Estudios geol., 45: 233-237 (1989)

ON THE TAYASSUID AFFINITIES OF *XENOHYUS* GINSBURG, 1980, AND THE DESCRIPTION OF NEW FOSSILS FROM SPAIN*

M. Pickford** and J. Morales***

ABSTRACT

In 1980, Ginsburg created the new genus *Xenohyus* for a large suiform artiodactyl which he considered to belong to the family Suidae. Among the distinguishing characters of the genus, Ginsburg cited the enlarged, strongly curved and inflated central upper incisors possessing a distal accessory cusplet, the shortened muzzle, the enlarged lower first and second incisors, and the close packing of the entire tooth row (i.e. reduced to absent diastemata). These and other characters, such as the vertically implanted mandibular canines, the symphyseal morphology, and the shape of the third upper incisor, suggest that *Xenohyus* belongs instead to the family Tayassuidae, subfamily Doliochoerinae.

Whereas Ginsburg suggested that *Xenohyus* had an unknown ancestry and that it represented an immigrant into Europe at about the beginning of zone MN2b, it now seems more likely that it represents a late doliochoere of the sort represented by *Doliochoerus quercyi* which occurs in late Stampian deposits (Ginsburg, 1974). In many ways it is merely an enlarged version of this species, but there are sufficient morphological differences to warrant retention of the genus *Xenohyus*.

Viewed within a tayassuid framework, *Xenohyus* is not seen to be unusual and not to run counter to evolutionary trends in the Suidae, the latter view being a necessity following its identifiation as a suid.

Some fundamental similarities between the molars of *Xenohyus* and *Kenyapotamus* could provide a link between late doliochoeres and early hippopotamids, an hypothesis already mentioned by Pickford (1983).

Newly discovered fossils from Loranca, Cuenca, Spain belong to two different species of *Xenohyus, X. venitor* and an undescribed larger species.

Key words: Xenohyus, *Tayassuidae, Lower Miocene, Spain.*

RESUMEN

Ginsburg (1980) creó un nuevo género *Xenohyus* para un suiforme de talla grande que consideró como perteneciente a la familia Suidae. Entre los caracteres que distinguían a este nuevo género, Ginsburg citaba la morfología peculiar del tercer incisivo superior; ensanchado, fuertemente curvado, centralmente hinchado y con un tubérculo accesorio distal. Así como el acortamiento del morro, los incisivos inferiores (I_1 e I_2) y la ausencia en la serie dentaria de diastemas. Este y otros caracteres, como son la implantación vertical de los caninos en la mandíbula, la morfología sinfisaria, y la forma del tercer incisivo superior, sugieren que *Xenohyus* pertenece más bien a la familia Tayassuidae, subfamilia Doliochoerinae.

Para Ginsburg, *Xenohyus* no tenía ningún ancestro conocido en Europa y por tanto, debía ser un inmigrante, cuya entrada se habría producido cerca de los comienzos de la unidad NM2b. *Xenohyus* es ahora visto como uno de los últimos miembros de los doliochoerinos, representados por *Doliochoerus quercyi* en los depósitos del Estampiense superior (Ginsburg, 1974). De alguna manera, *Xenohyus* es meramente una versión agrandada de esta especie, pero hay suficientes diferencias morfológicas que apoyan la retención del género.

Algunas similaridades fundamentales entre los molares de *Xenohyus* y *Kenyapotamus* podrían probar una relación entre los últimos doliochoerinos y los primeros hipopótamos, hipótesis ya ciertamente mencionada por Pickford (1983).

* Este trabajo ha sido posible gracias a las subvenciones de la Junta de Comunidades de Castilla-La Mancha para las excavaciones del yacimiento de Loranca del Campo (Cuenca).

** Institut de Paléontologie. 8, rue Buffon, 75005, Paris.

*** Museo Nacional de Ciencias Naturales. J. Gutiérrez Abascal, 2. 28006 Madrid.

Nuevos fósiles, descubiertos en Loranca (Cuenca, España), pertenecientes a dos diferentes especies de *Xenohyus; X. venitor* y *Xenohyus* sp. de talla mayor que el anterior, son también descritos en este trabajo.

Palabras clave: Xenohyus, *Tayassuidae, Mioceno inferior, España.*

Introduction

Ginsburg, 1980, described a new genus of suiform artiodactyl form zones MN2b and MN3b in France, as *Xenohyus.* Ginsburg placed the genus within the family Suidae, all his comparisons and comments of the genus being made with other suids. However, a re-examination of the material, including new specimens from Spain, leads us to propose a different hypothesis regarding the familial affinities of the genus. All the distinctive characters mentioned by Ginsburg for defining the new genus, are, in our opinion, typically doliochoerine tayassuid features, which relate the genus to the Old World peccaries rather than to the pigs.

This reassignment of the genus naturally affects the discussions made by Ginsburg regarding the palaeoethology and origins of *Xenohyus.*

New fossils from Spain

Collections of fossils from Loranca, Cuenca Province, during the past four years contain six specimens of *Xenohyus.* Three of these fall comfortably within the range of variation of *X. venitor* but three fossils fall well ouside this range. These latter specimens are appreciably larger than their homologues in *X. venitor* (Table 1) and may well represent a separate species. Morphologically, however, they are typical of the French species.

These three fossils are associated with a very rich fauna containing other large mammals as well as micromammals whose age is Ramblian, zone Z, more or less equivalent to MN3a of Mein's Biozonation (Ginsburg, et al, 1987).

The three smaller specimens were found in surface scatters of fossils at about 100 metres distance from where the series of larger teeth were found *in situ.* Their age could be Ramblian, but an age more recent cannot be excluded because relatively close to the area where they were found also exists a Middle Aragonian locality. Thus, the fossils found on the surface could have two different origins.

Systematic Paleontology

Class Mammalia Linneo, 1758.
Order Artiodactyla Owen, 1848.
Family Tayassuidae Palmer, 1897.
Genus *Xenohyus* Ginsburg, 1980.
Xenohyus venitor Ginsburg, 1980.
Locality: Loranca surface; Age: Ramblien or Middle Aragonian.

Description

Right upper central incisor lacking the root and a portion of the crown on the mesial edge: This tooth is moderatly worn, but shows the typical inflated and strongly curved external surface, the low lingual cingulum and the distal accessory cusp. The course of the central lingual ridge is shown by a curve in the outline of the wear facet near the lingual cingulum.

Left upper first or second molar: This unworn tooth crown lacks the roots and a small portion of the distolingual enamel near the cervix. The four principal cusps are bunodont and well separated from each other by grooves. There are anterior, median and posterior accessory cusps, those on the anterior and posterior parts of the crown being incorporated into the anterior and posterior cingula. The median accessory cusplet is close to the hypocone. The buccal cingulum is large.

Left lower third molar: This unworn rootless crown was found close to the upper molar described immediately above, and considering their compatible stage of wear, the two teeth might represent a single individual. There are four principal cusps arranged in two transverse pairs, and a fifth talonid cusp at the rear. There is a distinct median accessory cusp close to the entoconid. The hypoconulid lies between the hypoconid and the distal talonid cusp and is bordered lingually and labially by cingula. Anteriorly there is a large cingulum which extends onto the front part of the labial surface of the protoconid.

These three fossils closely resemble their homologues in *X. venitor,* both in their morphology and in size.

Xenohyus sp. indet.
Locality: Loranca; Age Ramblian, zone Z.

Description

Right upper central incisor: This tooth lacks most of the root and the distal accessory cusplet is damaged. The crown is lightly worn, and is in every res-

Table 1.—**Measurements (mm) of teeth of *Xenohyus* from Loranca (Cuenca, Spain)**

	Loranca Surface			Loranca *in situ*		
	I^1	M^X	M_3	I^1	p^3	M_3
MDL	17	20,2	32,5	18,7	20	39
BLB	21,7	18,2	17,3	24,5	15,2	21,5
H crown	—	10,3	12,5	—	17,5	—
H cing.	—	6,2	6,4	—	—	9

pect except for size, similar to those of *X. venitor.* The wear facet is principally at the apex and down the distal marginal ridge towards the distal accessory cusplet, as in material from France.

Left upper third premolar, unworn, lacking the roots: This specimen is closely similar, except for its larger size, to those from France. The only significant observable difference resides in the fact that the crest running from the apex of the principal cusp to the rear cingulum has two beads on it. These beads are very small, and with light wear would be unobservable.

The tooth lacks an external cingulum, although there is a slight swelling in the labial surface of the crown where a cingulum would normally appear. The distolingual cusplet and cingula are comparable in shape and position to those of *X. venitor.*

Worn right third molar in mandible fragment: This worn tooth has little detailed morphology remaining, but its general shape, and the presence of a cingulum on the front portion of the protoconid indicates that it belongs to the same group as the upper central incisor and the third premolar described above.

The talonid is simple, and has labial and lingual cingula leading forwards from it towards the hypoconid and entonocid. Between these two cingula lies the hypoconulid. The median accessory cusplet is closely attached to the entoconid, and is difficult to distinguish in this worn and cracked specimen.

The status of *Xenohyus*

Morphology

Upper incisors: The enlarged, strongly curved upper central incisors of *Xenohyus* lack the apical sulci

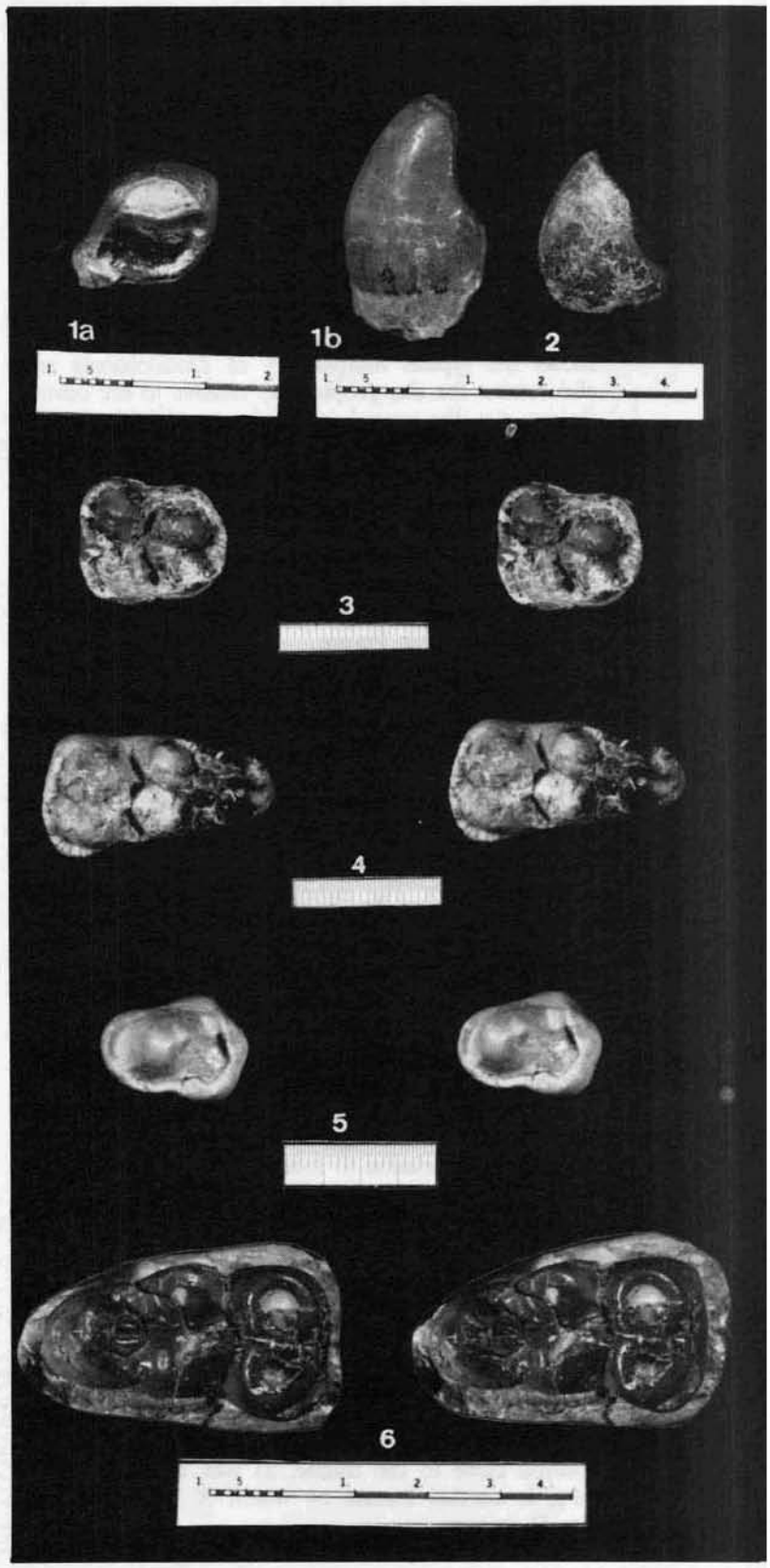

Plate 1.—*Xenohyus Ginsburg* from Loranca (Cuenca Province, Spain).—1. *Xenohyus* sp. right upper central incisor (I^1) lacking the root from Loranca *in situ,* a) occlusal view, b) lateral view.—2. *Xenohyus venitor* Ginsburg, right upper central incisor (I^1) lacking the root from Loranca surface, lateral view.—3. *Xenohyus venitor* Ginsburg, left upper first or second molar (M^1 or M^2) from Loranca surface, occlusal view (Stereophotography).—4. *Xenohyus venitor* Ginsburg, left lower third molar (M_3) from Loranca surface, occlusal view (Stereophotography).—5. *Xenohyus* sp., left upper third premolar (P^3) from Loranca *in situ,* occlusal view (Stereophotography).—6. *Xenohyus* sp., right lower third molar (M_3) from Loranca *in situ,* occlusal view (Stereophotography).

usually observed in suid teeth. They possess a lingual cingulum which joins the mesial and distal enamel ridges which form the lingual margins of the crown, and distally there is a small but distinct accessory cusplet. There is also a weak but broad central ridge running from the apex of the crown towards the lingual cingulum, and wear is predominantly apical and down the distal ridge to the distal accessory cusplet. This set of features and the overall shape of the tooth closely recalls, for example, *Doliochoerus quercyi* from Stampian deposits of Europe (Deschaseaux, 1959). The main difference is one of size.

The upper second incisor illustrated by Ginsburg shows the typical morphology of *Doliochoerus* and also retains the size proportions relative to the central incisors (i.e. the second incisor is considerable smaller than the central incisor).

Upper premolars: The third premolar of *Xenohyus* closely resembles its homologue in *D. quercyi* apart from its larger size. Ginsburg reports that most individuals of *X. venitor* possess labial cingula, but this feature seems to be variable, the spanish specimens having only an incomplete labial cingulum, as in a specimen from France.

The upper fourth premolars of *X. venitor* are closely similar to those of *D. quercyi* except for their larger size and more marked labial cingulum. In the position of the three main cusps (two labial, one lingual) and the degree of development of the anterior and posterior cingula, and in crown height, the upper fourth premolars of the two genera are difficult to distinguish from each other.

Upper molars: The rather bunodont, simple upper molars of *X. venitor*, resemble those of *D. quercyi* in a number of features including the proportions of the principal cusps, the positions and size relations of the anterior, median and posterior accessory cusplets and the strength of the anterior and posterior cingula. The only major difference in the available specimens, is that the labial cingulum in the upper molars of *Xenohyus* are more inflated and more complete than they are in *Doliochoerus*. Furthermore, the height of the cingula in relation to total crown height is similar in the two genera, and it should be pointed out that in this morphology the doliochoeres resemble the primitive hippopotamid *Kenyapotamus* described by Pickford (1983).

Lower incisors: The two central incisors of *Xenohyus* are enlarged, not only relative to the cheek teeth but also in relation to the third incisor. They have strongly developed central lingual ridges, and are bordered mesially and distally by marginal ridges. Their procumbent orientation in the symphysis and their position close to the canine, as was noted by Ginsburg, is another feature by which *X. venitor* resembles *D. quercyi*.

The third lower incisor of *Xenohyus* is a small tooth with a mesiodistally elongated crown, in which the distal part projects over the sloping root, precisely as in *Doliochoerus*.

Lower Canine: The position of the canine close to the incisors in front and the premolars behind, together with its vertical orientation within the jaw is a further indication of tayassuid rather than suid affinities for *Xenohyus*. The canine *in situ* in the mandibular fragment from La Fuye is a rather primitive, rooted tooth. A separate hypsodont canine illustrated by Ginsburg, resembles the canine of *D. quercyi*, but its association with *Xenohyus* must remain uncertain until specimens are found in place. The determination of sexual dimorphism in the genus must remain hypothetical for the time being, until better samples are known.

Lower Premolars: The morphology of the premolars of *Xenohyus* are closely compatible with those of *Doliochoerus* except for their larger size. Their position in a closed series close to the canine, the strongly developed «trigonid» in the fourth premolar (Deschaseaux, 1959), their gradual increase in size and complexity of crown morphology from mesial to distal is also typical of doliochoeres.

Lower Molars: Although at first glance the lower molars look like those of suids, there is nothing in their morphology to exclude them from being tayassuids. If anything, the close contact between the entoconid and the median accesory cusplet is more like the situation in Old World peccaries in general (Pickford, 1978) than it is in suids, but it must be admitted that in their molar morphology there has been a certain amount of convergent evolution between peccaries and pigs, as epitomised by the striking similarity between the molars of *Listriodon* and *Schizochoerus*.

Mandible: Ginsburg (1980) already noted the shortness of the snout in *Xenohyus*. Comparison of the symphyseal region with *Doliochoerus* reveals the following overall similarities: The symphyseal section, the shape, orientation and extent of the superior surface of the symphysis, its extension to the year as far as the second premolar, the shape of the geniohyoid fossae and the shape of the ventral surface, all recall *Doliochoerus* rather than suids. Furthermore, the absence of symphyseal splaying in the camine area is also a tayassuid character.

There are mental foramina below the second and fourth premolars about half way down the depth of the mandible. In this *Xenohyus* is similar to *D. quercyi*.

Maxilla: Although the maxilla of *Xenohyus* is poorly known, the available specimen from Laugnac accords well with the tayassuid hypothesis. The zygoma are placed forwards over the second molar and the anterior part of the third molar, whereas in many suids, the zygoma are located further to the

rear on the face of the maxilla. It is difficult to determine the distal extension of the palate in the sample of *Xenohyus*, but it seems reasonable to suggest, on the basis of specimen Lg 120, that there was a distal extension of the palate as in *Schizochoerus* as shown by Pickford (1978).

Discussion

It appears to us that it is likely that *Xenohyus* is an Old World doliochoerine tayassuid. Furthermore, it is probable that it evolved in Europe from an Oligocene doliochoere such as *Doliochoerus quercyi* or something similar. The latter is of late Stampian distribution according to Ginsburg (1974) while *Xenohyus* is known from lower Miocene strata of France (MN2b and MN3b) and Spain (Ramblian, zone Z), although the possibility that it can also be found in Middle Aragonian levels cannot be excluded until the relationships of the different Loranca sites is firmly established.

It was previously thought that *Xenohyus* became extinct before MN4, but the similarities between the molars of *Xenohyus* and *Kenyapotamus* may provide evidence that the lineage persisted after migrating to Africa in Faunal Set III (Pickford, 1981) where it gave rise to the hippopotamids. Clearly, however, a better sample of fossils would be needed in order to verify this possibility.

The detailed relationships of *Xenohyus* with respect to other Old World tayassuids such as *Schizochoerus*, *Taucanamo* and *Doliochoerus*, must await the discovery of substantailly better fossils of *Xenohyus*. Dentally, the closest relationships are undoubtedly to *Doliochoerus*.

ACKNOWLEDGEMENTS

We thank the Junta de Comunidades de Castilla-La Mancha for financial support and the Museo Nacional de Ciencias Naturales for facilities to study the fossil material. This report is part of a project initiated and headed by Margarita Díaz Molina, Universidad Complutense de Madrid (PB 85/0022).

References

Deschaseaux, C. (1959). Le genre *Doliochoerus*. *Ann. Paléont.* 45: 1-16.

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. and Locher, J. P. (1987). Les Suidae (Artiodactyla, Mammalia) du Miocène inférieur des Beilleaux à Savigné-sur-Lathan (Indre-et-Loire) *Bull. Mus. Natn. Hist. Nat.*, 10: 197-207.

Ginsburg L.; Morales, J. and Soria, D. (1987). Nouvelles faunes de grands mammifères d'âge Miocène inférieur dans la partie orientale du bassin du Tage (Espagne). Conséquences stratigraphiques. *Comptes rendus Acad. Sci. Paris*, 305: 629-632.

Pickford, M. (1978). The taxonomic status and distribution of *Schizochoerus* (Mammalia, Tayassuidae) *Tertiary Res.*, 2: 29-38.

Pickford, M. (1981). Preliminary Miocene mammalian biostratigraphy for Western Kenya. *J. Human Evol.*, 10: 73-97.

Pickford, M. (1983). On the origins of the Hippopotamidae together with a description of two new species, a new genus and a new subfamily from the Miocene of Kenya. *Geobios*, 16: 193-217.

Recibido el 31 de diciembre de 1988
Aceptado el 15 de marzo de 1989