Albanohyus, a small Miocene pig

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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 MN 7 (La Grive) to MN 9 (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* (HENDY, 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 M2 and M3, a left P3 and a fragment of a left mandible with M2 and M3. 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 M2 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 DEPERET'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 & FALCONE*, 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" *pygmaeus*. GINSBURG & BULOT (1987), referred the Steinhaim material to *T. sansaniense*. However, CHEN (1984) referred the same material to *T. pygmaeus*. 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 Przeworsko 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 basicania 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*. HENDNEY (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, *Cainchoerus africanus*, and transferred it to the Suidae. The resemblance

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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 Geologia, 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 (MNHN), Naturhistorisches Museum, Basel (NMB), Staatliches Museum für Naturkunde, Stuttgart (SMNS) and Université Claude Bernard, Lyon (UCBL).

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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 M₂; 2) the protocone is two 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 M₃); 2) the upper molars have two separate lingual roots, instead of fused lingual roots (Figs. 2A & 2B versus Figs. 3A & 3C); 3) the protocone is fused to the cingulum and not to the protocone (Figs. 1A, 2A & 2B versus Figs. 3A & 3C); 4) the upper male canine (C₃max) 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*,

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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 M₃ (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, Yumnanochoerus 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, Yumnanochoeus 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 Hyootherium, Aureliachoerus Ginsburg, 1974, Xenohyus Ginsburg, 1980 and others in the first six characters. Though the C₃ (character 4) does not always have three well developed bands in the earliest suids (Van der Made 1994, Pl. I, fig. 15), these bands do not occur in "tayassuids". Characters 1 - 6 seem to separate Suidae from the group formed by the Old World "Tayassuidae". 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 grandaeum from La Grive (old collections): A) LGr 1566 - left maxilla with M₂-M₃ (MGL), a) lingual view, b) occlusal view, c) buccal view; B) LGr 6003 - left C₃ (MGL), a) labial view, b) anterior view, c) lingual view, d) apical view; C) LGr 1575 - right M₂ (MGL), a) occlusal view, b) lingual view; D) LGr 1574 - right M₃ (MGL), a) anterior view, b) occlusal view, c) lingual view. Albanohyus pygmaeus from La Grive; E) LGr 6003 - left C₃ (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 Brujin* 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 M3. This either indicates variation within a "population" or that the

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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 grandaeum* from Steinheim (SMNS); black triangles points down – *Taucanamo grandaeum* from La Grive (old collections, MGL, IGF and NMB). (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

<table>
<thead>
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<th>Character</th>
<th>Doliachoerinae</th>
<th>Taucanamo</th>
<th>Suidae</th>
<th>Suidae</th>
<th>Suidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Roots of lower molars</td>
<td>fused</td>
<td>fused</td>
<td>separated at the lower end</td>
<td>separated at the lower end</td>
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<tr>
<td>2</td>
<td>Lingual roots of upper molars</td>
<td>fused</td>
<td>fused</td>
<td>separated</td>
<td>separated</td>
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<tr>
<td>3</td>
<td>Protocone fused to:</td>
<td>protocone</td>
<td>protocone</td>
<td>cingulum</td>
<td>cingulum</td>
</tr>
<tr>
<td>4</td>
<td>Number of enamel bands of C³</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>3?</td>
</tr>
<tr>
<td>5</td>
<td>Metapodials</td>
<td>no or no clear dorsal crest</td>
<td>no dorsal crest</td>
<td>clear dorsal crest</td>
<td>clear dorsal crest</td>
</tr>
<tr>
<td>6</td>
<td>First phalange with or without proximo-dorsal groove</td>
<td>without</td>
<td>without</td>
<td>with</td>
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Fig. 7. Morphological characters of Doliachoerinae 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 Suinae and Taucanamo belongs to a different group of Suinae, 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.

Note. When this paper was in press, a paper by Pickford appeared (1995, Old World Suoid Systematics, Phylogeny, Biogeography and Biostratigraphy. Paleontologia e Evoluzione, 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, Propalaeocherus and Palaeocherus (=? Doloichoerus). 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: Palaeocherininae Matthew, 1924; Doloichoerininae Simpson, 1945; Sanitherinae Simpson, 1945 and Schizochercini Golpe-Pessey, 1972. Pickford (1984) applied the name Sanitheridae, 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 papre and another one (Van der Made 1994) characters have been presented that unite the group, that separate them from the Suinae. 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 Palaeocherinidae Matthew, 1924. Taucanamo, Yunnanochoerus, Schizochoerus and probably Odoichoerus should be placed in the Schizocherininae Golpe-Pessey, 1972 and Propalaeocherinus, Palaeocherus and probably Sanitherium in the Palaeocherininae.

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