*, **45**, 1-16.

Fahlbusch, V. 1985. Säugetierreste *(Dorcatherium, Steneofiber)* aus der miozänen Braunkohle von Wackersdorf/Oberpfalz. *Mitteilungen der Bayerische Staatssammlung für Paläontologie und historische Geologie*, **25**, 81-94.

Filhol, H. 1880. Études des mammifères fossiles de Saint Gérand le Puy (Allier). Seconde Partie. *Annales des Sciences Géologiques*, **11**, 1-86, plates 1-20.

Filhol, H. 1882. Observations relatives à un nouveau genre de Mammifères allié à la famille des Suidés. *Comptes Rendus de l'Academie des Sciences*, 1258.

Filhol, H. 1884. Description d'une nouvelle espéce de Suidé fossile appartenant au genre Hyotherium. *Bulletin de la Société Philomatique*, **7 (9/10)**, 29-33.

Freudenthal, M. and Cuenca Bescos, G. 1984. Size variation of fossil rodent populations. *Scripta Geologica*, **76**, 1-28.

Gervais, P. 1859. *Zoologie et Paléontologie françaises.* Arthus Bertrand, Paris.

Ginsburg, L. 1974. Les Tayassuidés des phosphorites du Quercy. *Palaeovertebrata*, **6**, 55-85.

Ginsburg, L. 1980. *Xenohyus venitor*, suidé nouveau (Mammalia, Artiodactyla) du Miocène inférieur de France. *Geobios*, **13**, 861-877.

Ginsburg, L., Huin, J. et Locher, J.-P. 1988. Les Suidae (Artiodactyla, Mammalia) du Miocène inférieur des Beilleaux à Savigné-sur-Lathan (Indre-et-Loire). *Bulletin du Muséum national d'Histoire naturelle*, 4e série, 10, section C, **2**, 197-207.

Godina, A. Ya., Gromova, V. I., Sokolov, I. I., Trofimov, B. A., Flerov, K. K. and Khaveson, Ya. I. 1968. Order Artiodactyla. pp. 467-473 in: *Fundamentals of Palaeontology* (Yu. A. Orlov, editor), volume XIII (V. I. Gromova, volume editor). J. Sallkind & A. Kerew, English translation and edition. Israel Program for Scientific Translations, Jerusalem.

Golpe Posse, J. M. 1971. *Suiformes del Terciario Español y sus Yacimientos*, volume **1**, 1-558, volume **2**, 1-18, plates 1-27, figures. Unedited thesis, Barcelona. Copy in the Instituto de Paleontología Miquel Crusafont, Sabadell.

Golpe Posse, J. M. 1972. Suiformes del Terciario Español y sus yacimientos. *Paleontologia i Evolució*, **2**.

Gray, J. E. 1821. On the natural arrangement of vertebrose animals. *London Medical Repository*, **15 (1)**, 296-310.

Guan Jian and Made, J. van der in press. The Miocene Suid from Dingjiaergou near Tongxin. *Memoirs of Beijing Natural History Museum* volume of 1992 (Chinese with English abstract).

Hellmund, M. 1991. Schweineartige (Suina, Artiodactyla, Mammalia) aus oligo-miozänen Fundstellen Deutschlands, der Schweiz und Frankreichs I. *Hyotherium meissneri* (Suidae) aus dem Untermiozän von Ulm-Westtangente (Baden-Würtenberg). *Stuttgarter Beiträge zur Naturkunde. Serie B (Geologie und Paläontologie)*, **176**, 1-69.

Hellmund, M. 1992. Schweineartige (Suina, Artiodactyla, Mammalia) aus oligo-miozänen Fundstellen Deutschlands, der Schweiz und Frankreichs II. Revision von *Palaeochoerus* POMEL 1847 und *Propaleochoerus* STEHLIN 1899 (Tayassuidae). *Stuttgarter Beiträge zur Naturkunde. Serie B (Geologie und Paläontologie)*, **189**, 1-75.

Hünermann, K. A. 1968. Die Suidae (Mammalia, Artiodactyla) aus den Dinotheriensanden (Unterpliozän = Pont) Rheinhessens (Süd-westdeutschland). *Schweizerische Palaeontologische Abhandlungen / Mémoires Suisses de Paleontologie*, **86**, 1-96.

Kaup, J. J. 1859. *Beiträge zur näheren kenntnis der urweltlischen Säugethiere. Heft 4*, 16 p., 6 Pl. Darmstadt.

Lavocat, R. 1951. Révision de la faune des mammifères oligocènes d'Auvergne et du Velay. *Science et Avenir*, **153**, 1-153, 26 plates.

Legendre, S. 1986. Analysis of mammalian communities from the Late Eocene and Oligocene of southern France. *Palaeovertebrata*, **16 (4)**, 191-212.

Lydekker, R. 1885. *Catalogue of the Fossil Mammalia in the British Museum (Natural History). Part II Containing The Order Ungulata Suborder Artiodactyla*, 324 p. London.

Made, J. van der 1990a. Iberian Suoidea. *Paleontologia i Evoloció*, **23**, 83-97.

Made, J. van der 1990b. A range chart for European Suidae and Tayassuidae. *Paleontologia i Evoloció*, **23**, 99-104.

Made, J. van der 1990c. Masticatory adaptations, size and niches of related sympatric suids. *VI Jornadas de Paleontología, Granada 1990. Resúmenes*, 37.

Made, J. van der 1990d. The systematic value of the first upper incisor in pigs and peccaries. *VI Jornadas de Paleontología, Granada 1990. Resúmenes*, 38.

Made, J. van der 1991. Sexual bimodality in some recent pig populations and application of the findings to the study of fossils. *Zeitschrift für Säugetierkunde*, **56**, 81-87.

Made, J. van der y Alférez, F. 1988. Dos suidos (Listriodontinae) del Mioceno Inferior de Córcoles (Guadalajara, España). *Coloquio homenaje a Rafael Adrover: "Bioeventos y Sucesiones faunísticas en el Terciario continental Ibérico". Sabadell 14-16 dic. 1988. Resúmenes.*

Made, J. van der and Han Defen, submitted. Suoidea from the Late Miocene hominoid locality Lufeng, Yunnan province, China. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen.*

Mein, P. 1954. Les mammifères de la faune sidérolithique de Vieux-Collognes. *Nouvelles Archives du Muséum d'Histoire Naturel de Lyon*, **V**, 118 pp.

Mein, P. 1989. Updating of MN zones. In: *European Neogene Mammal Chronology* (Eds. E. H. Lindsay, V. Fahlbusch & P. Mein). Plenum Press, New York & London, 73-90.

Meisner, F. 1818. Über einige in der Schweiz gefundene fossile Knochen und Zähne verschiedener Landthiere. *Naturw. Anz. d. allg. Schweiz. Ges. f. d. ges. Naturwiss*, **1**, 38-39.

Meisner, F. 1820. Über einige in der Schweiz gefundene Osteoliten und Odontolithen. *Museum der Naturgeschichte Helvetiens*, **1 (9-10)**, 63-78, 1 plate. Bern.

Meyer, H. von 1829. Letter in *Zeitschrift für Mineralogie*, **1**, 151.

Meyer, H. von 1834. *Die fossilen Zähne und Knochen von Georgensmünd in Bayern.* J. D. Sauerlander, Frankfurt am Main, 1-126, plates 1-13.

Meyer, H. von 1841. Letter in *Neues Jahrbuch für Mineralogie, Geognosie und Petrefaktenkunde*, 101-104.

Meyer, H. von 1850. Der Schädel des *Hyotherium Meissneri* aus dem Tertiär- Kalke des Salzbachthales bei Wiesbaden. *Jahrbücher des Vereins für Naturkunde im Herzogtum Nassau*, **6**, 116-125.

Mottl, M. 1961. Die Dorcatherien der Steiermark. *Mitteilungen der Abteilung für Geologie, Paläontologie und Bergbau am Landesmuseum Joanneum*, **22 (1)**, 21-71.

Mottl, M. 1970. Die Jungtertiären Säugetierfaunen der Steiermark, Süd- Österreichs. *Mitteilungen des Museums für Bergbau, Geologie und Technik am Landesmuseum "Joanneum" Graz*, **31**, 1-92.

Pearson, H. S. 1927. On the Skulls of Early Tertiary Suidae, together with an Account of the Otic Region in some other Primitive Artiodactyla. *Philosophical Transactions of the Royal Society, London, series B*, **215**, 389-460.

Pearson, H. S. 1932. Some Skulls of *Perchoerus [Thynohyus]* from the White River and John Day Formations. *Bulletin of the American Museum of Natural History*, **48 (3)**, 61-96.

Pickford, M. (1988). Revison of the Miocene Suidae of the Indian Subcontinent. *Münchener Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie*, **12**, 1-91.

Pickford, M. and Morales, J. 1989. On the tayassuid affinities of *Xenohyus* Ginsburg, 1980, and the description of new fossils from Spain. *Estudios geológicos*, **45**, 233-237.

Pictet, F. J. 1844. *Traité élémentaire de paléontologie ou histoire naturelle des animeaux fossiles considérés dand leurs rapports zoologiques et geologiques. Tome premier*, 363 pp. Paris, J. B. Baillière.

Pictet, F. J. 1853. *Traité élémentaire de paléontologie ou histoire naturelle des animeaux fossiles considérés dand leurs rapports zoologiques et geologiques.* Tome premier. Second printing. 584 pp., Atlas volume 1, 28 Pl. J. B. Baillière, Paris.

Pilgrim, G. E. 1926. The fossil Suidae of India. *Palaeontologica Indica*, new series **(8 (4)**, 1-65, plates 1-20.

Pomel, A. 1847. Note sur les animaux fossiles découvertes dans le département de l'Allier. *Bulletin de la Société géologique de France*, 2ᵉ série, **4**, 378-385.

Pomel, A. 1848. Observations paléontologiques sur les hippopotames et les cochons. *Archives des sciences physisques et naturelle Genève*, **8**, 155- 162.

Pomel, A. 1853. *Catalogue méthodique et descriptif des vertébrés fossiles découverts dans le bassin hyderographique supérieur de la Loire et surtout dans la vallée de son affluent principal*, l'Allier, Paris, Baillères.

Repelin, J. 1930. Description Géologique Succincte du Département des Bouches-du-Rhône. *Bouches-du-Rhône, Encyclopedie Départementale*, **1**.

Ride, W. D. L., Sabrosky, C. W., Bernardi, G., Melville, R. V., Corliss, J. O., Forest, J., Key, K. H. L. and Wright, C. W. 1985. *International Code of Zoological Nomenclature*, third edition. 338 pp. International Trust for Zoological Nomenclature, British Museum (Natural History), London & University of California Press, Berkeley & Los Angeles.

Roman, F. 1907. Le Néogène continental dans la basse vallée du Tage (rive droite), 1ʳᵉ partie paleontologie. *Mémoires du Commission du Service Géologique du Portugal*, 1-78.

Schmidt-Kittler, N. (Editor) 1987. International Symposium on Mammalian Biostratigraphy and Paleoecology of the European Paleogene-Mainz, February 18th-21th 1987. *Münchener Geowissenschaftliche Abhandlungen. Reihe A Geologie und Paläontologie*, 1-311.

Stehlin, H. G. 1899/1900. Ueber die Geschichte des Suidengebisses. *Abhandlungen der schweizerischen paläontologischen Gesellschaft*, first part, 1899, **26**, 1-336, second part, 1900, **27**, 337-527, 10 plates.

Stehlin, H. G. 1929. Artiodactylen mit fünffingeriger Vorderextremität aus dem europäischen Oligocän. *Verhandlungen der naturforschenden Gesellschaft Basel*, **40**, 599-625.

Studer, Th. 1896. Die Säugetierreste aus den marinen Molasseablagerungen von Brütteln. *Abhandlungen der schweizerischen paläontologischen Gesellschaft*, **22**, 1-47, Taf. I-III.

Trofimov, B. A. 1949. The oldest representative of the primitive pigs in Asia. *Doklady Akademia Nauk SSR*, **67 (1)**, 145-148 (in Russian).

Truyols, J. 1962. El Aquitaniense de Cetina de Aragón y su fauna de Mamíferos. Unpublished thesis, University of Barcelona. Copy in the Instituto de Paleontologia, Sabadell.

Villalta Comella, J. F. de y Crusafont Pairo, M. 1945. Noticia preliminar sobre una fauna de mamíferos Aquitanienses en Cetina de Aragón (Zaragoza). *Las Ciencias*, **10 (4)**, 866-873.

Viret, J. 1929. Les Faunes de Mammifères de l'Oligocène supérieur de la limagne Bourbonnaise. *Annales de l'Université de Lyon, Nouvelle Série I, Sciences Médicines*, **47**, 1-328, 32 text Fig., 32 planches.

Wilkinson, A. F. 1976. The lower Miocene Suidae of Africa. In: *Fossil Vertebrates of Africa*, volume **4** (R. J. G. Savage & S. C. Coryndon Eds.). London & New York, Academic Press, 173-282.

Zittel, K. A. Schimper, W. Ph. und Schenk, A. 1891/93. *Handbuch der Paleontologie. IV. Band Mammalia.* 799 pp. R. Oldenburg, München & Leipzig.

Zittel, K. A. von 1895. *Grundzüge der Paläontologie (Paläozoologie).* 971 pp. R. Oldenburg Verlag, München & Leipzig.

Zittel, K. A. von 1911. *Grundzüge der Paläontologie (Paläozoologie).* Second printing, revised by F. Broili, E. Koken & M. Schlosser. 598 pp. R. Oldenburg Verlag, München & Berlin.

Zittel, K. A. von 1923. *Grundzüge der Paläontologie (Paläozoologie).* Fourth printing, revised by F. Broili & M. Schlosser. 706 pp. R. Oldenburg Verlag, München & Berlin.

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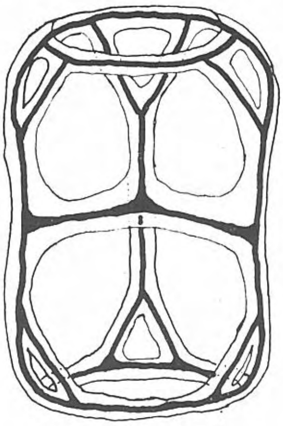
Note added in proof

Since the paper was in press, I have had the opportunity to study the holotype of *H. meisneri* in the Naturhistorisches Museum Bern (NMBe).

The type is still smaller than the cast in the NMB: P_4, DAP 12.1, DTa 7.4, DTp 7.6; M_1, DAP >12.0, DTa >9.3, DTp >8.5; M_2, DAP 14.6, DTa 11.5, DTp 11.4. The difference is probably due to the fact that the cast is painted. These smaller measurements show that the holotype of *H. meisneri* is even closer to the material from Cetina and even smaller than *H. major* from St.-Gérand and the fossils from Ulm-Westtangente.

I thank Dr. E. Büttiker allowing me to study fossils in the NMBe.



CORRECCIÓN DE ERRATAS

J. van der Made and M. Belinchón, 1991. *Korynochoerus palaeochoerus* from the uppermost Miocene of Alcoy. *Revista española de Paleontología,* n.º Extraordinario, 173-180.

There are some errors in the text, those which may hamper understanding are the following.

p. 173 bottom, first column: "... but the locality was a lignite mine ..." should be "... but the locality was known already before. The locality is a lignite mine ...".

p. 174: instead of "*Apreolus*" read "*Capreolus*".

p. 175: second column, eleventh line above "Discussion": instead of "and *S. arvernensis*" read "and *S. nanus*".

The legend of Figure 1 should read:

1) Suid from Alcoy, 2) *Korynochoerus palaeochoerus*, 3) *Korynochoerus provincialis*, 4) *Sus arvernensis*, 5) *Sus arvernensis* M^2 in the graph of the M^1, 6) *Hyotherium soemmeringi*, 7) *Hyotherium soemmeringi* M^2 in the graph of the M^1.

The legend of Plate I should read:

1. M_3 (Collection Villalta). 2. M_1 (Collection Villalta). 3. M^1 (Collection Villalta). 4. M^1 (Collection Villalta). 5. I^1 (Collection Villalta). 6. M^3 (MNCN). 7. M^3 (Collection Visedo). 8. M_x (Collection Villalta).