

A *CONOHYUS* - LINEAGE (SUIDAE, ARTIODACTYLA) FROM THE MIOCENE OF EUROPE

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ABSTRACT

The genus *Conohyus* belongs to the Tetraconodontinae: pigs with enlarged third and fourth premolars. There are two lineages in the Aragonian and the Vallesian of Europe: the *C. simorrensis* - *C. ebroensis* lineage and the *C. steinheimensis* lineage. The first lineage is the subject of this paper. It is characterized by a size increase in the molars and by premolars that do not increase in size or even decrease. Three forms can be distinguished: *C. simorrensis goeriachensis* nov. subsp. for MN 5, *C. simorrensis simorrensis* (Lartet, 1851) for MN 6 and MN 7 and *C. ebroensis* Azanza, 1986 for MN 8 and MN 9. The gradual loss of the tetraconodontine specialisation of enlarged premolars occurs not only in this line, but also in most other genera of the Tetraconodontinae. *C. simorrensis goeriachensis* nov. subsp. is one of the most primitive tetraconodontines in this respect and it is also one of the oldest.

Keywords: *Conohyus*, Suidae, Aragonian, Göriach

RESUMEN

El género *Conohyus* pertenece a los Tetraconodontinae: suidos con el tercer y el cuarto premolar agrandado. Hay dos líneas en el Aragoniense y el Vallesiense de Europa. La línea de *C. simorrensis* - *C. ebroensis* y la línea de *C. steinheimensis*. La primera línea es objeto de estudio en este artículo. Está caracterizada por el aumento del tamaño de los molares y por premolares que disminuyen de tamaño o bien no cambian. Se pueden distinguir tres formas: *C. simorrensis goeriachensis* nov. subsp. de la zona MN 5, *C. simorrensis simorrensis* (Lartet, 1851) de la zona MN 6 y la MN 7 y *C. ebroensis* Azanza, 1986 de la zona MN 8 y la MN 9. La pérdida gradual de la especialización tetraconodontina de premolares agrandados no sólo ocurre en esta línea, sino también en otros géneros de los Tetraconodontinae. *C. simorrensis goeriachensis* es uno de los más primitivos tetraconodontinos en este respecto así como uno de los más antiguos.

Palabras clave: *Conohyus*, Suidae, Aragoniense, Göriach.

INTRODUCTION

The genus *Conohyus* belongs to the *Tetraconodontinae*; pigs with enlarged third and fourth premolars, of which the P4 have only one cusp and the P4 have only one large labial cusp. It is the oldest known genus of this subfamily. It enters Europe in the middle Aragonian (MN 5), the Indian subcontinent in Kamlial and ranges up to MN 9 (lower Vallesian) and (lower?) Nagri.

In Europe there are three species: *Conohyus simorrensis* (Lartet, 1851), *C. ebroensis* Azanza, 1986 and *C. steinheimensis* (Fraas, 1870). For some time *C. steinheimensis* was considered to be synonymous

with *C. simorrensis*, but Chen Guanfang (1984) showed the species to be different on the basis of the greater width of the upper and lower last premolar in *C. simorrensis*. In addition the relative size of the third and fourth premolars in *C. steinheimensis* is smaller and the second upper incisor has a different shape. It is a different species but coincides in time and space with *C. simorrensis*. *C. ebroensis* was recently described by Azanza (1986). The only important differences between *C. ebroensis* and *C. simorrensis* are that in the former the molars are larger and small diastemae have developed between the canine and the P2. These characters are generally progressive in Suidae. The species replaces *C. simorrensis*; an ancestor-descendant relation seems likely.

	P ₁			P ₂			P ₃			P ₄			M ₁			M ₂			M ₃						
	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp			
<i>C. s. goeriachensis</i> from Göriach																									
mean	14,5	5,5	5,7	19,7	6,7	8,3	25,2	12,4	15,7	18,4	13,0	14,8	16,4	12,5	12,8	18,0	14,5	14,3	25,4	14,8	12,8	11,3			
<i>C. s. simorreensis</i> from Le Fousseret																									
lectotype										19,0		15,0	17,5		13,9	20,0		13,6	25,4	15,8					
<i>C. ebroensis</i>																									
Fonte do Pinheiro				19 ¹						22,1		11,8	20,0		15,8	20,4	14,6	15,0	23,7	17,9	17,0	34,4	18,5	16,4	12,2
El Buste												20,8			14,8 ¹	20,3	16,2	15,5	23,1	18,7	17,6				
<i>C. s. goeriachensis</i> 100%																									
<i>C. s. simorreensis</i>																									
Le Fousseret												103		101	107		109	111		105	100	107			
<i>C. ebroensis</i>																									
Fonte do Pinheiro							88		75	109				107	124		117	132	123	119	135	125	128	108	
El Buste										113				124		121	128	129	123						
<i>C. s. simorreensis</i> 100%																									
Fonte do Pinheiro												105		105	117		108	119		125	135	117			
El Buste												109			116		112	116		129					
	p ₁			p ₂			p ₃			p ₄			M ¹			M ²			M ³						
	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp				
<i>C. s. goeriachensis</i> from Göriach																									
mean	17,3	6,3	6,8	19,2	6,9	8,1	18,9	13,5	17,5	12,9	17,5	16,2	15,7	14,9	18,3	18,0	16,7	20,1	16,9	13,7					
<i>C. s. simorreensis</i> from Le Fousseret																									
composite							20 ¹		13,3	13,3	19,1	18,0	18,7		19,9	19,4		26,4	19,5						
<i>C. s. goeriachensis</i> 100%																									
<i>C. s. simorreensis</i>									76	103	109	111	119		109	108		131	115						

Table 3. The means of the measurements of the dentition from Göriach, compared with the measurements of the dentition of *Conohyus* from Le Fousseret, El Buste and Fonte do Pinheiro. The measurements are given in mm, but also as a percentage.

ret is stored in the Muséum National d'Histoire Naturelle in Paris and it is or will be described by Ginsburg, who will designate the mandible as a neotype of *Conohyus simorreensis*. The holotype of *C. ebroensis* is stored in the Instituto de Paleontología in Zaragoza and was described by Azanza (1986). A mandible from Fonte do Pinheiro is stored in the museum of natural history in Lisbon and was described by Roman (1907).

THE LINEAGE

In Tables 1 and 2 the measurements and the means of the Göriach materials are given. The teeth

FORTE DO PINHEIRO	MN 9	<i>Conohyus ebroensis</i>
EL BUSTE	MN 8	
LE FOUSSERET	MN 7	<i>C. simorreensis simorreensis</i>
MIRA	MN 6	
GÖRIACH HOMMES PUENTE VALLECAS	MN 5	<i>C. simorreensis goeriachensis</i>

Figure 1. Distribution of species and subspecies of the genus *Conohyus*.

		<i>Conohyus</i>	<i>Eotragus</i>	<i>Pliopithecus</i>	<i>Hemicyon</i>	<i>Plithocyon</i>
MN 6	SANSAN MIRA	<i>C. s. simorreensis</i>	<i>E. sansaniensis</i>	<i>P. antiquus</i>	<i>H. sansaniensis</i>	<i>P. armagnacensis</i>
MN 5	GÖRIACH	<i>C. s. goeriachensis</i>	<i>E. cf. sansaniensis</i>	<i>P. antiquus</i>	<i>H. sansaniensis</i>	<i>P. armagnacensis</i>
	FALUNS DE TOURAIN ET DE L'ANJOU	<i>C. s. goeriachensis</i>		<i>P. piveteaui</i>	<i>H. cf. sansaniensis</i>	<i>P. cf. armagnacensis</i>
	P. VALLECAS	<i>C. s. goeriachensis</i>				
	PONTLEVOY				<i>H. stehlini</i>	

Figure 2. Distribution of species and subspecies of *Conohyus* and *Eotragus* (personal observation) and *Pliopithecus*, *Hemicyon* and *Plithocyon* (Ginsburg, pes. comm.). Note that the "faluns de Touraine et de l'Anjou" represent a group of localities (including Hommes).

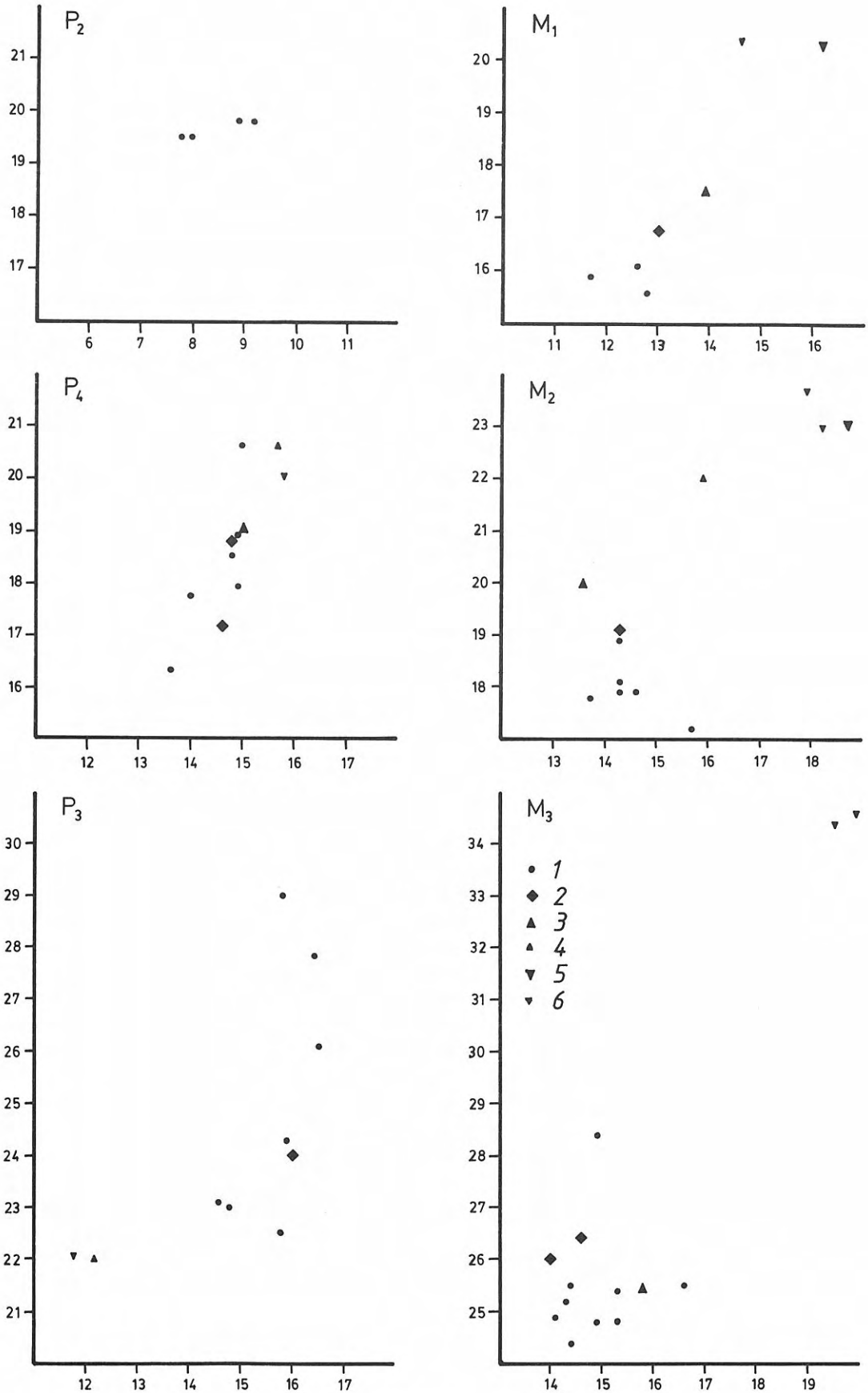


Figure 3. Length (vertical) versus largest width (horizontal) of the lower dentition of *Conohyus*. 1 *Conohyus simorrensis goeriachensis* from Göriach; 2 *Conohyus simorrensis goeriachensis* from Puente de Vallecas; 3 *Conohyus simorrensis simorrensis* from Le Fousseret; 4 *Conohyus simorrensis simorrensis* from Mira; 5 *Conohyus ebroensis* from El Buste; 6 *Conohyus ebroensis* from Fonte do Pinheiro.

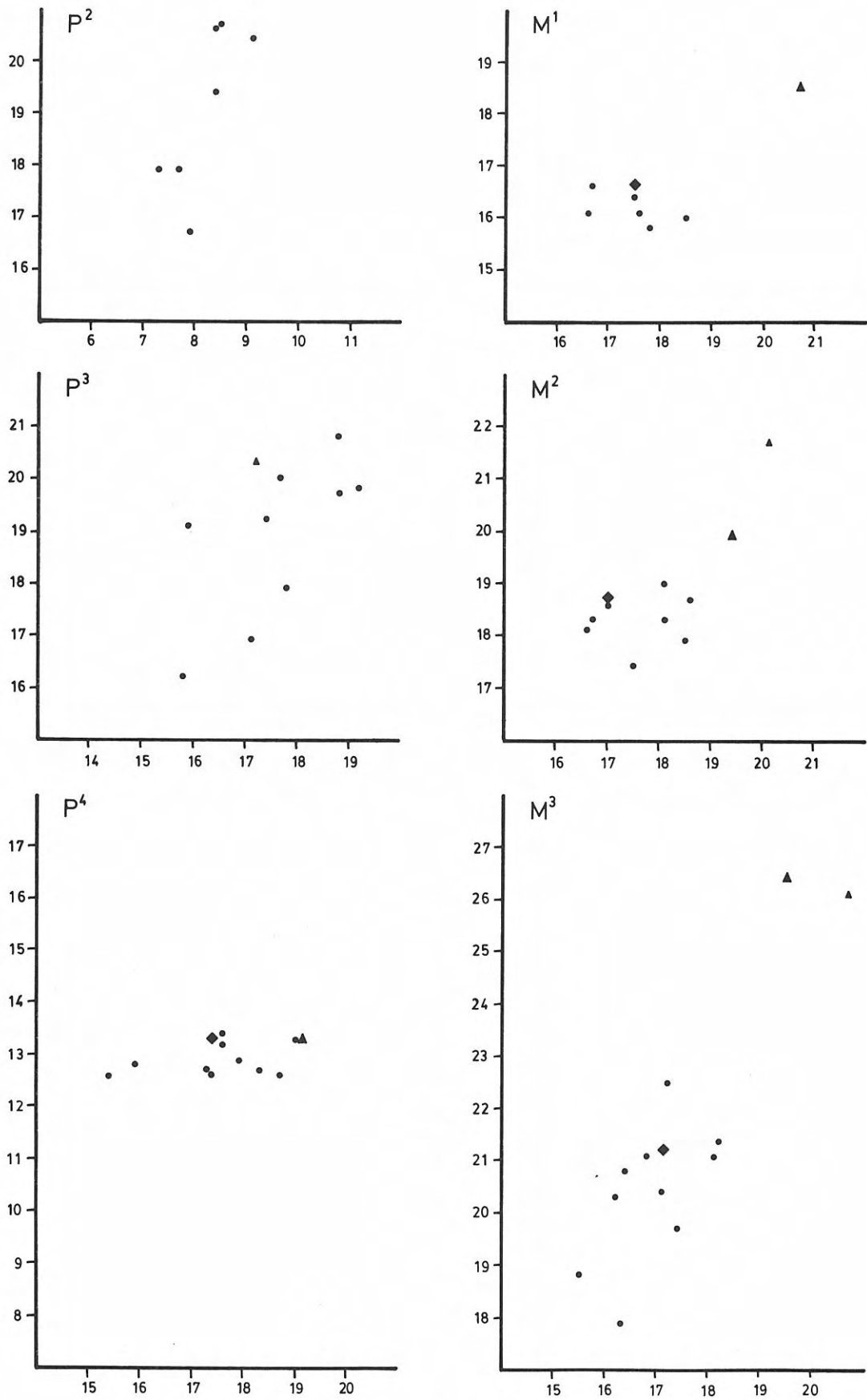


Figure 4. Length (vertical) and greatest width (horizontal) of the Upper dentition of *Conohyus*. Legend as in Figure 3.

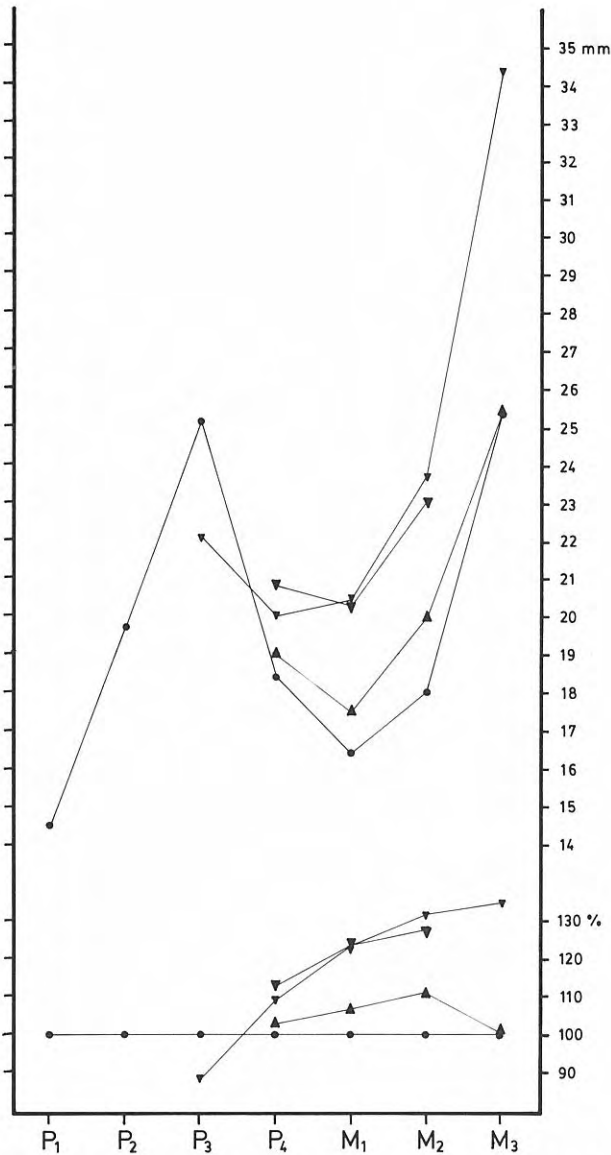


Figure 5. Lengths of the lower cheek teeth of *Conohyus* in millimetres and in percentages of the Göriach material. The values of *C. simorrensis goeriachensis* are the means of the population. Legend as in Figure 3.

are in a good state of conservation, but the bones are compressed, so that in some cases the right and left mandible are pressed against each other. For this reason the width of some of the teeth cannot be measured, or can be given only approximately. Table 3 also contains the measurements of the material from Le Fousseret, El Buste and Fonte do Pinheiro. In the case of the palate from Le Fousseret the measurements of P₃ - M₁ on the right side are given and the remaining values are for the left side. When I studied that material I was still in the habit of measuring only the greatest width of a tooth. For this reason only one measurement of the width of a tooth is given for the material from Le Fousseret.

Figures 4 and 3 are diagrams of length versus largest width. The abundant material from Göriach

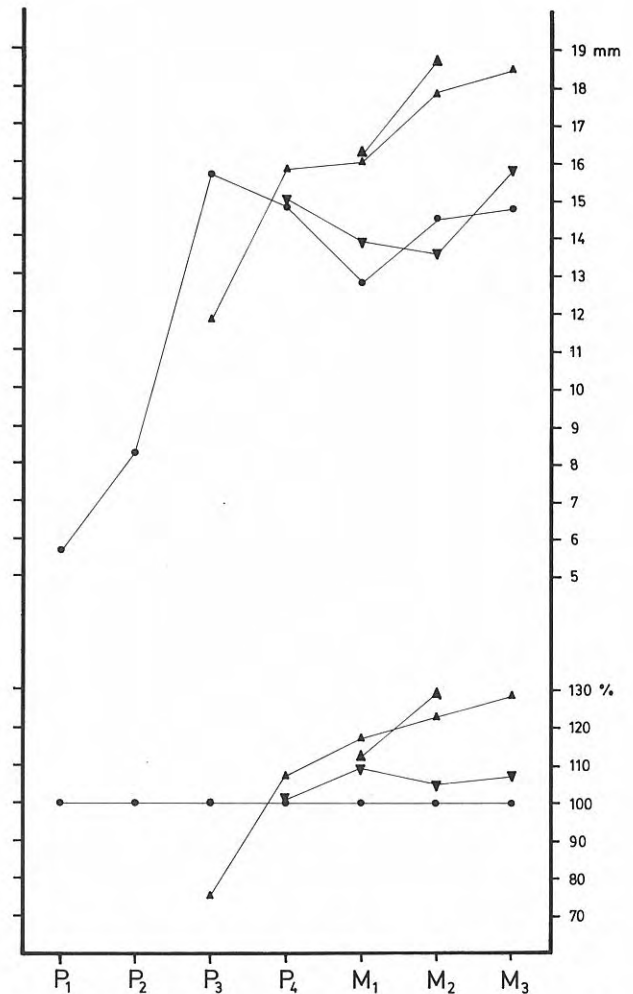


Figure 6. Largest widths of the lower cheek teeth of *Conohyus* in millimetres and in percentages of the Göriach material. The values for *C. simorrensis goeriachensis* are the means of the population. Legend as in Figure 3.

serves as a standard for the comparison. The lower teeth from Le Fousseret are large, but not in all cases are they larger than those from Göriach. The upper molars from Le Fousseret are all clearly larger; the last premolar is about the same size as the largest from Göriach and the P₃ is just about as long, but much narrower. The difference in the length of the longest M₃ from Göriach and the M₃ from Le Fousseret is nearly as much as the difference in the length of the shortest and the longest M₃ from Göriach. The palate from Le Fousseret seems to be from a large individual of a population, whereas the mandible is from a small individual of that population. The P₃ of *C. ebroensis* is smaller than the P₃ from Göriach, whereas the last premolar is as long as the longest premolar from Göriach and all molars of *C. ebroensis* are clearly larger. The molars of *C. ebroensis* are very much larger, than the molars in the material from Le Fousseret.

In Table 3 the means of the measurements from Göriach are compared with the measurements of the material from the other localities. The Göriach

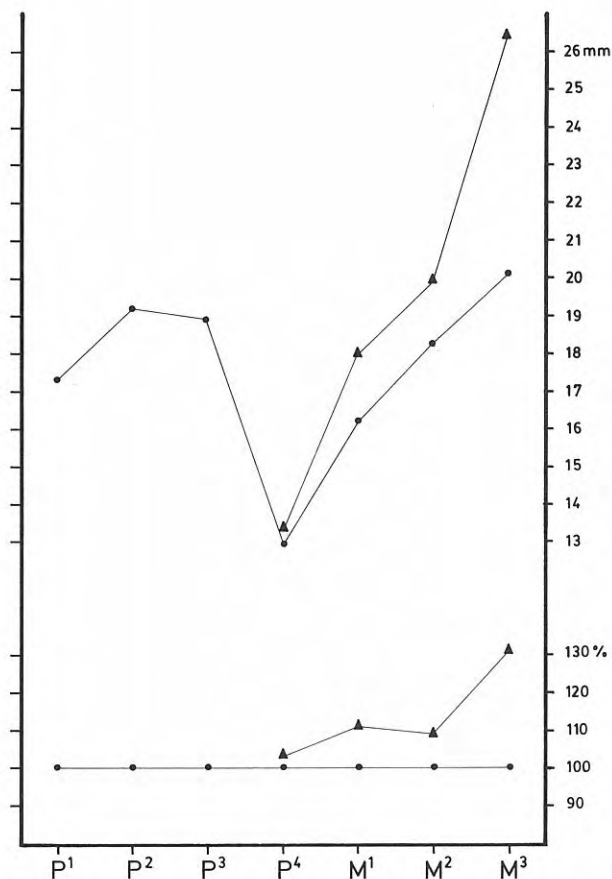


Figure 7. Lengths of the upper cheek teeth of *Conohyus* in millimetres and in percentages of the Göriach material. The values for *C. simorrensis goeriachensis* are the means of the population. Legend as in Figure 3.

values are taken as 100% and for each tooth the other values are expressed as a percentage. In the same way the material from Le Fousseret is taken as a standard for *C. ebroensis*. In Figures 5 to 8 the absolute values and the percentages are graphically compared. There is a strong size increase in the distal direction in the upper tooth row from Le Fousseret compared to the mean values of each type of tooth in the Göriach population. The measurements of the mandible from Le Fousseret are slightly greater than the means from Göriach. The mandibles of *C. ebroensis* show a marked relative size increase distally; the P3 is even small, but the molars are much enlarged. *C. ebroensis* is large, even compared to the material from Le Fousseret, the differences in the lower cheek teeth being larger than the differences between the upper cheek teeth of the material of Le Fousseret and Göriach.

There are three forms with increasing size; the size increase is greatest distally, whereas the P3 may even reduce in size.

DISCUSSION

Material from Mira (stored in the Instituto de

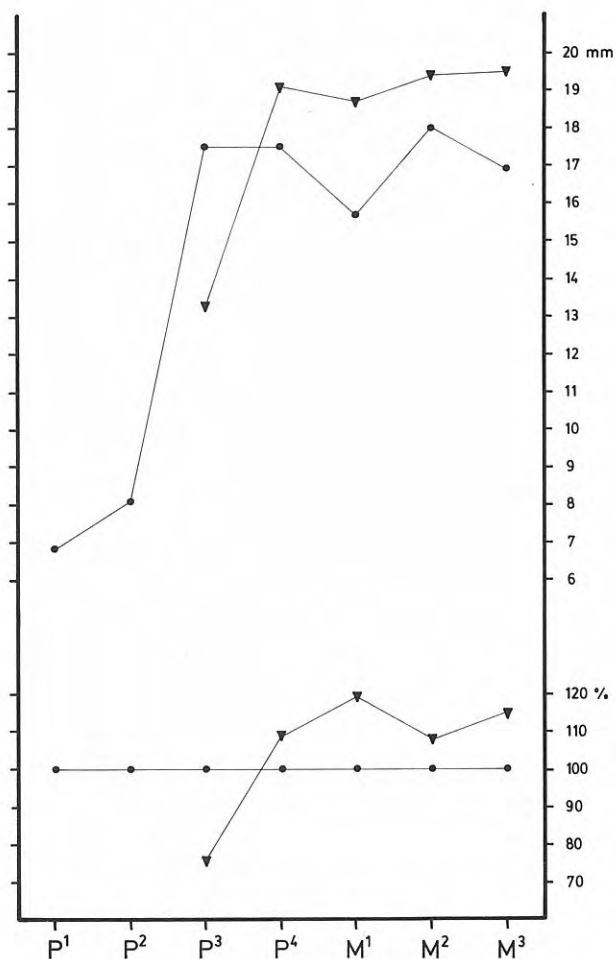


Figure 8. Largest widths of the upper cheek teeth of *Conohyus* in millimetres and in percentages of the Göriach material. The values for *C. simorrensis goeriachensis* are the means of the population. Legend as in Figure 3.

Paleontología, Sabadell) is almost the same size as the material from Le Fousseret (see Figures 1, 3 & 4). Mira is currently thought to be MN 5.

The measurements of the Göriach material are similar to those of the material from Puente Vallecas (Colección Rotondo), see Figures 4 and 3 (my measurements). This locality is dated MN 5. Part of the material is figured by Morales & Soria (1985). Also a P3 from Hommes, a locality that is dated MN 5, has measurements like the Göriach material (Ginsburg, 1977).

Göriach is currently considered to be MN 6 (Mein 1975, Ginsburg 1986). It was thought that in Styria *Conohyus* replaced *Hyotherium* (Mottl, 1970). This is one of the reasons why Göriach is dated younger than Seegraben (Leoben) which is dated MN 5 (Mein, op cit.). But *Hyotherium soemmeringi* does not only occur in Seegraben but also in Göriach. The I1 figured by Thenius (1956, fig. 20 c & d) is not *Conohyus*, but *H. soemmeringi*; in addition, there are two I2 of this species in the Joanneum. We also know that *Conohyus* occurs in MN 5, so this reason to date Göriach younger than Seegraben is not valid.

Other reasons for placing Göriach in MN 6 are the presence of *Pliopithecus anticius*, *Hemicyon sansaniensis* and *Plithocyon armagnacensis* in Göriach. *Pliopithecus piveteaui*, *H. cf. sansaniensis* or *H. stehlini* and *P. cf. armagnacensis* are present in MN 5 (Ginsburg 1986 & pers. comm.). (Fig. 2).

Eotragus increases in size from *E. artenensis* to *E. sansaniensis*. The *Eotragus* material from Göriach has the same size as the *Eotragus* material from Seegraben. On average the material is intermediate in size between *E. artenensis* and *E. sansaniensis*. From Göriach I studied several mandibles and maxillae in the Joanneum and from Sansan I studied approximately 70 mandibles and many maxillas in

the Muséum national d'Histoire naturelle (size variation in approximately 70 horn cores from Sansan is much greater than size variation in roughly the same number of teeth from Sansan; it is better to use teeth).

The *Hyotherium* I1 from Göriach, that was mentioned before, has a very small labio-distal cusplet, like other *Hyotherium* incisors from MN 4b and MN 5. In MN 6 this cusplet is bigger on average as is shown by the abundant Sandelzhausen material. Variation in the size is wide, and small cusps like those of MN 5 may occur. So the *Hyotherium* I1 indicates that Göriach more probably is MN 5 than MN 6, although it may be MN 6.

Eotragus, *Conohyus* and *Hyotherium* indicate that Göriach should be placed in MN 5 (or at least that Göriach is older than Sansan, Mira and Sandelzhausen). But *Pliopithecus*, *Hemicyon* and *Plithocyon* indicate that Göriach should be placed in MN 6 (or at least that Göriach is younger than faunas with *P. piveteaui*, *H. cf. sansaniensis* and *P. cf. armagnacensis*). In the first case large amounts of material are used for comparison, which increases the reliability.

If Göriach is dated MN 5 and Mira MN 6 we arrive at a model in which the Göriach form is typical for MN 5, the larger Le Fousseret form is typical for MN 6 and MN 7 and the still larger *C. ebroensis* is typical for MN 8 (El Buste) and MN 9 (Fonte do Pinheiro).

In this lineage the tetraconodontine specialization (enlarged P3 and P4) becomes less pronounced. All Tetraconodontinae are thought to be descendants of *Conohyus*. Fig. 9 shows that most other Tetraconodontinae have less enlarged premolars than *Conohyus* from Göriach, which is one of the oldest and one of the most primitive tetraconodontines. ("*Conohyus*" *betpakdalensis* Trofimov, 1946 is not a Tetraconodontine: it might be the same species as *Xenohyus venitor* Ginsburg, 1980.)

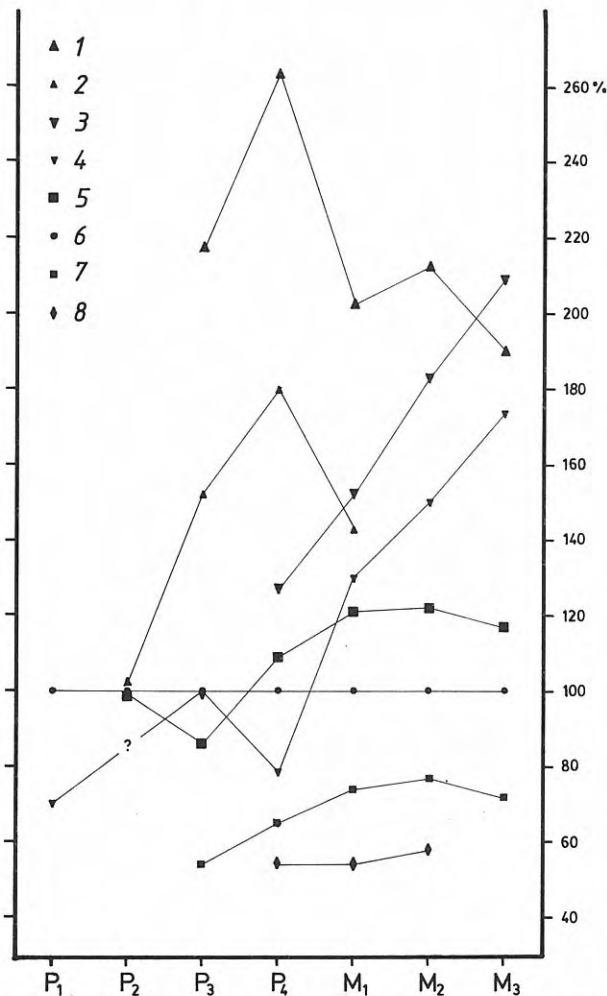
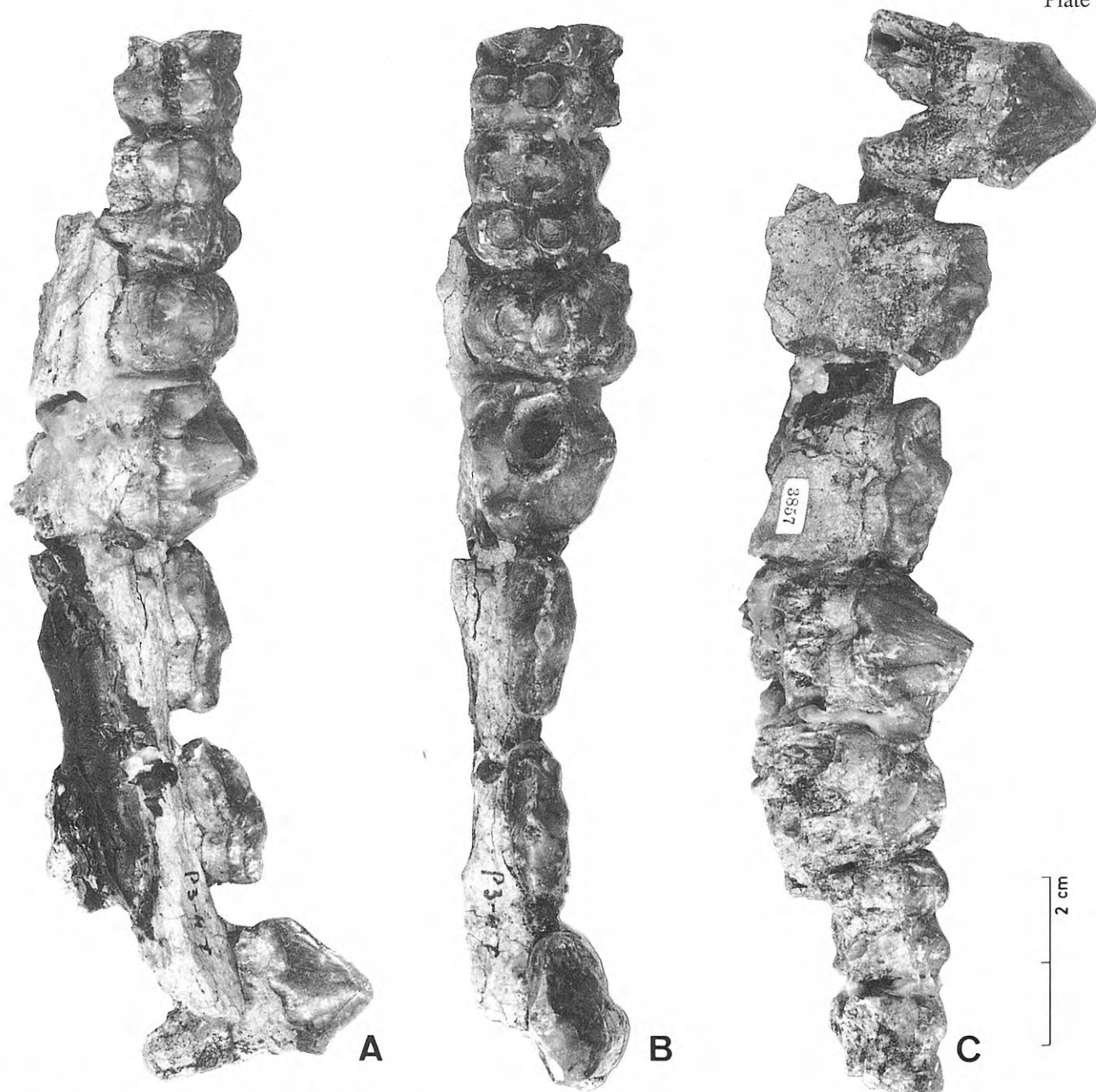


Figure 9. The lengths of the cheek teeth of Tetraconodontinae, expressed as a percentage of the mean of the Göriach population. 1 *Sivachoerus prior* Pilgrim, 1926, Indian Museum B 697; 2 *Tetraconodon magnus* Falconer, 1868, Indian Museum B 828; 3 *Sivachoerus/Nyanzachoerus* from Sahabi, University of Rome; *Tetraconodon minor* Pilgrim, 1926, Indian Museum B 771; *Conohyus steineheimensis* (Fraas, 1870) from Castell de Barberà, Instituto de Paleontología, Sabadell; 6 *C. simorrensis goeriachensis* nov. subsp., mean of the Göriach population; 7 *Parachleuastochoerus crusafontii* Golpe, 1972, Instituto de Paleontología Sabadell IPS 1019; *Lophochoerus nagrii* Pilgrim, 1926, Indian Museum B 693.

THE GÖRIACH FORM

The form from El Buste and Fonte do Pinheiro has been named *C. ebroensis* and the form of Le Fousseret has been named *C. simorrensis*. Since the Göriach form is really different from the typical *C. simorrensis* it should also be given a name. I do not think that differences are great enough to erect a new species, besides it is not practical: an isolated mandible with measurements like that from Le Fousseret could not be assigned to a species. (The bigger the samples the smaller the problem.) Another reason is that in all probability the material under consideration is one lineage: this will be made clear in systematics if only one species name is used.

ORDER ARTIODACTYLA Owen, 1849
Family Suidae Gray, 1821
Subfamily Tetraconodontinae Simpson, 1945
Genus *Conohyus* Pilgrim, 1925



REVISTA ESPAÑOLA DE PALEONTOLOGÍA, 4. 1989.

Plate I. *Conohyus simorrensis goeriachensis* nov. subsp. Holotype. No. 3857, stored in the Joanneum, Graz. Right maxilla, A: lingual view, B: occlusal view, C: labial view. (Photos by J. v. d. Made.)

Conohyus simorrensis (Lartet, 1851)

Conohyus simorrensis goeriachensis nov. subsp.

Plate I

Derivatio nominis: the new subspecies is based on material from Göriach.

Locus typicus: Göriach in Austria.

Stratum typicum: Middle Aragonian (MN 5)

Material

Holotype: a right maxilla with number 3857 which is stored in the Joanneum in Graz.

Paratypes: the pieces mentioned in tables 1 and 2.

Diagnosis

Conohyus simorrensis with large premolars and molars that are smaller on average than in *C. simorrensis*

Description

The holotype has a canine, all premolars and the first two molars. The canine shows that it is a female. It is premolariform and has two roots. The crown is very low and elongated. The first two premolars have long, narrow, low crowns, as is nor-

mal in *Conohyus*. The last two premolars are very wide. The P3 has one wide main cusp, there is a wide postero - lingual cingulum which does not bear a cusp. The P4 has one main labial cusp, although posteriorly a second smaller one is indicated by the enamel that curves inward; this cusplet is not individualized. The molars have a simple structure and are wide, as is common in primitive Suidae.

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