# Albanohyus, a small Miocene pig

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Accepted for publication: 15 March, 1995

MADE J. VAN DER. 1996. *Albanohyus*, a small Miocene pig. Acta. zool. cracov., **39**(1): 293-303.

Abstract. There has long been confusion regarding the small Miocene Suoidea Albanohyus pygmaeus (Depéret, 1892) and Taucanamo grandaevum (Fraas, 1870). A number of characters separate not only these species, but Suidae and Old World "Tayassuidae" as well. Albanohyus appears to be a suid and not a "tayassuid". In Europe, Albanohyus is characterized by size increase: the small A. pygmaeus is found in La Grive, and the larger A. castellensis (Golpe-Posse, 1977) in Castell de Barberà and Doué-la-Fontaine; Albanohyus from Przeworno 2 is intermediate. The known time range of the lineage is MN7 (La Grive) to MN9 (Doué-la-Fontaine). African material from the Middle Miocene of Fort Ternan and the Ngorora Formation is also assigned to Albanohyus. The Pliocene suid Cainochoerus africanus (Hendey, 1976) is believed to be a descendant of Albanohyus.

Key-words: Albanohyus, Suidae, Miocene, Aragonian.

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#### I. INTRODUCTION

There has long been confusion regarding European "Tayassuidae" and Suidae. At first all were believed to be suids, then some fossils were recognized to be different and to resemble tayassuids in certain characters. These fossils were then (and are still) considered Tayassuidae, but might well represent a third group of Suoidea. At the same time wrong species or genus names were applied to these fossils. As a result, the distinction between the two groups of suoids became blurred. For *Palaeochoerus* POMEL, 1847 and *Hyotherium* MEYER, 1834 the problems were largely resolved by GINSBURG (1974), but unfortunately his results have often been ignored (see also VAN DER MADE 1994). *Taucanamo* SIMPSON, 1945, *Albanohyus* GINSBURG, 1974 and *Barberahyus* GOLPE POSSE, 1977 present a similar chaos.

DEPÉRET (1892) described the species "Choeromorus" pygmaeus on the basis of three fossils from La Grive, a right maxilla with M<sup>2</sup> and M<sup>3</sup>, a left P<sup>4</sup> and a fragment of a left mandible with M<sub>2</sub> and M<sub>3</sub>. The first two specimens are housed in the Université Claude Bernard, Lyon (UCBL) under no. 65652 and the latter specimen is possibly LGr 699 in the Muséum Guimet, Lyon (MGL) but if this is the case the M<sub>2</sub> is lost. Apparently, the maxilla and not the mandible was considered to be the holotype (p. 89). "Colobus" grandaevus FRAAS, 1870, from Steinheim, a "peccary" and

not a primate, was considered as a possible (senior) synonym of the new species. It seems that later authors agreed on the synonymy and applied DEPÉRET's (junior) species name.

Choeromorus GERVAIS, 1848-1852 and Choerotherium LARTET, 1851 were based on the "tayassuid" from Sansan, for which several names were introduced (see GERVAIS 1859, 185-187), but which is nowadays commonly known under the name Taucanamo sansaniense (LARTET, 1851). SIMPSON (1945) noted that Choerotherium CAUTLEY & FALCONER, 1835 antedates Choerotherium LARTET and introduced the name Taucanamo. However, Choeromorus has the same type species (the "peccary" from Sansan), and has priority. SIMPSON did not indicate why he believed Choeromorus to be an invalid name. Since the name Taucanamo is widely used, it is applied here.

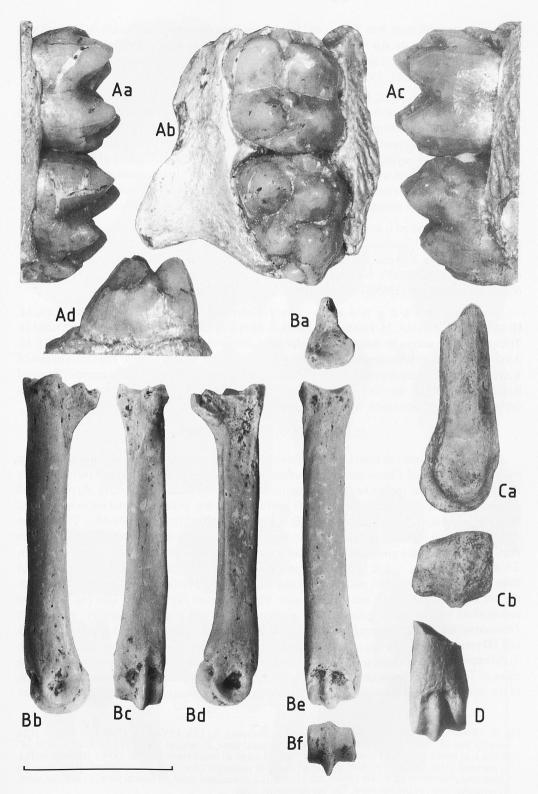
GINSBURG (1974) believed that the suoids from Artenay and La Grive belong to the same species, one distinct from *Taucanamo sansaniense*, and introduced the generic name *Albanohyus* for "*Taucanamo*" *pygmaeum*. GINSBURG & BULOT (1987), referred the Steinheim material to *T. sansaniense*. However, CHEN (1984) referred the same material to *T. pygmaeum*. FORTELIUS & BERNOR (1990) drew attention to the possibility that *T. grandaevum* may be the valid name for the material from Steinheim.

Golpe Posse (1977) introduced the genus and species names *Barberahyus castellensis* for what she believed to be a peccary from Castell de Barberà. CHEN (1984) tentatively referred material from Przeworno 2 to *Barberahyus castellensis*; this material had been assigned to *Taucanamo sansaniense* by Kubiak (1981). Later it was noted that, apart from *Taucanamo, Barberahyus castellensis* seemed also to be present in La Grive (VAN DER MADE 1990). FORTELIUS et al. (in press) recognized *Taucanamo sansaniense* for the material from Sansan, *Taucanamo grandaevum* for the material from Steinheim and part of the material from La Grive, *Albanohyus pygmaeus* for other material from La Grive and left the possibility open that the material from Castell de Barberà could be specifically different from La Grive and should be named *Albanohyus castellensis*. There is a size difference between the holotype of *A. pygmaeus* and the type material of *A. castellensis* and at that time it was not clear whether this was due to inter- or intraspecific variation.

It is obvious that there has been great confusion on both the specific and generic levels. This has obscured the higher level relationships of the taxa involved. PEARSON (1927) studied basicrania of artiodactyla and concluded that a number of Old World suoids should be placed in the Tayassuidae, which at that time were generally seen as exclusively American. Her work was a great advance, but she used names that were common at the time, and now appear to be incorrect. The material studied and figured by her under the name *Palaeochoerus* belongs to *Hyotherium* and her *Choerotherium pygmaeum* (a skull from Steinheim) is now placed in *Taucanamo grandaevum*. It seems that in quite a number of cases authors have related the characters found by PEARSON to the wrong taxa and therefore placed them in the wrong family. This might be the case in COLBERT (1935), SIMPSON (1945), ROMER (1966, p. 389), HÜNERMANN (1968), GOLPE POSSE (1972, 1975, 1977), GINSBURG (1974, 1980), PICKFORD (1984, 1988a, p. 10), CARROLL (1988, p. 640) and many others.

GOLPE POSSE (1975, 1977) assigned "Barberahyus" to the Tayassuidae, but without presenting any arguments for this. The fossil was compared to Pecarichoerus? africanus. HENDEY (1976) described the latter species on fossils from Langebaanweg and placed it in the Tayassuidae on the basis of the orientation of the canines and fused metatarsals. PICKFORD (1988b) placed the species in a genus of its own, Cainochoerus africanus, and transferred it to the Suidae. The resemblance

Fig. 1. Albanohyus pygmaeus from La Grive (old collections): A) 65652 – holotype, right M²-M³ (UCBL), a) buccal view, b) occlusal view, c) lingual view; B) 287 – right third metatarsal (IGF), a) proximal view, b) external view, c) posterior view, d) internal view, e) anterior view, f) distal view. Taucanamo aff. sansaniense from Vieux Collonges (= Mont Ceindre); C) MC 125 – distal part of metapodial (MGL): a) external view, b) distal view. Albanohyus castellensis from Castell de Barberà; D) IPS 1945 – distal metapodial (IPS), anterior view. The bar represents 1 cm for fig. A and 2 cm for the other figures.



between some teeth from Fort Ternan and those from Langebaanweg and Castell de Barberà was repeatedly noted (PICKFORD 1986, 1988b), but the former teeth were not assigned to any of the taxa. A skull without dentition from the Ngorora Fm. was tentatively assigned to *Schizochoerus* CRUSAFONT & LAVOCAT, 1954, a "tayassuid" (PICKFORD 1986).

It is the aim of this paper: 1) to illustrate the differences between Albanohyus and Taucanamo; 2) to indicate which of these are of importance at the family level; 3) to show that Albanohyus is a suid; 4) to study and interpret size changes in Albanohyus; 5) to briefly discuss the affinities between European Albanohyus and the small suoids from Fort Ternan, the Ngorora Formation and Langebaanweg. It is beyond the scope of this paper to assign Albanohyus to any of the subfamilies of the Suidae, to discuss whether Taucanamo really belongs to the Tayassuidae or to discuss the affinities of Pecarichoerus Colbert, 1933. Old World "Tayassuidae" are indicated here as Tayassuidae, though a reassessment of their status at the family level is necessary.

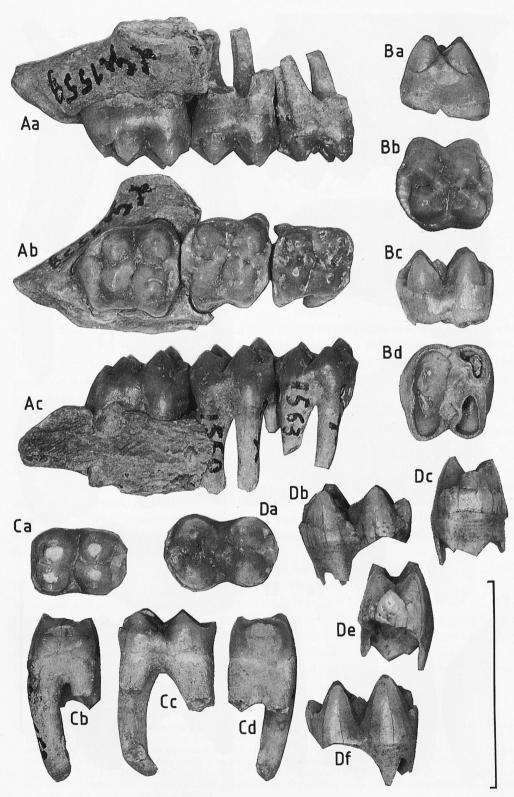
The material studied is stored in the Istituto di Geología, Firenze (IGF), Instituto de Paleontología, Sabadell (IPS), Institute of Systematics and Evolution of Animals, Kraków (ISEAK), Kenya National Museums, Nairobi (KNM), Museum Guimet, Lyon (MGL), Museum national d'Histoire naturelle, Paris (MNHNP), Naturhistorisches Museum, Basel (NMB), Staatliches Museum für Naturkunde, Stuttgart (SMNS) and Université Claude Bernard, Lyon (UCBL).

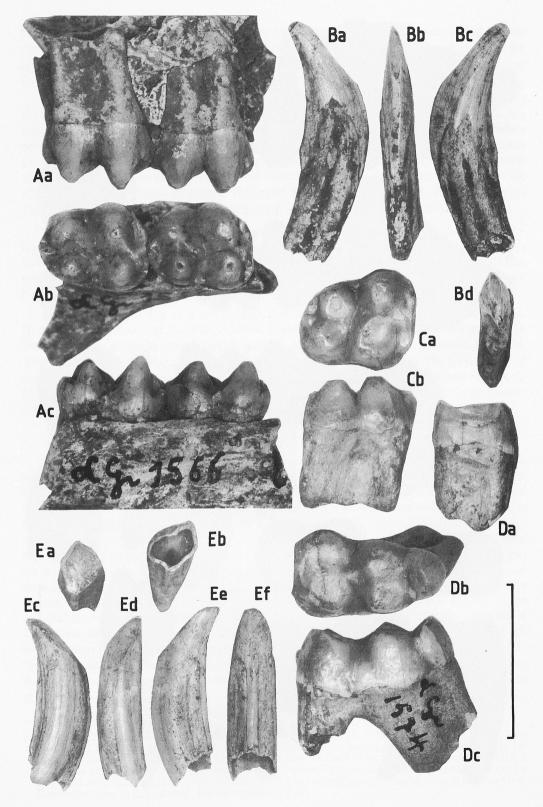
A c k n o w l e d g m e n t s . Drs. J. AGUSTÍ, B. ENGESSER, E. P. J. HEIZMANN, M. HUGUENEY, H. KUBIAK, M. LEAKEY, P. MEIN, S. MOYÀ-SOLÀ, M. MUNNGU, M. PHILIPPE and D. TORRE gave me access to material and helped me during my stays in their institutes. Dr. D. M. AVERY and P. HAARHOFF sent me information on and casts of *Cainochoerus*. The Government of Kenya supplied a research permit and the Netherlands Foundation for the Advancement of Tropical Research (WOTRO) the financial means to work in Nairobi. Dr. P. PELAEZ-CAMPOMANES critically read the manuscript. All these persons and institutions are thanked for their help.

### II. RESULTS AND DISCUSSION

Study of old collections from La Grive show that both Taucanamo grandaevum and Albanohyus pygmaeus are present. Characters of Albanohyus that separate it from Taucanamo include: 1) the lower first and second molars have four roots instead of two and the anterior lobe of M3 two instead of one (though the roots lateral to each other are fused for a few millimeters and not as separate as in say, Hyotherium) (Fig. 2C versus Fig. 2D & Fig. 3D, for the first lobe of the M<sub>3</sub>); 2) the upper molars have two separate lingual roots, instead of fused lingual roots (Figs. 2A & 2B versus Figs. 3A & 3C); 3) the protoconule is fused to the cingulum and not to the protocone (Figs. 1A, 2A & 2B versus Figs. 3 A & 3C); 4) the upper male canine (C<sup>m</sup>) has a crown from which depart three enamel bands (anterior, posterior and lingual) instead of two (in the "tayassuids" the canines are not sexually dimorphic, but differ in size; Fig. 3E versus Fig. 3B; see also Fig. 4); 5) the metapodials have a distal roller with a median crest which continues dorsally, whereas in Taucanamo the dorsal surface of the distal roller is nearly flat in the transverse direction (Fig. 1B and 1D versus Fig. 1C); 6) this morphology is reflected in the proximal facet of the first phalanges; 7) the upper and lower cheek teeth of Albanohyus are wider (have a lower length/width index) than those of Taucanamo (upper cheek teeth: Fig. 5); 8) the premolars are shorter relative to the length of the molars than in Taucanamo (Fig. 5); 9) the cusps of the molars are rounded in Albanohyus,

Fig. 2. Albanohyus pygmaeus from La Grive (old collections): A) LGr 1559, LGr 1560, LGr 1563 – right maxilla and M¹-M³ (MGL), a) buccal view, b) occlusal view, c) lingual view; B) LGr 1566 – right M² (MGL), a) anterior view, b) occlusal view, c) buccal view, d) basal view; C) LGr 1558 – left M₂ (MGL), a) occlusal view, b) anterior view, c) buccal view, d) posterior view. Taucanamo grandaevum from La Grive (old collections); D) LGr 1566 – left M₂ (MGL), a) occlusal view, b) buccal view, c) anterior view, d) posterior view, e) lingual view. The bar represents 2 cm.





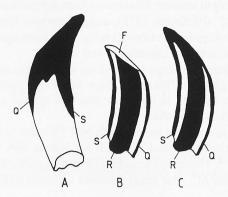


Fig. 4. The lingual side of the upper canines of A) *Taucanamo grandaevum* (LGr 6003, sex unknown, left); B) *Albanohyus pygmaeus* (LGr 6003, male, right); C) the same specimen as B, but reconstructed as if without wear. F = wear facet, Q = anterior enamel band, R = lingual enamel band, S = posterior enamel band.

whereas those of *Taucanamo* have crests that seem to be in an early stage of developing into lophs [Fig. 1A versus Fig. 3A; Within the group formed by *Taucanamo*, *Yunnanochoerus* and *Schizochoerus*, there seems to be a tendency towards lophodonty (VAN DER MADE & HAN 1994). This group may well originate from the Paleogene *Odoichoerus* TONG & ZHAO, 1986. True lophodonty seems to be derived from a morphology that includes crestlike structures. True bunodonty as in *Albanohyus* is probably also a derived character.], 10) *Albanohyus pygmaeus* is smaller than *Taucanamo grandaevum* (Fig. 5). Characters 3 and 10 can be observed in the holotype of *Albanohyus* (Figs. 1A and 5). With so many differences, it is obvious that *Taucanamo* and *Albanohyus* should be considered different genera.

In the first six characters *Taucanamo* resembles the "Tayassuidae" *Palaeochoerus* and *Propalaeochoerus* Stehlin, 1899 (Hellmund 1992, Plate 1, Plate 5, figs. 5 and 6, Plate 6, figs. 6-8, Plate 7, fig. 1). The "Tayassuidae" *Schizochoerus*, *Yunnanochoeus* VAN DER MADE & HAN, 1994 and *Pecarichoerus* resemble *Taucanamo* in the known characters. *Sanitherium* MEYER, 1866 resembles this group in the known characters.

Albanohyus resembles Suidae such as Hyotherium, Aureliachoerus GINSBURG, 1974, Xenohyus GINSBURG, 1980 and others in the first six characters. Though the C<sup>m</sup> (character 4) does not always have three well developed bands in the earliest suids (VAN DER MADE 1994, Pl. I, fig. 15), three bands do not occur in "tayassuids". Characters 1 - 6 seem to separate Suidae from the group formed by the Old World "Tayaşsuidae". In addition, there are other characters such as: 1) the universally accepted outwardly flaring canines in the suids (but are weakly flaring in the earliest species); 2) the skull characters described by PEARSON (1927). The first six characters indicate that Albanohyus belongs to the Suidae (Fig. 7).

Fig. 3. Taucanamo grandaevum from La Grive (old collections): A) LGr 1566 – left maxilla with M<sup>2</sup>-M<sup>3</sup> (MGL), a) lingual view, b) occlusal view, c) buccal view; B) LGr 6003 – left C<sup>x</sup> (MGL), a) labial view, b) anterior view, c) lingual view, d) apical view; C) LGr 1575 – right M<sup>3</sup> (MGL), a) occlusal view, b) lingual view; D) LGr 1574 – right M<sub>3</sub> (MGL), a) anterior view, b) occlusal view, c) lingual view. Albanohyus pygmaeus from La Grive: E) LGr 6003 – left C<sup>m</sup> (MGL), a) apical view, b) basal view (showing the basal section), c) lingual view, d) anterior view, e) labial view, f) posterior view. The bar represents 2 cm for figs. B and E and 1.5 cm for the other figures.

Characters 7 and 8 serve to separate *Taucanamo* from *Schizochoerus* (VAN DER MADE & HAN 1994), another "tayassuid" (PICKFORD 1978), and *Albanohyus* from certain suids, but do not separate *Taucanamo* or *Schizochoerus* from all suids. Thus these characters are not significant at the family level. The same is true of characters 9 and 10.

The M1 and M2 of *Albanohyus* from La Grive are smaller than those from Castell de Barberà and Doué-la-Fontaine (Fig. 5 & 6). This seems also to be the case for the scarce foot bones (Fig. 1B & 1D). This suggests an increase in body size and two species are recognized, the small *A. pygmaeus* and the larger *A. castellensis*.

Most of the localities in La Grive are placed in MN 7 (or low in MN 7+8 sensu DE BRUIJN et al. 1992), Castell de Barberà is placed in MN 8 (or high in MN 7+8 or even in MN 9) and Doué-la-Fontaine in MN 9. This seems to indicate a size increase. The holotype of A. pygmaeus is very small, especially the M<sup>3</sup>. This either indicates variation within a "population" or that the

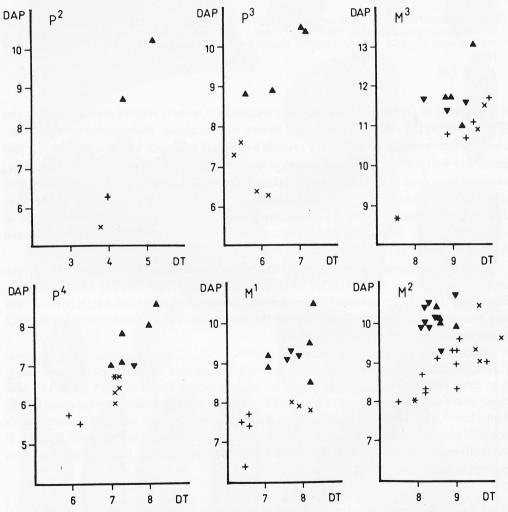


Fig. 5. Bivariate plots of length (DAP, in mm) versus greatest width (DT, in mm) of the upper cheek teeth. Legend: crosses – Albanohyus pygmaeus from La Grive (old collections, MGL, IGF and NMB); asterix – holotype and paratype of Albanohyus pygmaeus from La Grive (old collections, UCBL); oblique crosses – Albanohyus castellensis from Castell de Barberà (IPS); black triangles points up – Taucanamo grandaevum from Steinheim (SMNS); black triangles points down – Taucanamo grandaevum from La Grive (old collections, MGL, IGF and NMB). (Size indicated in mm.)

	M <sub>1</sub>		M <sub>2</sub>			M <sub>3</sub>					
	7	8	9	8	9	10	11	11	12	13	14
	1	1	1	1	1	1	1	1	1	1	1
Doué-la-Fontaine						•					
Castell de Barberà		•••	•		•	•	•			. :	
Przeworno II					•	•			•	•••	•
La Grive				8	-14	••			• • •	••	

Fig. 6. Size increase in the lower molars in *Albanohyus*. La Grive (MGL, IGF and NMB), Przeworno 2 (ISEAK), Castell de Barberà (IPS), Doué-la-Fontaine (MNHNP). (Size indicated in mm.)

sample is not homogenous in its provenance. The exact provenance of the old collections is not known.

In Przeworno 2 the same two small suoids are found as in La Grive. Przeworno has been placed in either MN 7 (GINSBURG 1986) or MN 8 (MEIN 1986). The size of *Albanohyus* from Przeworno is intermediate between that of La Grive and Castell de Barberà (Fig. 3). This suggests an intermediate age. Comparing the Przeworno material with that from Castell de Barberà, it seems that, the general size increase notwithstanding, the M3 does not increase in size and the premolars become even smaller.

Cainochoerus africanus resembles Albanohyus pygmaeus in the general appearance of the incisors, canines, premolars and molars, as well as in characters 1-9, except possibly character 4 (PICKFORD 1988b, p. 9). It differs in the further reduction in the relative size of the premolars and M3, the better developed metaconid in the P4, the slightly smaller size and the partial fusion of the metatarsals in Cainochoerus. The teeth from Fort Ternan (PICKFORD 1986) are identical to those of Albanohyus. The skull from the Ngorora Formation (PICKFORD 1986, Fig. 80) has alveoli for

Character		Doliochoerinae	www.millery.	Suidae			
		Doliochoerinae	Taucanamo	Albanohyus	Cainochoerus	Suidae	
1	Roots of lower molars	fused	fused	separated at the lower end	separated at the lower end	separated	
2	Lingual roots of upper molars	fused	fused	separated	separated	separated	
3	Protoconule fused to:	protocone	protocone	cingulum	cingulum	cingulum	
4	Number of enamel bands of C <sup>m</sup>	2	2	3	3?	3	
5	Metapodials	no or no clear dorsal crest	no dorsal crest	clear dorsal crest	clear dorsal crest	clear dorsal crest	
6	First phalange with or without proximo-dorsal grove	without	without	with	with	with	

Fig. 7. Morphological characters of Doliochoerinae and Suidae compared. The numbers of the characters refer to the numbers given to those characters in the text.

four roots per upper molar; the lingual roots are not fused. This indicates that the skull more likely belongs to some suid than to a "tayassuid" like *Schizochoerus*. The size of this skull and the proportions of the cheek teeth, indicated by the alveoli, are as in *Albanohyus* from Castell de Barberà. Nothing in this skull, including the orientation of the canines, argues against referral to *Albanohyus*. It seems likely that *Albanohyus* had a wide geographical distribution during approximately the late Aragonian and early Vallesian and that *Cainochoerus* evolved from this genus.

## III. CONCLUSIONS

Albanohyus belongs to the Suidae and Taucanamo belongs to a different group of Suoidea, usually placed in the Tayassuidae. There are two species of Albanohyus, the smaller and earlier A. pygmaeus and the later and larger A. castellensis. The localities have the following species: La Grive – A. pygmaeus, Fort Ternan – A. cf. pygmaeus, Przeworno 2 – A. cf. castellensis, the Ngorora Fm. – A. cf. castellensis, Castell de Barberà – A. castellensis, Doué-la-Fontaine – A. castellensis.

Albanohyus had a wide geographic distribution during the Middle and early Late Miocene, including Kenya, Poland, France and Spain. After the early Vallesian, the genus disappeared from Europe and apparently lived on in Africa where the Pliocene *Cainochoerus* is a descendant of *Albanohyus*.

N o t e. When this paper was in press, a paper by PICKFORD appeared (1995, Old World Suoid Systematics, Phylogeny, Biogeography and Biostratigraphy. Paleontologia i Evolució, no. 26-27: 237-270). In this paper he introduced, the subfamily Cainochoerinae for the genus *Cainochoerus*. I agree fully to place this form in a new subfamily. However, I would like to include also *Albanohyus* and possibly *Kenyasus*.

The Old World "Tayassuidae" include: Odoichoerus, Taucanamo, Yunnanochoerus, Schizochoerus, Propalaeochoerus and Palaeochoerus (=? Doliochoerus). This group seems to be homogenous to a certain extend and seems to differ in various characters from the American Tayassuidae. Several names of the family group have been applied to this group or members of this group: Palaeochoerinae MATTHEW, 1924; Doliochoerinae SIMPSON, 1945; Sanitheriinae SIMPSON, 1945 and Schizochoerini GOLPE-POSSE, 1972. PICKFORD (1984) applied the name Sanitheriidae, because he believes this group to be different at the family level. This is not the place to discuss the phylogeny of this group in great detail. However, I have been criticized at length for being so cautious to place some of the genera in "Tayassuidae subfamily indet" or in "Tayassuidae incertae sedis" (PICKFORD 1995, 257-259). In the present paper and another one (VAN DER MADE 1994) characters have been presented that unite the group, that separate them from the Suidae. There is no indication that there was any relation with the American tayassuids later than the earliest Oligocene. A family rank status of the "Old World tayassuids" seems justified and should be Palaeochoeridae MATTHEW, 1924. Taucanamo, Yunnanochoerus, Schizochoerus and probably Odoichoerus should be placed in the Schizochoerinae GOLPE-POSSE, 1972 and Propalaeochoerus, Palaeochoerus and probably Sanitherium in the Palaeochoerinae.

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