

Iberian Suoidea

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RESUMEN

En este trabajo se presenta una síntesis de los Suoidea de la Península Ibérica.

Los Suoidea ibéricos están compuestos por treinta especies y subespecies. Para cada taxón se presenta una lista de localidades y se presenta una distribución temporal.

ABSTRACT

There is a good record of Suoidea (= Suidae + Tayassuidae; Mammalia, Artiodactyla) from the Miocene of the Iberian peninsula, besides Suidae are also known from the Iberian Pliocene and Pleistocene.

The Iberian Suoidea (30 species and subspecies) are briefly described or reference is made to a recent description. For each taxon a list of localities where it is found is presented and a range-chart has been compiled.

The Suoidea of the Iberian peninsula are compared to those of the rest of Europe. Some of the differences are the absence of *Taucanamo*, *Sanitherium* and *Microstonyx antiquus* in Spain and Portugal and the presence or abundance in Spain of *Schizochoerus* and *Parachleuastochoerus*. Further differences are in some ranges: *Bunolistriodon*, *K. provincialis* and *S. arvernensis* are known from older localities in Spain than in France; *K. provincialis* also enters early in Italy.

Species diversity was high during the Early Aragonian and near the transition from the Aragonian to the Vallesian. Like in other parts of Europe, species diversity became very low after the Vallesian. *K. palaeochoerus* is the only species crossing the MN 9 - MN 10 limit for a substantial period. The cause of this change must be an important ecological event because in Africa and the Indian Subcontinent suoid species diversity remained high.

INTRODUCTION

This paper has several goals. One is to give a list of the Iberian species and the localities where they occur. Another goal is to compile a range-chart for the

Iberian Suoidea and to study the changes in the suoid fauna. A last goal is to compare the Iberian Suoidea to the rest of Europe and to study the changes in the Suoid record. In some cases it was necessary to discuss systematics or determinations of individual pieces.

I studied most of the Iberian material. A large part of the Spanish material described or mentioned here was described or mentioned before by GOLPE (1972). If a comparison is made the reader will find that my

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determinations differ many times from those by GOLPE. One of the main differences between my determinations and those by GOLPE concerns *Hyotherium soemmeringi*. The majority of the material referred to this species by GOLPE belongs in my opinion to *Conohyus steinheimensis*. I studied the *Conohyus* material from Steinheim, the large population of *Hyotherium soemmeringi* from Sandelzhausen and the publication in which the types of *H. soemmeringi* are figured (VON MEYER, 1834).

Dr. Antunes was so kind to show me the Portuguese material which is under study. So I make only some brief remarks on this material.

The suoids will be treated per species or subspecies, 30 forms all together. For each species a table is given with all localities where the species occurs (in the case of a possible presence this will be indicated by a question mark), the collection, useful descriptions of the material, the biozone and a reference on the dating. I did not try to be complete when giving references of descriptions (for instance: I did not refer each time to GOLPE, 1972). When a reference of a description of material is given this does not imply that I agree with the determination of that author. If the collection is mentioned this means that I studied the material, if it is not mentioned I know the material only from literature.

There is some Iberian Suoid material older than MN 2a but this is not taken into consideration as it is very scarce.

Usually the biozonation by MEIN (1975) is used and not the one by DAAMS & FREUDENTHAL (1981) and DAAMS, FREUDENTHAL & ALVAREZ (1986). The reason for this is that the ages of many localities can be found in literature in the MN zonation, but not in the other zonation (for instance Portuguese and Catalan localities).

COLLECTIONS

CEPUNL. Centro de Estratigrafia e Paleobiologia da Universidade Nova de Lisboa

CST. Colegio La Salle, Teruel

IPS. Instituto de Paleontología de Sabadell

ITGE. Instituto Tecnológico y Geominero de España (Madrid) (formerly called IGME)

IVAU. Instituut voor Aardwetenschappen Utrecht = Faculteit Geologie en Geofysica, Rijksuniversiteit te Utrecht

MAMCVMA. Museu Arqueològic Municipal "Camil Visedo Moltó", Alcoy

MGB. Museo de Geología, Barcelona

MGSCB. Museo Geológico del Seminario Conciliar, Barcelona

MHMN. Museu Històric Municipal de Novelda

MNCN. Museo Nacional de Ciencias Naturales (Madrid)

MPZ. Museo de Paleontología de la Universidad de Zaragoza

MPV. Museo Paleontológico de Valencia
RGM. Rijksmuseum voor Geologie en Mineralogie, now called National Museum of Natural History (Leiden).

UC. Universidad Complutense, Madrid

UCBL. Université Claude Bernard, Lyon

LM. Museum of natural history of Lisbon

In addition material of various private collections was studied.

THE TAXA AND THEIR RANGES

Tayassuidae PALMER, 1897

The Iberian Tayassuidae belong to Doliochoerinae SIMPSON, 1945 or to an other group of old world peccaries.

Palaeochoerus typus POMEL, 1847

This small tayassuid is typified by upper molars with the paraconule fused to the protocone and separated from the cingulum and by a size inferior to *Hyotherium meissneri*. It resembles much *Aureliachoerus*, but its premolars are more hypsodont and the upper molars have a different paraconule morphology.

Postcranial material from Valquemado might belong to another species, like the species of Navarrete or may belong to *Aureliachoerus aurelianensis*. Although the entry of *A. aurelianensis* should be in MN 2b (GINSBURG, 1980) this species is not known for certain before MN 3b in Spain.

locality	collection	description	biozone	reference
Cetina	MNCN	V.d. MADE in prep.	Y/MN2a	GINSBURG et al. 1987
Moheda	MNCN		Z	MORALES pers. com.
?Valquemado	MNCN		Y/2b	GINSBURG et al. 1987

Doliochoerinae indet.

A much worn molar and a piece of a maxilla from Navarrete represent another tayassuid. The maxilla has a vertical canine and a diastema between P¹ and P². The molar indicates a size comparable to *P. typus*, but this animal does not have a diastema.

A molar from Colmenar has enamel with a very smooth surface, resembling tayassuids and it is too large for *P. typus*. The known Miocene tayassuids are smaller or are lophodont. Tayassuids with molars of this size and morphology (*P. gergovianus* and *Doliochoerus*) are thought to be older (GINSBURG, 1973 & 1980).

locality	collection	description	biozone	reference
Navarete	MNCN		Z	
Colmenar	MNCN			

***Barberahyus castellensis* GOLPE, 1977**

This is the smallest European Miocene suoid. Its molars are bunodont and have smooth enamel, giving them a very simple appearance. The canines are of the tayassuid type, but are more hypsodont than in *Taucanamo*. The ridges on the distal articulations of the metapodials continue dorsally. This is also the case in recent peccaries and Suidae but it is not the case in *Taucanamo* and probably not in *Palaeochoerus*. This tayassuid does not seem to be closely related to either *Palaeochoerus/Dolichochoerus* on one hand nor to *Taucanamo/Schizochoerus* on the other. It is probably an immigrant in Europe. HENDEY (1976) described a peccary from South Africa that resembles *Barberahyus* in size and morphology (as far as can be judged from the pictures).

locality	collection	description	biozone	reference
Castell de Barberà	IPS	GOLPE 1975, 1977	MN 8	MEIN 1975
Nombrevilla II	MNCN	MORALES pers. com.	MN 8	see paragraph on <i>Parachleuastochoerus</i>

***Schizochoerus vallesiensis* CRUSAFONT & LAVOCAT, 1954**

Schizochoerus is a large peccary and is probably related to *Taucanamo*. In Europe *Schizochoerus* is an immigrant and not a direct descendant of this genus. The genus is known only from Spain and eastern Europe and from outside of Europe. Its molars are lophodont and resemble those of *Listriodon*, but are more elongated, the incisors and canines are entirely different. More information on this taxon is given by PICKFORD (1978).

In Spain the species is restricted to two localities both attributed to the lower part of MN 10 (AGUSTI *et al.*, 1985).

locality	collection	description	biozone	reference
Villadecavalls (= Can Purull)	IPS	CRUS&LAV 1954	MN 10	MEIN 1975
La Tarumba		GOLPE 1972	MN 10	AGUSTI <i>et al.</i> 1985

Suidae GRAY, 1821

Primitive Suidae resemble Tayassuidae very much, they differ however in the structure of the basicranium and the shape and orientation of the canines (PEARSON,

1927) and they differ in having relatively longer premolar rows, the individual premolars being less hypsodont and frequently being more elongate. In the Hyotheriinae and Listriodontinae upper molars with the paraconule fused to the protocone still occur, but also a type with the paraconule fused to the cingulum and separated from the protoconule occurs. The last type is the only one occurring in Tetraconodontinae and Suinae.

Listriodontinae SIMPSON, 1945

Listriodontinae (including *Kubanochoerus*) are Suidae with I¹, I₁ and I₂ with low and wide crowns. The shape of the incisors is a derived character of the whole group. The incisors are well described by LEINDERS (1977a), who compared them to the incisors of *Sus*. However, it should be kept in mind that the starting point of development of the listriodont incisors were not *Sus*-like hypsodont incisors. Primitive suoid incisors are low crowned; the listriodont incisors became wide and the incisors of *Sus* became hypsodont.

In the genus *Bunolistriodon* the paraconule sometimes is fused to the protocone and sometimes to the cingulum; this may change even within one tooth row. In *Listriodon* the protocone, paraconule and paracone are fused to form a lophe.

The astragalus of the listriodonts is typical and is well described by LEINDERS (1976), but the astragalus from Munébrega which he referred to *B. lockharti* more likely represents *Hyotherium* (V. d. MADE & ALFÉREZ in prep.).

The lineage "*Listriodon*" *lockharti* - *Listriodon splendens* was proposed by LEINDERS (1975) and he included *B. lockharti* in the genus *Listriodon* because of the supposed close relation. Such a lineage seems unlikely because of reduction of the facet for the second cuneiform on the navicular in *Bunolistriodon*, this facet is not reduced in *Listriodon*.

***Bunolistriodon lockharti* (POMEL, 1848)**

Large listriodontines with bunodont dentition. The premolar row is somewhat shortened (compared to, for instance, *B. jeanelli* and Hyotheriinae).

B. lockharti occurs in localities of MN 4a to MN 5, or zone D and E.

The holotype of *Palaeochoerus giganteus* GOLPE, 1972 is an upper molar of *Bunolistriodon*, it is either an M¹ of *B. lockharti* or an M² of *B. latidens*. The trapezoidal form that is mentioned in the diagnosis is caused by deformation.

B. lockharti is cited from Puente Vallecas (GOLPE, 1972 and MORALES & SORIA, 1985). GOLPE mentions an incisor and an M³. MORALES and SORIA mention a maxilla and an M³ (the same one?). The incisor certainly is not *Bunolistriodon*, the maxilla belongs to *Conohyus* and the M³ to *B. latidens*.

locality	collection	description	biozone	reference
Córcoles	UC	V.d. MADE & ALFÉREZ in prep.	MN 4a	MOYA-SOLA & ALFÉREZ 1988
Buñol	IVAU/IPS/MPV	BELINCHON 1987	MN 4a	MEIN 1975
Lisbon Va (various localities)	CEPUNL		MN 4a	ANTUNES 1984
Can Canals	IPS		MN 4	AGUSTI et al. 1984
Puente de Toledo		MORALES & SORIA 1985	MN 4	ALBERDI et al. 1985
?Villafeliche 3	IVAU			
?Villafeliche "bocht"	IVAU			
La Hidroeléctrica				
Lisbon Vb (various localities)	CEPUNL		MN 4b	ANTUNES 1984
Monteagudo	IPS	ASTIBIA et al. 1987	MN 4/5	ASTIBIA et al. 1987

becomes shorter (which is an unusual trend in Suidae) and the P2 and P3 get additional cusps. The lower premolars get a second large cusp internally of the main cusp (like the P4) and the upper premolars get a second labial cusp behind the main cusp. The talonids of the lower premolars become elevated and get a distinct small cusp. The lingual cusplet of the upper premolars becomes larger. *L. splendens major* TORRES, 1907 is the progressive subspecies. Although the changes occur gradually one might say that *L. s. splendens* occurs in MN 6 and 7 and *L. s. major* occurs in MN 8 and 9.

Listriodon splendens MEY. var. *aragoniensis* GOLPE, 1972 is a *Listriodon splendens* from Arroyo del Val IV, and in my opinion represents *Listriodon splendens splendens*. The material is not more hypsodont than normal, it is however less worn.

Some material from Arroyo del Val I, Manchones I, Cerro del Otero and Paracuellos III is much larger than the normal *L. splendens*.

***Bunolistriodon latidens* (BIEDERMANN, 1873)**

A small *Bunolistriodon*, 85 % the size (linear) of *B. lockharti*. Both species of *Bunolistriodon* are well represented in Córcoles (V. d. MADE & ALFÉREZ, 1988) and a description of this material is in preparation (V. d. MADE & ALFÉREZ).

locality	collection	description	biozone	reference
Córcoles	UC	V.d. MADE & ALFÉREZ in prep.	MN 4a	MOYA-SOLA 1988
La Artesilla Armantes I	MPZ/IVAU		MN 4b	ANTUNES 1984
Munébrega I	IVAU		MN 4b	ANTUNES 1984
Munébrega II	IVAU			
Munébrega II	IIVAU			
Munébrega AB	IVAU	LEINDERS 1975		
Torraiba II	IVAU			
Tejar			MN 4b	ANTUNES 1984
Manzanares				
Hidroeléctrica	MNCN/IPS			
Lisbon Vb (various localities)	CEPUNL		MN 4b	ANTUNES 1984
Puente de Toledo	ITGE	MORALES & SORIA 1985	MN 4	ALBERDI et al. 1985
Moratines	IPS/MNCN		MN 4	ALBERDI et al. 1985
?Can Canals	IPS		MN 4	AGUSTI et al. 1984
Puente Vallecas	IPS	MORALES & SORIA 1985	MN 5	ALBERDI et al. 1985

locality	collection	description	biozone	reference
Paracuellos V	MNCN	MORALES & SORIA 1985	MN 6	ALBERDI et al. 1985
Arroyo del Val I + IV	IVAU/RGM	LEINDERS 1975, 1976, 1977	MN 6	MEIN 1975
VI	IPS			
Manchones I + II	IVAU/IPS		MN 6	MEIN 1975
Murrero	IVAU			
Paracuellos III	MNCN	MORALES & SORIA 1985	MN 6/7/8	ALBERDI et al. 1985
Cerro del (=Palencia)	MNCN	HERNÁNDEZ PACHECO 1915	MN 7	MEIN 1975
Torrii III	coll. Langa			
La Ciesma	MPZ	AZANZA 1986	MN 8	presence <i>C. ebroensis</i> and absence <i>Hipparion</i> see paragraph on <i>Parachleuastochoerus</i>
Nombrevilla II	MNCN		MN 8	see paragraph on <i>Parachleuastochoerus</i>
Castell de Barberá	IPS		MN 8	MEIN 1975
S. Quirze (=Trinchera coll. Villalta de Ferrocarril)	IPS		MN 8	MEIN 1975
Aveiras de Baixo	LM	ROMAN 1907	MN 9	ANTUNES 1984
Hostalets	IPS		MN 8 + 9	AGUSTI et al. 1985
coll. Villalta				
Can Ponsic I	IPS		MN 9	MOYA-SOLA 1983
Mas del Olmo	ITGE			
Azambujeira inf.		ANTUNES et al. 1983	MN 9	ANTUNES et al. 1983
Santiga	IPS			
La Cisterniga	MNCN/IPS			
Can Feliu	IPS			
Can Cunilé	IPS			

***Listriodon splendens* VON MEYER, 1846**

Listriodon splendens is a lophodont suid, with wide incisors, which become even wider in the younger subspecies of *L. splendens*. Also the talon of the M3

Hyotheriinae COPE, 1888

Hyotheriinae are a group of pigs that usually lack striking specializations. It is not absolutely sure that the subfamily, as presently used, is monophyletic. The Iberian Hyotheriinae form a group of animals with dentition with roughly the same morphology but with differences in size. There is a series of contemporaneous species in which each smaller species has 85% the linear size of the larger species. This means that the smaller species had approximately half the body weight of the larger species.

Hyotherium meissneri VON MEYER, 1829

This small hyotheriine pig is well represented in Cetina de Aragón, a description is in preparation (V. d. MADE in prep.). The paraconule and the crown height of the premolars indicate that it is a suid and not a tayassuid. It is not related to the *Palaeochoerus* from Coderet. This tayassuid is more progressive in having larger last molars relative to the M1.

H. meissneri has 86 % the linear size of *H. major*. Scanty material from Horta das Tripas and Moratilla has the same size, a P³ from Torralba II in the MNCN collection might belong to this species as well as an M³ in the IVAU collection (although it has a paraconule fused to the protocone). An astragalus from Olival Suzana may belong to this species or to *H. major* or *Aureliachoerus*.

locality	collection	description	biozone	reference
Cetina	MNCN/IPS IVAUI	V.D. MADE in prep.	Y/MN 2a	GINSBURG et al. 1987
?Horta das Tripas	LM	ROMAN 1907	MN 3a	ANTUNES Lisbon I 1984
?Moratilla	MNCN		A / 3b	GINSBURG et al. 1987
?Torralba II	IVAUI			
Torralba II	MNCN			
?Olival Suzana	CEPUNL		MN 4b	ANTUNES Lisbon Vb1984

Hyotherium major (POMEL, 1847)

H. major is 93 % the size (linear measurements) of *H. soemmeringi*, morphological differences are a distal cusplet on the I¹ and elongation of the premolars in *H. soemmeringi*. But these characters are not always clearly present in the earliest *H. soemmeringi*. *H. soemmeringi* replaced *H. major*, but it is not known whether one species evolved into the other or whether *H. soemmeringi* is an immigrant. In the case that *H. soemmeringi* is an immigrant it is possible that it coexisted for some time with *H. major*.

An M₃ and D⁴ from Valdemoros 3a and 3c may be referred to *H. major* on the basis of size. Premolars and

molars from Armantes I are closer in size to *H. major* than to *H. soemmeringi*.

The holotype of *Conohyus cuspidatus* GOLPE, 1972 from Armantes I has the size of *H. major* and as far as I can judge, nothing indicates that it belongs to *Conohyus*.

locality	collection	description	biozone	reference
Cetina	IPS MPZ		Y/MN 2a	GINSBURG et al. 1987
?Valdemoros3a	IVAUI		MN 4b	MEIN 1975
?Valdemoros3c	IVAUI		MN 4b	MEIN 1975
?Armantes I	IVAUI		MN 4b	ANTUNES 1984

Hyotherium soemmeringi VON MEYER, 1829

I¹ from Munébrega I and Munébrega AB show (faintly developed) the labio-distal cusps that are typical for *H. soemmeringi*. The dimensions of other teeth are not in contradiction to such a determination. The fact that the P4 from Munébrega has two well separated cusps led LEINDERS (1975) to figure it as an example of the variation in morphology in *B. lockharti*. The same tooth is also a paratype of *Conohyus cuspidatus* GOLPE, 1972. Astragali from Torralba IV, Munébrega I, Q. Flamengas and Sant Mamet have the size of the *H. soemmeringi* astragali from Sandelzhausen. Other postcranial from Munébrega I and poor dental remains from A. de la Vega and Q. Musqueira also resemble *H. soemmeringi*. No Iberian locality has yielded good material.

locality	collection	description	biozone	reference
Sant Mamet	IPS		MN 4a	AGUSTI et al. 1985
Munébrega I	IVAUI	LEINDERS, 1976	MN 4b	ANTUNES 1984
Munébrega II	IVAUI			
Munébrega AB	IVAUI	LEINDERS, 1975 (fig. II,3)		
Torralba IV	IVAUI			
Lisbon Vb	CEPUNL	(various localities)	MN 4b	ANTUNES 1984
?Montejo de la Vega	MNCN		MN 6	MORALES pers. comm.

Aureliachoerus aurelianensis (STEHLIN, 1899)

A small hyotheriine pig that is 85 % the (linear) size of *H. meissneri*. It has a shorter premolar row and a relatively longer last molar. It is larger than *A. minus* and *P. typus*.

An M¹ or M² from Rubielos de Mora is either *A. aurelianensis* or *A. minus*.

The species is found from MN 3b to MN 4b. According to GINSBURG (1980) *P. typus* is replaced by *A. aurelianensis* in MN 2b. In Spain this does not seem

to be the case.

locality	collection	description	biozone	reference
Molí Calopa	IPS		MN 3b	MEIN 1975
Agreda	MNCN			
St. Andreu de la Barca	IPS		MN 3	AGUSTI et al. 1984
?Rubielos de Mora	MNCN		MN 4a	ALVAREZ 1987
Buñol	MNCN	BELINCHÓN 1987	MN 4a	MEIN 1975
Can Canals	IPS		MN 4b	AGUSTI et al. 1984

***Aureliachoerus minus* (GOLPE, 1972)**

This small species was first described from El Canyet (the type locality) and from Can Canals. It is very close to *A. aurelianensis*, but differs in having smaller M3 and a P4 with two well separated labial cusps. Sizes of other teeth are very close and may even overlap, but size variation of all material together is too large for one species. M1-3 from Costa Blanca I probably represent *A. minus* but are also close in size to *P. typus*, a species that probably was already extinct.

locality	collection	description	biozone	reference
Costa Blanca I				
Can Canals	IPS	GOLPE 1981	MN 4b	AGUSTI et al. 1984
El Canyet	IPS	GOLPE 1981	MN 4b	AGUSTI et al. 1984

***Xenohyus venitor* GINSBURG, 1980**

X. venitor is a large hyotheriine. The P₄ usually have two main cusps. This is a progressive character. But these cusps probably are not always well separated, like in other Hyotheriinae. "*Conohyus*" *betpakdalensis* TROFIMOV, 1949 from Russia has the same measurements, but differs in having a P₄ with a blunt main cusp. The tooth is very different from the pointed *Conohyus* P₄, but resembles P₄ with only one main cusp that occur in the Cetina *H. meissneri* and St. Gérard *H. major* samples. As "*C.*" *betpakdalensis* and *X. venitor* are of about the same age they might well be synonymous.

A large metapodial from Molí Calopa cannot belong to another suid than *Xenohyus*. A P₁ from Moratilla might represent this species. A mandible from Q. da Farinheira has roughly the morphology of *H. soemmeringi*, but is too large and its P₄ is not elongated as in *H. soemmeringi*; it has the size of *X. venitor*. A P₄ and some postcranial material from Buñol most likely belongs to this species for the same reasons. If all this material represents *X. venitor* the range of this species is much longer than recognized. If it is *H. soemmeringi* it implies that this species decreased in size, which is not uncommon in pigs. It also would imply

that the entry of *H. soemmeringi* was much earlier, which means that it coexisted a long time with a smaller *Hyotherium*. What is difficult to explain in this case is why *H. soemmeringi* would decrease in size and would start to resemble much more the smaller species, causing of course a stronger competition.

locality	collection	description	biozone	reference
Loranca	MNCN	PICKFORD & MORALES 1989	Z	GINSBURG et al. 1987
Molí Calopa	IPS		MN 3b	MEIN 1975
?Moratilla	MNCN		A / 3b	GINSBURG et al. 1987
Buñol	MPV	BELINCHÓN 1987	MN 4a	MEIN 1975
Quinta da Farinheira	CEPUNL		MN 4b	ANTUNES (Lisbon Vb) 1984

Hyotheriinae indet.

A large suid, probably a hyotheriine is found in Loranca and Valquemado. It is larger than *B. lockharti*. It is possible that two large M3 and an elongated large P3 from Quinta la Barbacena belong to the same species. If this is not the case they represent the largest *B. lockharti*.

locality	collection	description	biozone	reference
Valquemado	MNCN		Y / 2b	GINSBURG et al. 1987
Loranca	MNCN	PICKFORD & MORALES 1982	Z	GINSBURG et al. 1987
?Quinta la Barbacena	CEPUNL		MN 4a	ANTUNES (Lisbon VA) 1984

Tetraconodontinae SIMPSON, 1945

Tetraconodontinae are suidae that retained P₄ with one main cusp and P⁴ with one main labial cusp and they have the derived character of a much enlarged and relatively narrow P₃; the P₄ frequently are enlarged and relatively wide, the P₁ and P₂ often are low, narrow and very long.

***Conohyus simorrensis goeriachensis* VAN DER MADE, 1989**

The lineage *C. simorrensis goeriachensis* - *C. s. simorrensis* - *C. ebroensis* is described by me elsewhere. It is characterized by increase in body size (which is related to the size of the M1 - LEGENDRE, 1986), a relative greater increase in the size of the last molars and a size decrease of the premolars.

The subspecies *C. s. goeriachensis* is typical of MN 5.

A maxilla from Puente Vallecas, figured by MORALES & SORIA (1985) as *B. lockharti* was described by GOLPE (1972) as "*?Hyotherium soemmeringi* MEY. *matritensis* n. sp.". This is a strange way of writing a species name, but it is repeated elsewhere, except for the question mark. The question mark indicates that GOLPE was in doubt whether the new species should be placed in the genus *Hyotherium* (as there can be no doubt about the type species *H. soemmeringi*). The mandible represents *C. simorrensis goeriachensis* and the species *?Hyotherium matritensis* is synonymous to *C. simorrensis*. In figure 1 the maxilla is compared to other *Conohyus* material.

locality	collection	description	biozone	reference
Puente Vallecas	coll. Rotondo	MORALES & SORIA 1985 V. d. MADE 1989	MN 5	ALBERDI et al. 1985
	IPS	MORALES & SORIA 1985		

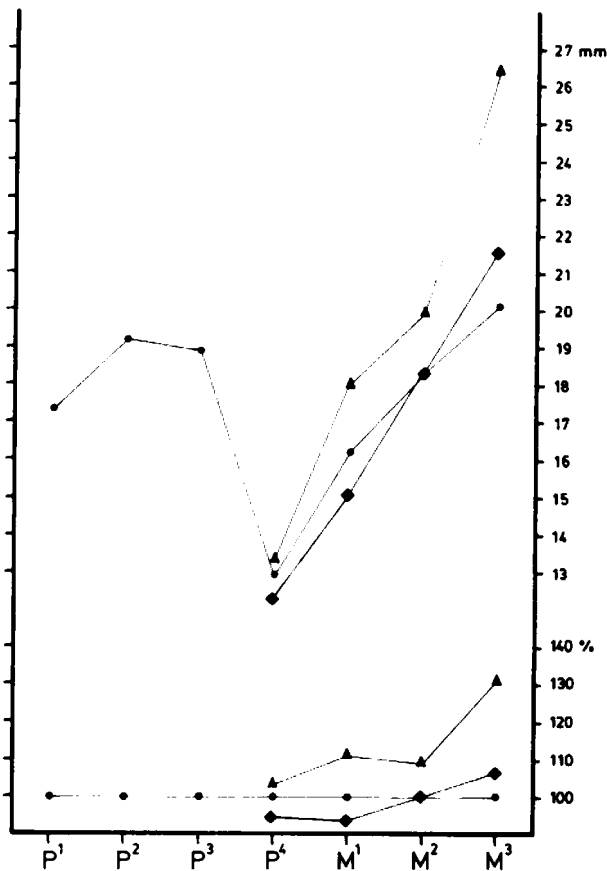


FIGURE 1. The lengths of the upper cheek teeth of the holotype of "*?Hyotherium soemmeringi* MEY. *matritensis* GOLPE, 1972" (= *Conohyus simorrensis*) (diamonds) compared with *Conohyus simorrensis* from Göriach (means of population) (dots) and with *Conohyus simorrensis* from Le Fousseret (triangles).

Conohyus simorrensis simorrensis (LARTET, 1851)

The material from Pero Filho probably represents *C. s. simorrensis*, more likely than *C. steinheimensis*.

In the Iberian peninsula the animal is rare and is found only in two localities belonging to MN 6.

The material from Mira was described by GOLPE (1972) as *Conohyus melendezi*, but it represents *Conohyus simorrensis simorrensis*.

locality	collection	description	biozone	reference
Mira	IPS	V. d. MADE 1989	MN 6	V. d. MADE 1989
Pero Filho		ANTUNES & MEIN 1977	MN 6	ANTUNES & MEIN 1977

Conohyus ebroensis AZANZA, 1986

The holotype of this species comes from El Buste. An upper molar from La Ciesma is too wide for *Suinae* or *C. steinheimensis*.

Localities with *C. ebroensis* are younger than those with *C. simorrensis* but include Fonte do Pinheiro (Simorre and Le Fousseret are MN 7), so the range must be MN 8 to MN 9. ANTUNES *et al.* (1983) described a P³ from Azambujeira inf. as *C. simorrensis*, it represents either *C. ebroensis* or *C. steinheimensis*. An M₃ from La Bisbal and two M³ from Can Ponsic II are very large. The M₃ is larger than any of the M₃ of *K. palaeochoerus* from the Deinotheriensande (HÜNERMANN, 1968). The M³ are much too large for *K. palaeochoerus*, but too small for *M. major* (MN 10 - 12) or the much larger *M. antiquus* (MN 9). The teeth are also too old to belong to *K. provincialis*. The M² from Aveiras de Baixo probably is an M₂ of *C. ebroensis*, it also might be an M¹ of *M. antiquus* or a large M¹ of *M. major*; it is wider than any *K. palaeochoerus* M₂ and about as long as the longest M² of this species. All this material might belong to *C. ebroensis*, but we do not have any good information on the ranges of size of this species.

locality	collection	description	biozone	reference
El Buste	MPZ	AZANZA 1986	MN 8	V. d. MADE 1989
La Ciesma	MPZ	AZANZA 1986	MN 8	presence <i>C. ebroensis</i> , absence <i>Hipparion</i>
Fonte do Pinheiro	LM	ROMAN 1907	MN 9	
?Aveiras de Baixo	LM	ROMAN 1907	MN 9	ANTUNES 1984
?Azambujeira inf.		ANTUNES et al. 1983	MN 9	ANTUNES et al. 1983
?Can Ponsic II	IPS		MN 9	MOYA SOLA pers. com.
?La Bisbal de L'Empordà	coll. Villalta		MN 9	MOYA SOLA 1983

Conohyus steinheimensis (FRAAS, 1870)

C. steinheimensis is a tetracondont comparable in size to *C. simorrensis*, but with a morphology like *Parachleuastochoerus*. (Consequently, *C. steinheimensis* might better be placed in *Parachleuastochoerus*, but such a discussion is beyond the scope of this paper.) It differs in having relatively smaller premolars, narrower P4 and molars and by the retention of an I³, which probably is lost in *C. simorrensis*. A recent description of the Steinheim material is by CHEN GUANFANG (1984). The species shows a size increase with time; there are minor morphological changes too. The material from Can Almirall seems to be too advanced for MN 6.

The oldest localities with this species are Manchones and Arroyo del Val (MN 6) the last occurrence seems to be in MN 9. Material from Santiga, Solera, Can Cunilé and Nombrevilla II is poor and might represent also *C. simorrensis/ebroensis* or *Korynochoerus*.

locality	collection	description	biozone	reference
Arroyo del Val I + VI + IV?	IVAU		MN 6	MEIN 1975
Manchones I	IVAU		MN 6	MEIN 1975
	IPS			
Can Almirall	IPS		MN 6 (?)	AGUSTI et al. 1984
Castell de Barberá	IPS		MN 8	MEIN 1975
Can Feliu	IPS			
?Nombrevilla II	MNCN		MN 8	See section on <i>Parachleuastochoerus</i> MEIN 1975
S. Quirze	IPS		MN 8	
	coll. Villalta			
?Solera	MNCN		G	DAAMS & V.D. MEULEN 1984
Hostalets	IPS		MN 8 + 9	AGUSTI et al. 1985
	coll. Villalta			
Can Ponsic I	IPS		MN 9	
?Can Cunilé	IPS			
?Santiga	IPS		MN 9	MOYA SOLA 1983

***Parachleuastochoerus crusafonti* GOLPE, 1972 and *Parachleuastochoerus huenermanni* (HEISSIG, 1989)**

Parachleuastochoerus resembles very much *C. steinheimensis*, to which it is probably closely related: the premolars are less enlarged than in *C. simorrensis*, the P4 are narrower and the I² are more elongated than in *C. simorrensis* and there is still an I³. The species shows a size decrease with time (interestingly *C. steinheimensis* becomes larger during the same period). The material from S. Quirze, Castell de Barberá and Seu d'Urgell (all MN 8) is larger than the material from Can Llobateres (MN 9); the Can Ponsic material is intermediate. *Dicerorhinus sansaniensis* is typical of the Upper Aragonian, but is found also in Can Ponsic, in Can Llobateres the species is replaced by *D. schleiermayeri*, a form that is known also from the Upper Vallesian (CERDENO, 1988). MN 9 can be separated in an upper biozone (the *Cricetulodon* zone) and lower zone, both Can Llobateres and Can Ponsic are placed in the upper zone (AGUSTI et al., 1984). These data indicate that there was a notable size decrease during the later part of MN 9 (figure 2).

A third metacarpal from La Tarumba is approx. 10 % smaller than a metacarpal of *P. crusafonti* from Can Llobateres and has the same morphology. Metacarpals of *Schizochoerus* (also occurring in La Tarumba) are expected to be larger. La Tarumba is dated the older part of MN 10 (AGUSTI et al., 1985).

HEISSIG (1989) described "*Conohyus*" *huenermanni* from the Upper Sweet Water Molasse of Krumbach. The holotype is slightly larger than material from Wissberg and the larger Spanish material and smaller than the material from Steinheim. Similarly a P⁴ from Doué-la-Fontaine is slightly larger than those from Wissberg and Spain. It is likely that the material from France and Germany belongs to the same lineage as the Spanish *Parachleuastochoerus*. The type of *P. crusafonti* is from Can Llobateres. The larger material from Krumbach, Doué-la-Fontaine, Wissberg, San Quirze, La Seu d'Urgell, Can Ponsic and Castell de Barberá belongs to *P. huenermanni* and the smaller material from Can Llobateres and La Tarumba belongs to *P. crusafonti*.

	AGUSTI et al. 1984		CERDENO 1988	This paper
U. Vallesian	MN 10		<u><i>Dicerorhinus schleiermayeri</i></u>	<u><i>Parachleuastochoerus small</i></u>
L. Vallesian	MN 9 upper part	Can Llobateres	<u><i>D. schleiermayeri</i></u>	<u><i>Parachleuastochoerus small</i></u>
	<u><i>Cricetulodon</i> zone</u>	Can Ponsic I	<u><i>D. sansaniensis</i></u>	<u><i>Parachleuastochoerus intermediate</i></u>
	MN 9 lower part			
U. Aragonian	MN 8		<u><i>D. sansaniensis</i></u>	<u><i>Parachleuastochoerus large</i></u>

FIGURE 2. Size decrease in *Parachleuastochoerus* and changes in the rodent and rhino faunas.

locality	collection	description	biozone	reference
Castell de Barberá	IPS		MN 8	MEIN 1975
S. Quirze coll. Villalta	IPS	PICKFORD 1981	MN 8	MEIN 1975
?Nombrevilla II	MNCN		MN 8	presence of <i>Parachleuastochoerus</i> , absence of <i>Hipparion</i>
Hostaletes	IPS		MN 8 + 9	AGUSTI et al. 1985
Seu d'Urgell	MGB		MN 9	
Can Llobateres	IPS	PICKFORD 1981	MN 9	MEIN 1975
Santiga		PICKFORD 1981	MN 9	MOYÀ SOLÀ 1983
Can Ponsic I	IPS	PICKFORD 1981	MN 9	MOYÀ SOLÀ 1983
La Tarumba	coll. Villalta		MN 10	AGUSTI et al. 1985

Suinae VON ZITTEL, 1893

Morphological descriptions of *Korynochoerus*, *Microstonyx* and *Sus* are given by V. d. MADE & MOYÀ (1989) and will not be repeated here.

Korynochoerus palaeochoerus (KAUP, 1833)

The anterior half of a lower molar from Los Valles de Fuentidueña might represent this species or several other species occurring in MN 9: it might be an M₁ of *M. antiquus* or an M₃ of *C. ebroensis*. Material from La Balsilla, Molina de Aragón and Terrassa is tentatively referred to this species. A description of material from Alcoy is in press (V. d. MADE & BELINCHÓN).

K. palaeochoerus is well represented in MN 8 and MN 9. The decrease in abundance of the species might be related to the "Mid Vallesian Crisis".

locality	collection	description	biozone	reference
Castell de Barberá	IPS		MN 8	MEIN 1975
Hostaletes	IPS		MN 8 + 9	AGUSTI et al. 1985
?Los Valles de Fuentidueña		MORALES & SORIA 1981	MN 9	ALBERDI et al. 1981
S. Quirze inf.	IPS		MN 9	ANTUNES et al. 1983
Azambujeira		ANTUNES et al. 1983	MN 9	ANTUNES et al. 1983
Molina de Aragón	MNCN			
Can Llobateres	IPS		MN 9	MEIN 1975
Can Ponsic I	IPS		MN 9	MOYÀ SOLÀ 1983
Ballestar	IPS		MN 9	MOYÀ SOLÀ 1983
Terrassa (=Can Jofresa)	IPS		MN 10	MOYÀ SOLÀ 1983

locality	collection	description	biozone	reference
Alcoy	MNCN	V.D. MADE & BELINCHÓN	MN 13	MEIN 1975
	MPV	in press		
	MAMCVMA			

Korynochoerus provincialis (GERVAIS, 1859)

Good material of this species is only known from Venta del Moro, a P₄ and an M³ fragment from Arenas del Rey are morphologically closer to this species than to *K. palaeochoerus*. Postcranial material from La Librilla and Milagros have the size of *K. provincialis*, but are not sufficient for a determination to specific level.

locality	collection	description	biozone	reference
Venta del Moro	MNCN	MORALES 1984	MN 13	MEIN 1975
Arenas del Rey	IPS		MN 13	MONTOYA pers. comm.
?Milagros			MN 13	MOYÀ SOLÀ 1983
?La Librilla	IPS		MN 13	MOYÀ SOLÀ 1983

Microstonyx major major (GERVAIS, 1848 - 1852)

M. major does not present great difficulties in determination, because of its size. The Spanish material is being described by V. d. MADE, MONTOYA & ALCALÁ (in press.).

locality	collection	description	biozone	reference
Terrassa	IPS	GOLPE 1978, 1979a, 1979b	MN 10	AGUSTI et al. 1985
La Roma 2 Masía del Barbo	coll. Esteban CST		MN 10	
Das	MGSCB		MN 10	
Peralejos	MNCN		MN 10?	
La Cantera	MNCN		MN 10/11	
Piera	IPS, MGB		MN 11	MOYÀ SOLÀ 1983
	MGSCB			
Crevillente 2 (= Aspe)	MHMN		MN 11	ALCALÁ et al. 1987
	MPV			
Puente Minero	MNCN		MN 11	
Crevillente 15	MPV		MN 12	
Crevillente 16	MPV		MN 12	
Concud	MNCN, IVAU		MN 12	MEIN 1975
Cerro de la Garrita)	MPZ, IPS			
	coll. Orrios, coll. Esteban, coll. Marco			
Concud Barranco de las Calaveras)	IVAUA		MN 12	MEIN 1975
Concud (which?)	UCBL		MN 12	MEIN 1975
Las Pedrizas	MNCN		MN 12	

cf. *Microstonyx major erymanthius* (ROTH & WAGNER, 1854)

An aberrant dicoryphochoerine from Terral d'en Maties is much too small for *M. major major*. It is close to *M. major erymanthius* from Pikermi and Kerassia, but in the M2 it still is smaller. Unfortunately no micromammals were collected at this locality (AGUSTI pers. comm.) so that the age is not known.

locality	collection	description	biozone	reference
Terral d'en Maties	IPS	GOLPE 1972		

***Sus arvernensis* CROIZET & JOBERT, 1828**

S. arvernensis is a little smaller than *K. palaeochoerus*. It is known only from two localities.

locality	collection	description	biozone	reference
Gorafe IV	IPS		MN 14A	AGUSTI 1986
Piedrabuena	MNCN	MAZO & TORRES in prep	MN 16a	MAZO & TORRES 1988

***Sus strozzii* FORSYTH MAJOR, 1881**

S. strozzii is known from only one Spanish locality. The material consists of the last lower two molars. Their size and the simple morphology of the third lobe of the M₃ indicate that they belong to *S. strozzii*.

locality	collection	description	biozone	reference
Valdeganga II		MEIN et al. 1978	MN 17	AGUSTI et al. 1987

***Sus scrofa* Linnaeus, 1758**

The oldest Spanish locality with *S. scrofa* is Bovila Ordís (Moyà Solà, pers comm.).

locality	collection	reference	biozone	reference
Bovila Ordís	Moya SOLA	MmQ 2 pers. comm.	Moya SOLA	pers. comm.

DISCUSSION

The ranges of the species are given in figure 3. These ranges are compared to those for Europe as given elsewhere (GINSBURG, 1973 & 1980; GUÉRIN & FAURE, 1975 and V. d. MADE, this volume).

Some taxa are completely absent in Spain and Portugal. Striking is the absence of *Taucanamo*. This genus is found in Europe from MN 4a to MN 9. There is no reliable record of this genus south of the Pyrenees. GOLPE (1972) referred three teeth from Hostalets to *T. pygmaeum*. I could not find these teeth in the IPS. Other citations are based on wrong determined milk dentition or bones. Also *Sanitherium* is absent; in Europe it is restricted to south-eastern Europe. *Microstonyx antiquus* is rare in Europe and totally absent in the Iberian peninsula.

Other taxa are rare in Europe, but are known from the peninsula and may be even abundant. *Schizochoerus* is found in Spain in the older part of MN 10. Apart from Spain it is not found in western Europe, but in it is found in eastern Europe and Turkey. *Parachleuastochoerus* is abundant in Spain, it is known from but few other places. And the very large suid from Loranca is until now known from Spain only and possibly from Portugal.

In other cases the entry of a species is earlier in the Iberian peninsula than in other parts of Europe. *Bunolistriodon* enters in MN 4a in Spain and in Portugal. In France it seems to enter in MN 4b (GINSBURG, 1980). *C. steinheimensis* enters in MN 6 in Spain, outside Spain the oldest known occurrences are Steinheim, La Grive and Przeworno (MN 7). *K. provincialis* is found in Spain only in MN 13, in France it is only known from MN 14 and 15 (GUÉRIN & FAURE, 1985), but in Italy it is also found in MN 13 (Casino). In France *Sus arvernensis* is not known before MN 15 (GUÉRIN & FAURE, 1985), but in Spain it is found in MN 14.

In other cases the entry of taxa is later in the Iberian peninsula. Until now *Barberahyus* is known from two places outside Spain: Przeworno II and La Grive (some metapodials in the museum of natural history in Florence), both localities are MN 7; in Spain the species is only known from MN 8.

The large suid from Loranca, *Barberahyus*, *Microstonyx antiquus* and *Schizochoerus* are so rare that any differences between the Iberian peninsula and the rest of Europe are likely to be due to an incomplete record. This may also be the case with *Parachleuastochoerus*, although it is really abundant in some Catalan localities. It is also rare in other parts of the peninsula.

The absence of *Taucanamo* in Spain and Portugal probably is the result of some ecological cause. Also the early entry (compared to France) of *K. provincialis* (in Spain and in Italy) and *S. arvernensis* (in Spain) may have some ecological significance, as it is repeated and in both cases it seems to be related to latitude. It is striking that the same thing occurs with *Bunolistriodon*: this genus also enters later in France.

In some other cases the ranges of certain species need further discussion.

H. soemmeringi ranges from MN 4b to MN 6 in the Iberian peninsula. According to GINSBURG (1980, 1973) the last occurrence of the species is MN 9, but he does

not cite a locality. HÜNERMANN (1968) referred two teeth from Wissberg to *Hyotherium* sp. and he placed *Korynochoerus palaeochoerus* in *Hyotherium*. In a rangechart for suid genera compiled by HÜNERMANN (1969) the genus *Hyotherium* has a continuous range "Burdigalium" - "Panonium". In older literature a lineage *H. soemmeringi* - "*Hyotherium*" (= *Korynochoerus*) *palaeochoerus* is supposed (STEHLIN 1899/1900 and many others). Maybe this is the reason for extending the range of *H. soemmeringi*. GOLPE (1972) cited *H. soemmeringi* from several MN 8 and MN 9 localities, but this material proved to be *C. steinheimensis*. The occurrence of *H. soemmeringi* in MN 7, 8 and 9 is doubtful, also outside Spain and Portugal.

The tayassuid from Navarete (that probably is related to *Palaeochoerus* or *Doliochoerus*) is not comparable to any other known European material of the same age. It might represent species that has a longer range than was supposed until now. The genus *Aureliachoerus* is supposed to enter in MN 2b in Selles sur Cher (GINSBURG, 1980). The known range of *A. aurelianensis* in Spain is from MN 3b to MN 4b. The known range of *A. minus* is MN 4a to 4b. The material from Selles sur Cher might represent also a tayassuid. *Xenohyus venitoris* found in France from MN 2b to MN 3 (GINSBURG, 1980). If this species occurs together with *Bunolistriodon* the possibility exists that isolated molars are attributed to *Bunolistriodon* and isolated

premolars to *Hyotherium*. Material from Quinta do Farinheira and Buñol indicates that the range of *X. venitor* is longer, this may also be the case in France.

Many of the Suoidea mentioned are not particularly abundant, but *Listriodon splendens*, *Bunolistriodon*, *Korynochoerus palaeochoerus* and *Microstonyx major* often form an important part of the fauna in numbers of individuals and are known from a lot of localities, not only in the Iberian peninsula, but all over Europe. If there is sufficient material identification is easy. They might be considered as guide fossils.

It was mentioned before that Hyotheriinae form a series of more or less similar forms that differ in body size. *A. aurelianensis* - *H. meissneri* - *H. major* and possibly *Xenohyus venitor* may represent a series in which each following form has approximately twice the body weight of the preceding form. These forms coexisted for some time. It is possible that these suids formed a stable part of the ecosystem and that the size differences prevented the niches from overlapping much. *H. soemmeringi* did not fit in this system of doubling of body size. The entry of *H. soemmeringi* more or less coincided with the disappearance of most of the hyotheriines forming the series with a regular size increase. Coexistence of more or less similar animals that differ only in body size is common. Four species of *Dorcatherium* that differed in size coexisted and three species may be found in one locality (FAHLBUSCH, 1985). Two species of *Bunolistriodon*

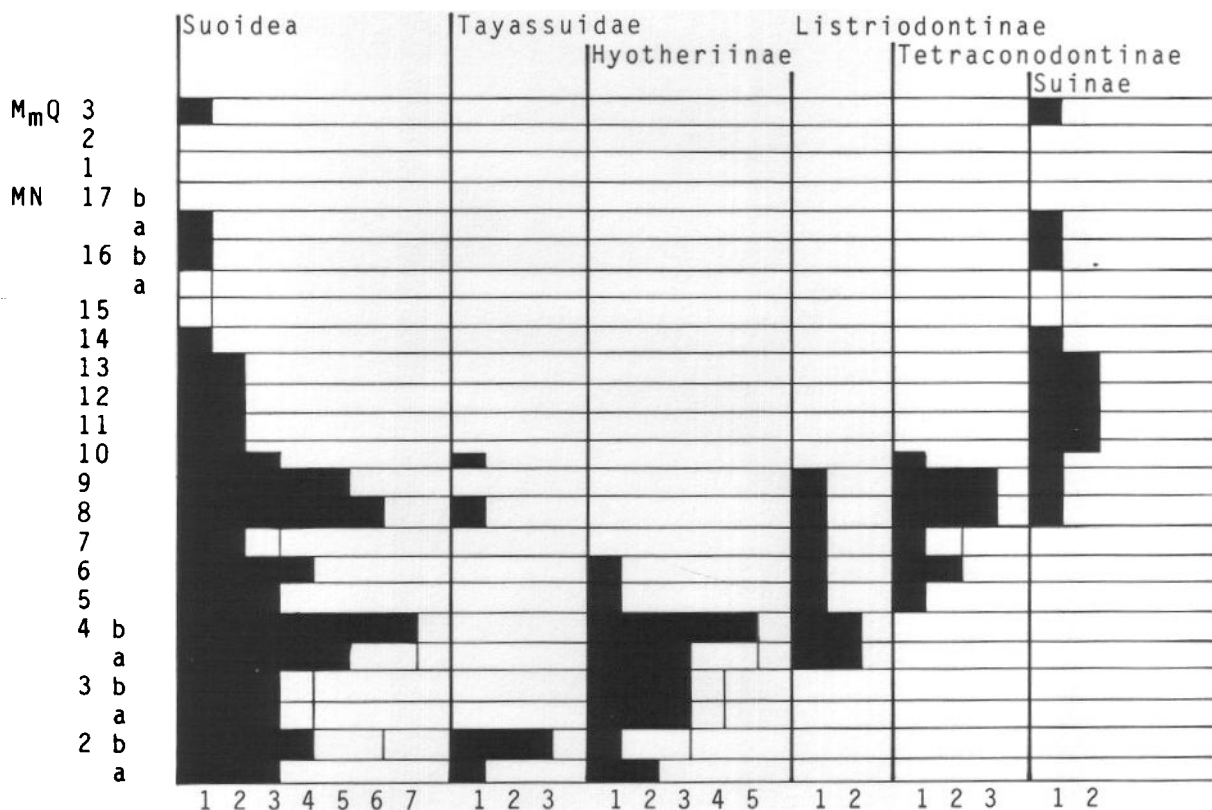


FIGURE 4. The numbers of species per biozone for all Suoidea together and for the Tayassuidae and subfamilies of the Suidae. Species that are present in earlier and later zones are assumed to be present in the intermediate biozone, but are indicated by a line only.

coexisted. In the Indian subcontinent two lophodont listriodonts coexisted and in Africa may be even more (belonging to *Listriodon* and to *Lopholistriodon*). In the Indian subcontinent a series of Dicoryphochoerini of different sizes coexisted. Often a set of such animals enters within a short period and often also the exit is more or less at the same time. This may prove to be a frequent and important pattern in faunal evolution. It seems to be an interesting field for further investigation.

An abundance of Suoidea (in number of individuals and in number of species) generally is interpreted as an indication of a more humid climate and a denser vegetation, but might also be related to temperature. In figure 4 the number of species per biozone is given. MN 4 and MN 9 have high species diversity. In MN 10

the number of species declines to two and in later zones the diversity becomes even less. The same occurs also in other parts of Europe. At the same moment suoid diversity in the Indian subcontinent remained high (PICKFORD, 1988). Also in the Pliocene and Pleistocene of Africa there is a high species diversity: first there is a high number of Tetraconodontinae (which also survived in India, but which became extinct during the Vallesian in Europe) and later there are up to 8 species of Suinae at a moment (COOKE & WILKINSON, 1978). The decrease of the number of suoid species during the Vallesian in Europe certainly has an ecological significance. Also in the Bovidae there is a great change during the Vallesian (ALCALÁ *et al.*, 1988).

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