

THE PIG *CONOHYUS SIMORRENSIS* FROM THE UPPER ARAGONIAN OF ALHAMBRA, MADRID, AND A REVIEW OF THE DISTRIBUTION OF EUROPEAN *CONOHYUS*

J. van der Made* and J. Morales*

ABSTRACT

The suid remains from Alhambra (Madrid, late Aragonian, Middle Miocene; MN6, zone F) are described and assigned to *Conohyus simorrensis*. *Conohyus* is well known in Spain from late MN5, or zone E, MN7+8, or zone G, and MN9. The material from Alhambra fills the gap in the Iberian record. The Iberian record shows that *Conohyus* became larger, with relatively larger posterior molars and with reduced premolars. This evolution occurred in a large area that extends from western Europe to Anatolia. We present an overview of the European and Anatolian localities with *Conohyus*.

Key words: *Conohyus*, *Tetraconodontinae*, *Suidae*, *Aragonian*, *Miocene*, *biogeography*.

RESUMEN

Los restos de suido de Alhambra (Madrid, Aragoniense Tardío, Mioceno Medio, MN6, zona F) son descritos y asignados a *Conohyus simorrensis*. Este género se conoce bien en España de la unidad MN5, o zona E, y MN7+8, o zona G, y en MN9. El material de Alhambra llena un hiato en el registro ibérico. La evolución de *Conohyus* ocurrió en una vasta área que se extiende de Europa occidental hasta Anatolia. Presentamos un sumario de yacimientos europeos y turcos con *Conohyus*.

Palabras clave: *Conohyus*, *Tetraconodontinae*, *Suidae*, *Aragoniense*, *Mioceno*, *biogeografía*.

Introduction

The locality of Alhambra was discovered in 1991 by the geologist Javier González when a new street was constructed near to the banks of the Manzanares river in the La Latina quarter in the center of Madrid. The locality was excavated during two campaigns, the first one in november 1991 was directed by Laureano Merino and Susana Consuegra and the second one in november 1994 was directed by Esther Herráez and Susana Consuegra (Herráez *et al.*, 2000).

The fossils were found arcose sandy clays, corresponding to the middle levels of the Unidad Superior (upper unit) of the Madrid basin (Peláez-Campomanes *et al.*, 2000).

The faunal association is typical of the earlier part of the Upper Aragonian, biozone F (Soria *et al.*, 2000) and includes:

Reptilia

Ophisaurus sp.
Chelonia indet.

Aves

Aves indet.

Mammalia

Soricinae indet.

Galerix sp.

Pseudaelurus quadridentatus

Hemicyoninae indet.

Lagopsis verus

Democricetodon darocensis

Megacricetodon gersii

Megacricetodon rafaeli

Armantomys tricristatus

Heteroxerus rubricati

Heteroxerus grivensis

Gomphotherium angustidens

Anchitherium cursor

Alicornops simorrensis

Conohyus simorrensis

Hispanomeryx aragonensis

Heteroprox moralesi

Bovidae indet.

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

Conohyus is a suid with enlarged premolars, which is typical for the Tetraconodontinae, to which it belongs. It is assumed to have evolved from the Indian form *Sivachoerus sindiense* when it spread into Europe (Van der Made, 1999). In west and central Europe, it appeared late in MN5 or zone E and is becoming known from an increasing number of localities of this age. *Conohyus* became larger, increased the size of its posterior molars and reduced the size of its premolars (Van der Made, 1989, 1998, 1999; Van der Made & Ribot, 1999; Mazo *et al.*, 1998). During the Vallesian, the genus spread from Europe to the Indian Subcontinent and Africa and went extinct in Europe. *Conohyus* is becoming known from an increasing number of European localities, especially from late MN5, or zone E and from MN7+8, or zone G. There are relatively few MN6, or zone F, localities. The locality of Alhambra is of this age and thus increases our knowledge of a less well known section of this lineage.

Methods and material

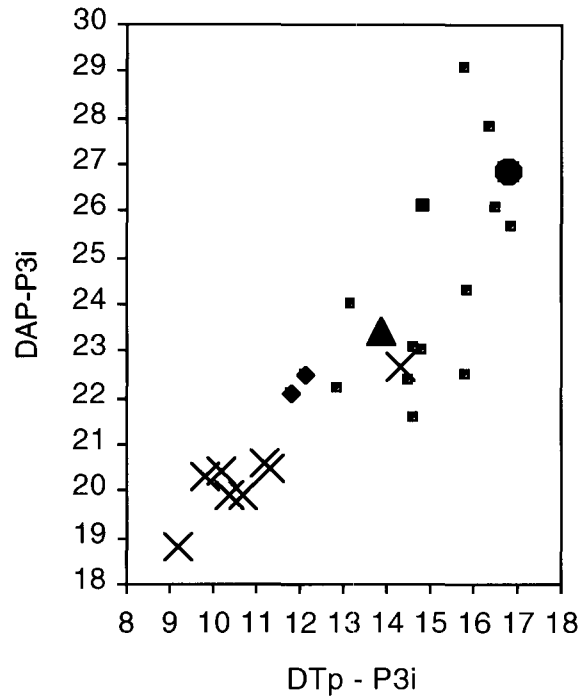
Here we use the MN units (Mein, 1975; De Bruijn *et al.*, 1992) and the zonation of the Aragonian (zones B-G; Daams *et al.*, 1999).

The classification of the Tetraconodontinae is after Van der Made (1999) and the nomenclature of the teeth and measurements are after Van der Made (1996). All measurements in this paper are in mm. Abbreviations:

- DAP = antero-posterior diametre or length.
- DT = transverse diametre or width.
- DTa = DT of the anterior lobe.
- DTp = DT of the posterior lobe.
- Ha or H1 = Height measured at the first lobe of a tooth.
- Hp or H2 = Height measured at the second lobe of a tooth.

The material studied is stored in the following institutions:
IGGML = Institut für Geowissenschaften / Geologie der Montan Universität Leoben.

- IPS = Institut Paleontologic M. Crusafont, Sabadell.
- IPUW = Institut für Paläontologie der Universität, Wien.
- LM = Geological Museum of Lisbon.
- MNCN = Museo Nacional de Ciencias Naturales, Madrid.
- MNHN = Muséum National d'Histoire Naturelle, Paris.
- MGL = Muséum Guimet, Lyon.
- MGPUSB = Museo di Geologia e Paleontologia, Università degli Studi di Bologna.
- MPZ = Museo Paleontológico de la Universidad de Zaragoza.
- MTA = Maden Tetkik ve Arama (geological survey of Turkey, Ankara).
- NMB = Naturhistorisches Museum Basel.
- NMW = Naturhistorisches Museum, Wien.
- PDTFAU = Palaeoantropoloji, Dil ve Tarih Coğrafya Fakültesi, Ankara Üniversitesi.
- PIMUZ = Paläontologisches Institut und Museum der Universität, Zürich.
- SLJG = Steiermärkisches Landesmuseum Joanneum, Graz.
- UCM = Université Claude Bernard, Lyon.



- *Conohyus*
- ▲ Alhambra
- ◆ Fonte do Pinheiro
- Tutzing
- Hommes
- × *P. steinheimensis*

Fig. 1.—Bivariate plot of the P₃ of *Conohyus* and *Parachleus-tochoerus steinheimensis*. Length (DAP) against width (DT). *Conohyus* from Göriach (SLJG, NMW; data given by Van der Made, 1998), Puente de Vallecas (cast in MNCN), Villefranche d'Astarac (cast in MNHN), Paşalar (PDTFAU), Klein Hadersdorf (IPUW), Mira (IPS), St. Gaudens? (cast in MGPUSB), Fonte do Pinheiro (LM), Hommes (Ginsburg, 1989) and Alhambra (MNCN). *Parachleus-tochoerus steinheimensis* is from La Grive (old collections in MGL).

Description

- Family SUIDAE Gray, 1821
- Subfamily TETRACONODONTINAE Lydekker, 1876
- Tribe NYANZACHOERINI Van der Made, 1999
- Genus *Conohyus* Pilgrim, 1926
- Species *Conohyus simorreensis* (Lartet, 1851)

Material

- Tu534 - right P₃ (DAP = 23.4; DTa = 11.1; DTp = 13.9).
 - Tu863 - left M₂ (DAP = 20.1; DTa = 14.7; DTp = 13.9; Ha = 11.7; Hp = 10.0).
 - sn - right M₂ (DAP = 19.4; DTa = 14.9; DTp = 13.6; Ha = 11.2; DTp = 9.8).
- (The prefix Tu stands for Tüneles, a name initially applied for the locality.)

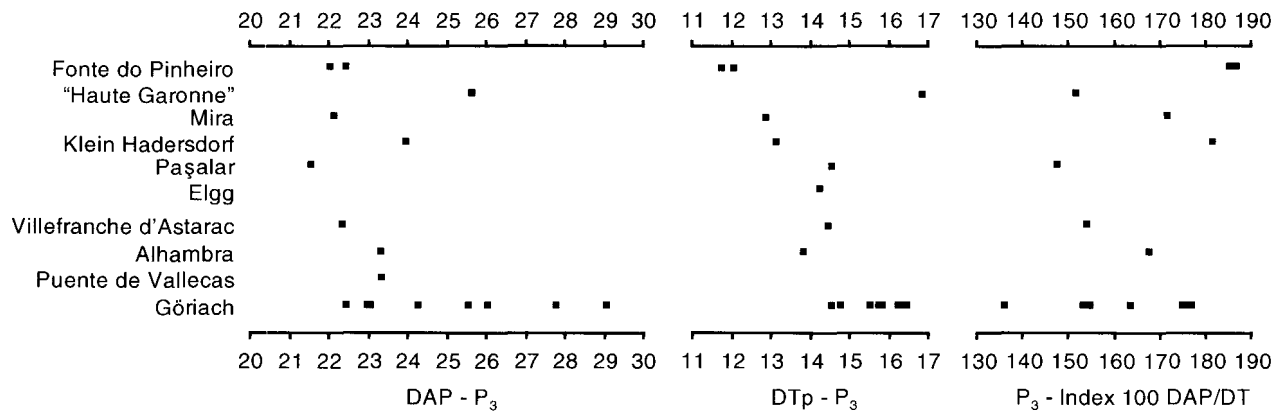


Fig. 2.—The length (DAP), width of the posterior lobe (DTp) and index (100 DAP/DTp) of the P₃ in *Conohyus simorrensis*. The localities are in approximate order from old to young: Göriach (SLJG, NMW, NMB; data given by Van der Made, 1998), Puente de Vallecás (cast in MNCN), Alhambra (MNCN), Villefranche d'Astarac (cast in MNHN), Elgg (NMB), Paşalar (PDTFAU), Klein Hadersdorf (IPUW), Mira (IPS), St. Gaudens? (cast in MGPUSB), Fonte do Pinheiro (LM).

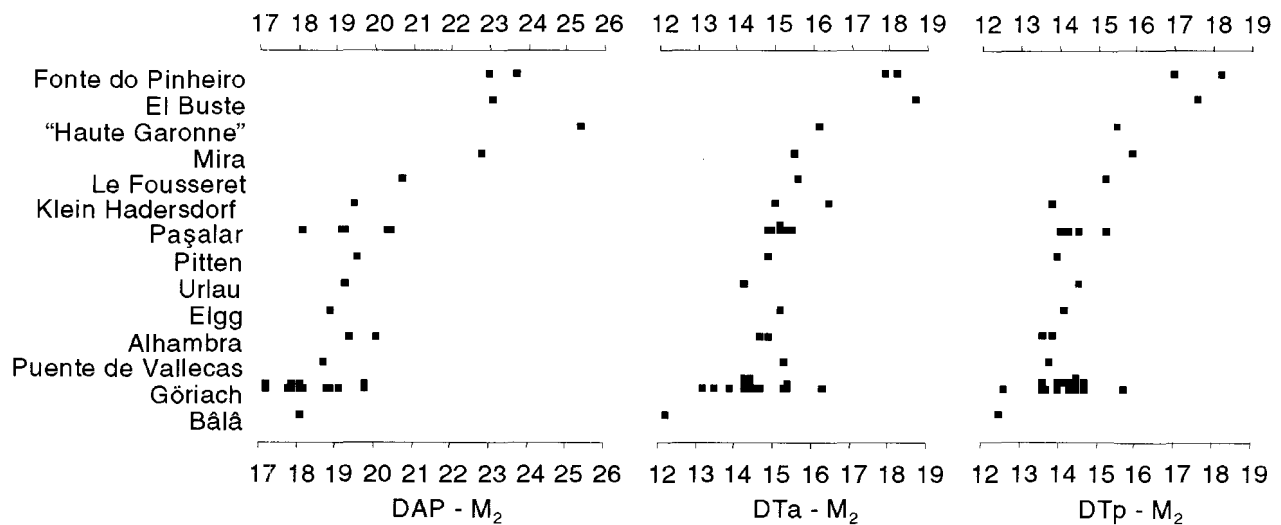


Fig. 3.—The length (DAP) and width of the first (DTa) and second (DTp) lobes of the second lower molar in *Conohyus*. The localities are in approximate order from old to young: Bâlâ (MTA), Göriach (SLJG, NMW, IGGML, NMB; data given by Van der Made, 1998), Puente de Vallecás (cast in MNCN), Alhambra (MNCN), Elgg (NMB), Paşalar (PDTFAU), Klein Hadersdorf (IPUW), Le Fousseret (MNHN), Mira (IPS), St. Gaudens? (cast in MGPUSB), El Buste (MPZ), Fonte do Pinheiro (LM).

Description and comparison

The P₃ (Plate 1, fig. 3) is a massive tooth with a high protoconid and protopre- and protopostcristids that end very low. There are two posterior roots, which is common in the Tetraconodontinae, but not in other Suidae. Teeth of this size and morphology are typical of the Tetraconodontinae. In Europe, *Conohyus* and *Parachleuastochoerus steinheimensis* have P₃ of about this size. The P₃ of *P. steinheimensis* tends to be smaller than that of *Conohyus*, but in the sample from La Grive there is one abnormally large specimen (fig. 1). The specimen from Alhambra is even larger than this largest specimen from La Grive and is well within the ranges of *Conohyus*. Within this

genus there is a tendency to reduce this tooth (fig. 2). This reduction seems to be clearest in the width. The variation in the length is bigger, but also seems to reduce. However, not all specimens fit this tendency well and apparently, reduction is accompanied by an increase in variability. If there is a tendency in the length-width index, the tooth becomes more elongate. None of the values of the Alhambra specimen is indicative for a very old, nor for a very young age.

Both M₂ (Plate 1, figs. 1 & 2) are wide bunodont molars with low crowns. Molars of Suinae tend to be much more elongate. The specimens have the size of the M₂ of *Conohyus simorrensis* and *Parachleuastochoerus steinheimensis* or of the M₁ of the latest Aragonian and Vallesian *Conohyus*. Because of the tendencies in *Conohyus* in increase in the size of the posterior

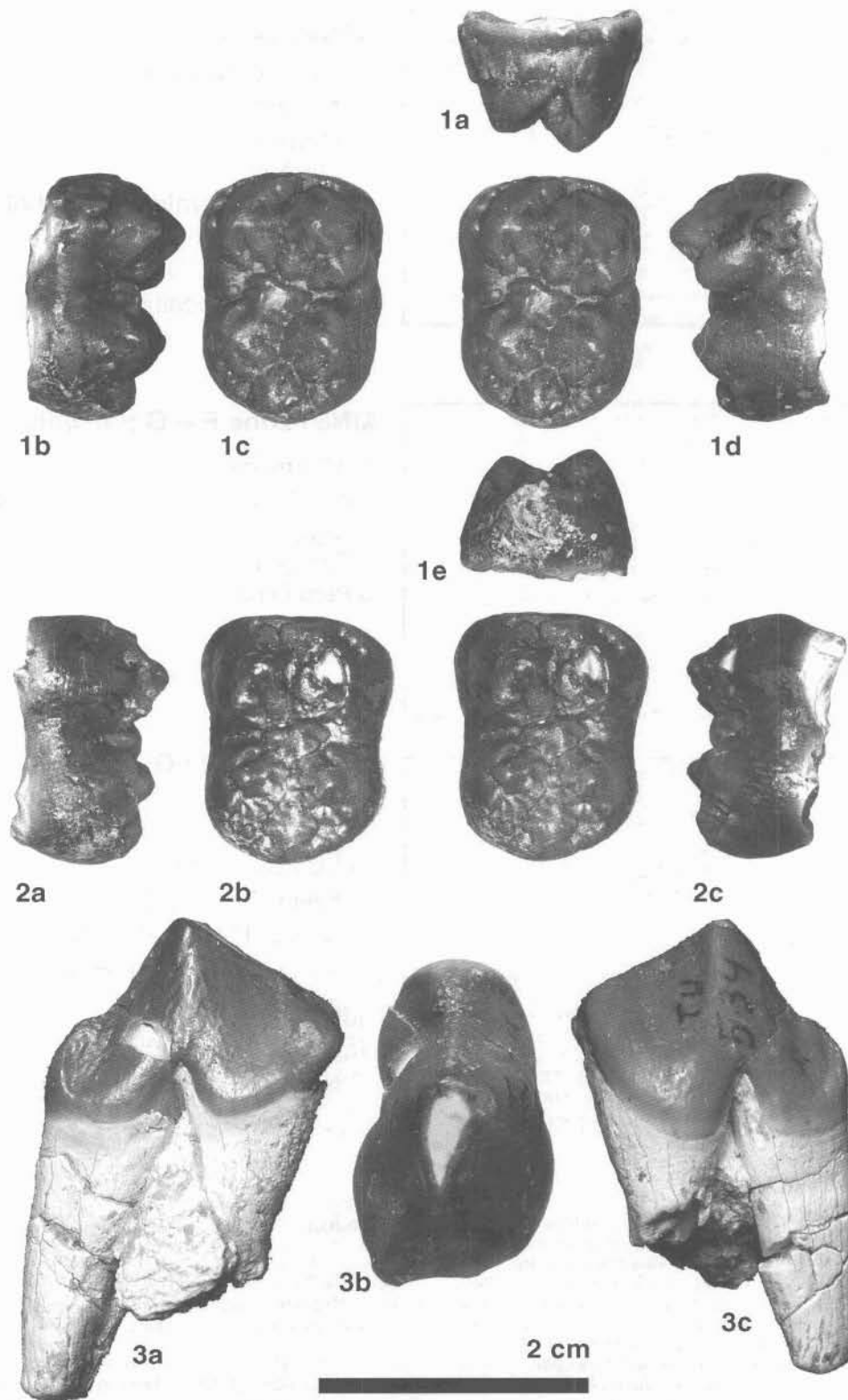
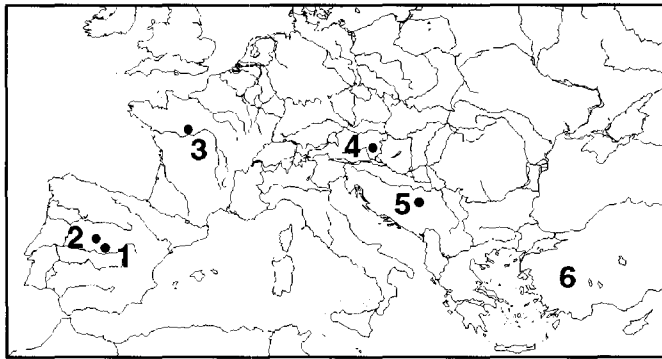
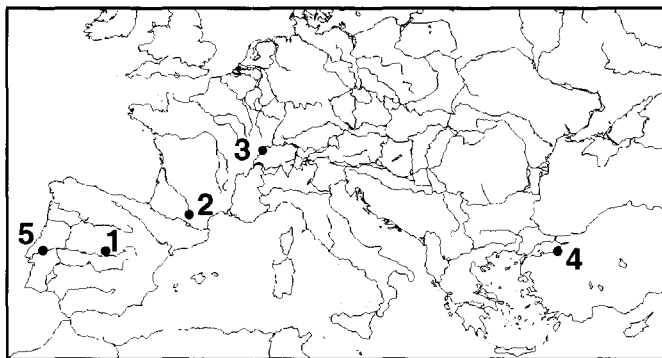


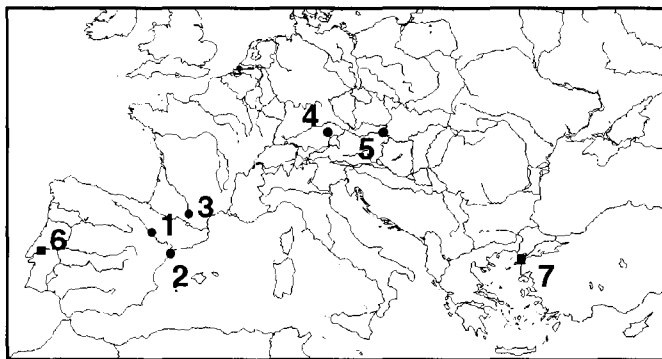
Plate I.—(1) Tu863, left M_2 : *a*) anterior view, *b*) buccal view, *c*) occlusal view, stereopair, *d*) lingual view, *e*) posterior view. (2) right M_2 : *a*) lingual view, *b*) occlusal view, stereopair, *c*) buccal view. (3) Tu534, right P_3 : *a*) lingual view, *b*) occlusal view, *c*) buccal view.

**MN5 / zone E**

- 1 Puente de Vallecas, Somosaguas
- 2 Montejo de la Vega
- 3 Hommes, Channay
- 4 Göriach
- 4 Au, St. Oswald, Rosenthal (MN5/6?)
- 5 Mala Miliva (zone D/E?)
- 6 Bâlâ (zone D/E? - exact geographic position?)

**MN6 / zone F + G partially**

- 1 Alhambra
- 2 Simorre, Villefranche, Sansan
- 3 Elgg
- 4 Paşalar
- 5 Pero Filho

**MN7+8 / zone G**

- 1 El Buste
- 2 Mira
- 3 Le Fousseret
- 4 Klein Eisenbach
- 4 Urlau, Tutzing (MN 6/7?)
- 5 Klein Hadersdorf, Pitten

MN9

- 6 Fonte do Pinheiro
- 7 Nuri Yamut (?)

Fig. 4.—Geographical position of the European and Anatolian localities with *Conohyus*.

molars, and decrease in size of the premolars, and the large size of the P_3 from Alhambra, it is more likely, that the molars are M_2 than M_1 . The M_2 tend to have relatively thicker enamel than M_1 , and absolutely much thicker enamel (Van der Made, 1996). However, in the specimens from Alhambra, enamel thickness could not be measured in the standard way, since the teeth are not worn. It is possible that there are differences in crown height between M_1 and M_2 , but this character has not yet been studied in a detailed way. In *Conohyus*, the molars increased in size (Van der Made, 1989, 1998, fig. 9, 1999, figs. 12-14; Van der Made & Ribot, 1999, fig. 6; Mazo *et al.*, 1998, figs. 10-11). The molars from Alhambra fit well with the M_2 of *Conohyus simorreensis* (fig. 3).

Discussion

As appears from the description, the material from Alhambra fits best *Conohyus simorreensis* and in particular the early, but not very early stages. Alhambra is placed in MN6, or zone F, what is consistent with the aparent stage of evolution indicated by the fossils. The area with the most “complete” record of *Conohyus* is the Iberian Peninsula, where the genus is known from MN5, or zone E, MN7+8,

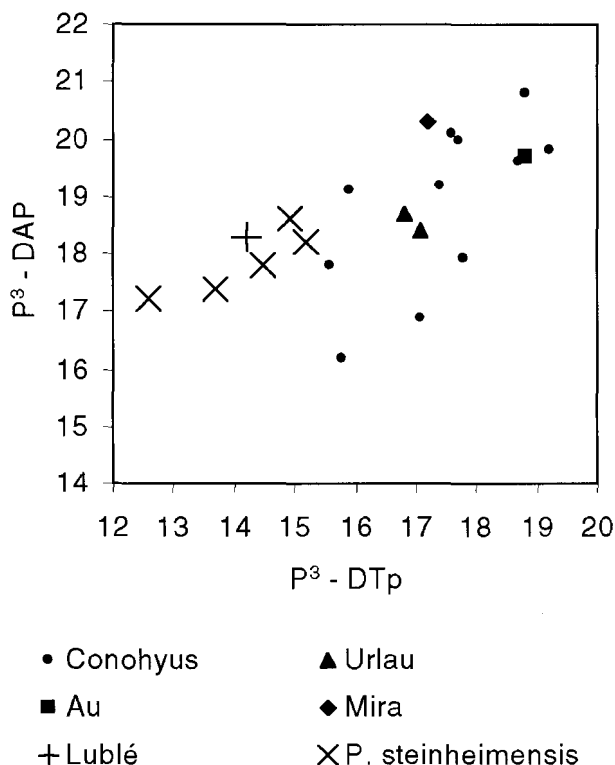


Fig. 5.—Bivariate plot of the P³ of *Conohyus* and *Parachleuastochoerus steinheimensis*. Length (DAP) against width (DT). *Conohyus* from Göriach (SLJG, IPUW; data given by Van der Made, 1998), Urlaub (SMNS), Elgg (PIMUZ), Au (SLJG), Paşalar (PIMUZ) and Mira (IPS). *Parachleuastochoerus steinheimensis* is from La Grive (old collections in MGL) and Lublé (data from Ginsburg, 1987).

or zone G, and MN 9. The remains from Alhambra fill a gap in the record of the genus in the Iberian Peninsula.

Review of the European and Anatolian *Conohyus*

Though the Tetraconodontinae have a long range from the earliest Middle Miocene to the end of the Pliocene, their presence in Europe is restricted to the Middle and earliest Late Miocene (late MN5 - MN9). They are represented with by two genera, *Conohyus*, with one lineage and two species, and *Parachleuastochoerus*, with two lineages and three species (Van der Made, 1990b, 1999). The *Conohyus* lineage starts with *C. simorreensis*, which evolved into the larger *C. giganteus* (= *C. ebroensis*). *Parachleuastochoerus* has one lineage of small size (*P. huenermanni* - *P. crusafonti*) and one of larger size (*P. steinheimensis*). *Conohyus simorreensis* and *Parachleuas-*

tochoerus steinheimensis are of similar size, differing mainly in the relative size of their premolars, those of *Parachleuastochoerus* being smaller. Till relatively recently, *P. steinheimensis* was not considered to be a different species, or a subspecies of *C. simorreensis* (eg. Hünemann, 1968; Thenius, 1952, 1956; Ginsburg, 1980), but Chen (1984) proved them to be different species, and Fortelius *et al.* (1996) transferred "*Conohyus*" *steinheimensis* to *Parachleuastochoerus*. The separation of the two species (and genera) is sometimes difficult and there are localities for which there is no recently published opinion as to which of the two is present.

In Table 1 we list the localities where we believe the presence of *Conohyus* reasonably sure and in Figure 4 we give their approximate geographic positions. The first column in Table 1 gives the name of the locality, occasionally with a question mark, when there is doubt as to the correct name of the locality or presence of *Conohyus*. The second column gives the age of the locality, in terms of MN units or zonations of the Aragonian. The third column gives a reference for the age; sometimes the age (in MN units) is plainly given, but sometimes the age had to be interpreted on the basis of information in that paper, in that case the reference is between brackets. The fourth column indicates the place where we studied or consulted the fossils or casts. The fifth column gives a reference for a paper that describes or figures the material or gives measurements, or a recent paper that indicates the material to be *Conohyus* (and not *P. steinheimensis*).

Material from Urlaub and Tutzing mentioned by Stehlin (1899-1900) is in the range for *Conohyus* (figs. 3 & 5), as well as material from Au in Styria, mentioned by Mottl (1970).

A cast of a mandible with P₃ - M₂ in the MGPUSB is of a large *Conohyus* and is indicated to be from "Haute Garonne". Stehlin (1899-1900, p. 140) mentions this cast and states that the original is in Toulouse and is from Le Fousseret. However, the specimen is very much larger than a specimen from Le Fousseret in the MNHN. Its size suggests that it is late MN7+8 or MN9. Richard (1946) gave an overview of the faunas, and cited *Conohyus* from St. Gaudens. We do not know on what material this citation is based. The cast in the MGPUSB should be from one of these localities. A skull from St. Gaudens-Valentine is the type of "*Sus valentini*" and is placed by Stehlin (1899-1900, p. 139) in "*Hyotherium*" *simorreense*. We do not know this material; it might belong to *Conohyus* or to *Parachleuastochoerus steinheimensis*.

A specimen from Nuri Yamut might represent *Conohyus* or *Sivachoerus* (Van der Made & Tuna, 1999).

Tabla 1.—European and Anatolian localities with *Conohus*.

Locality	Age	Ref. to age	Collection	Description, figures, measurements or citation of taxon
Puente de Vallecas	MN5, E		MNCN	Morales & Soria, 1985; Van der Made, 1990a
Somosaguas	MN5, E	López <i>et al.</i> , 2000	UCM	Van der Made & Salesa, in press
Montejo de la Vega	MN5, E	Mazo <i>et al.</i> , 1998	MNCN	Mazo <i>et al.</i> , 1998
Göriach	MN5, E	Mazo <i>et al.</i> , 1998 Van der Made & Ribot, 1999	SLJG, NMW, NMB, IGGML	Hofmann, 1893; Thenius, 1956; Van der Made, 1989, 1998
Au	MN5/6	(Mottl, 1970)	SLJG	Van der Made, 1998
St. Oswald	MN5/6	(Mottl, 1970)	SLJG	Van der Made, 1998
Rosenthal	MN6/6	(Mottl, 1970)	SLJG	Van der Made, 1998
Pero Filho	MN6	Antunes & Mein, 1977		Antunes & Mein, 1977
Mala Miliva	MN5	De Bruijn <i>et al.</i> , '90 Van der Made, '96		Petronievic, 1967
Bâlâ	MN5	Van der Made, '99	MTA	Pickford & Ertürk, 1979; Van der Made, 1999
Alhambra	MN6, F		MNCN	this paper
Simorre	MN6	(Ginsburg, 1971)	MNHN	Lartet, 1851
Sansan	MN6	Mein, 1990		Ginsburg, 1977
Elgg	MN6	Van der Made & Ribot, 1999		Van der Made, 1999; Van der Made & Ribot, 1999; Kaup, 1859
Pasalar	MN6	Van der Made & Ribot, 1999	PDTFAU, MTA, PIMUZ MNHN	Fortelius & Bernor, 1990; Van der Made, 1999; Van der Made & Ribot, 1999
Villefranche	MN6/7		NMB	Stehlin, 1899-1900
Tutzing	MN6/7		MPZ	Azanza, 1986; Van der Made, 1989, 1999
El Buste	MN7+8	Azanza, 1986	MPZ	Azanza, 1986
?La Ciesma	MN7+8	Azanza, 1986	MPZ	Azanza, 1986
Pichelsberg	MN7+8		BSPHGM	Fortelius <i>et al.</i> , 1996
Mira	MN7+8	(Golpe, 1972)	IPS	Golpe Posse, 1972; Van der Made, 1989, 1999
Le Fousseret	MN7+8	(Ginsburg, 1971)	MNHN	Van der Made, 1989, 1999
"Haute Garonne"	MN7+8		MGPUSB	Stehlin, 1899-1900 (p. 140)
Klein Eisenbach	MN7+8	Mein, 1990	BSPHGM	Fortelius <i>et al.</i> , 1996
Urlau			NMB, SMNS	Stehlin, 1899-1900
Klein Hadersdorf	MN7+8	Van der Made & Ribot, 1999	NMW	Van der Made & Ribot, 1999
Pitten	MN7+8		NMW	Van der Made, 1998
Hombres	MN9	Ginsburg, 1987		Ginsburg, 1977, 1987
?Channay	MN9	Ginsburg, 1987		Ginsburg, 1977, 1987
?Lublé	MN9	Ginsburg, 1987		Ginsburg, 1977, 1987
Fonte do Pinheiro	MN9	Roman, 1907	LM	Van der Made, 1989, 1999
?Nuri Yamut	MN9	Van der Made & Tuna, 1999		Van der Made & Tuna, 1999

Ginsburg (1977) described teeth from three localities in the Faluns de Touraine and assigned them to *Conohyus simorreus*, and believed them to be of a "falun" that is older than Sansan. The teeth would be MN5 in age. However, Ginsburg (1989) described some more material and now thought them to be of the younger "falun à Arca" (MN9). The P_3 from Hommes is much larger than that of *P. steinheimensis* and is even large for *Conohyus* (Fig. 1). The P_4 from Fonte do Pinheiro (MN9) are small (Van der Made, 1989), suggesting a size decrease in this tooth (which would imply that the large specimen from Hommes is not that young), but then the cast from "Haute Garonne" discussed above has also very large premolars. The P_3 from Lublé is narrow, is out of the known range for *Conohyus* and within that of *Parach-*

leuastochoerus steinheimensis (Fig. 5) A partial P^3 from Channay (DTp = 14.4) is also narrow for *Conohyus*. A P^4 from Channay is within the ranges for early *Conohyus* but probably not of the later *Conohyus*, since the genus seems to acquire wider P^4 in evolution (Fig. 6). Two P_4 from Channay are large compared to *P. steinheimensis* and are in the lower range of *Conohyus* (Fig. 7). The specimen from Hommes and some of the specimens from Channay certainly belong to *Conohyus*, while part of the material from Channay and the specimen from Lublé might represent *P. steinheimensis*, or alternatively reduced premolars of late *Conohyus*. This latter option would fit well the mandible from Fonte do Pinheiro. However, no upper tooth row of *Conohyus* of this age is known from Europe.

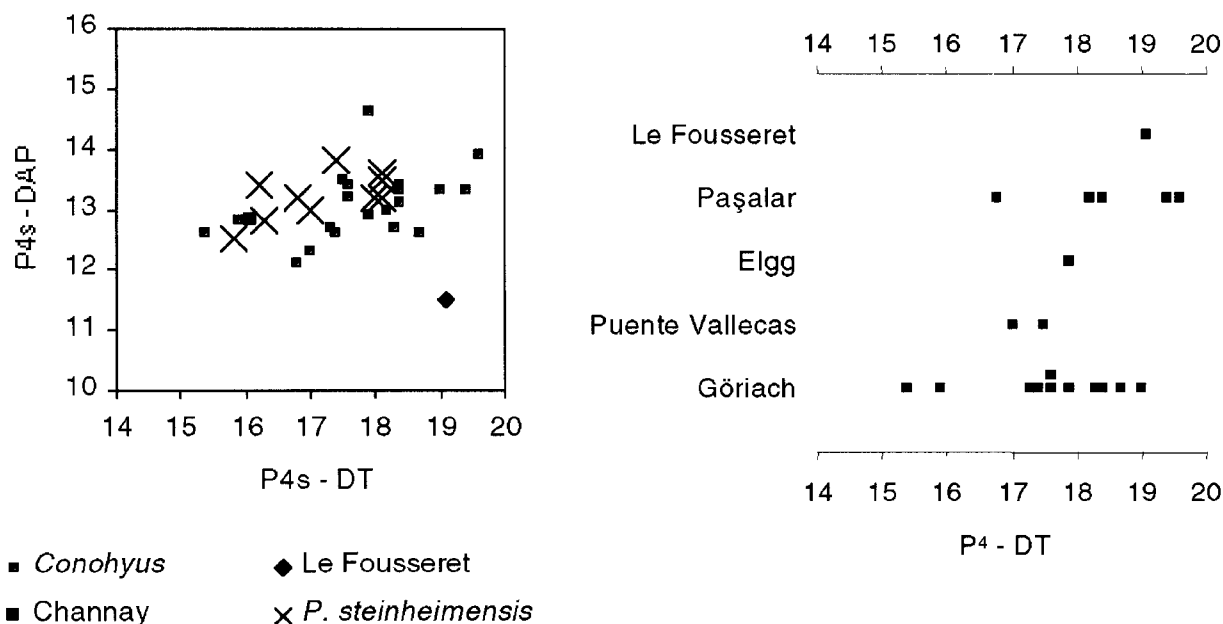


Fig. 6.—The P^4 of *Conohyus* and *Parachleuastochoerus steinheimensis*. Left part: length (DAP) against width (DT), right part: localities in approximate stratigraphical order. *Conohyus* from Göriach (SLJG, NMW, IPW; data given by Van der Made, 1998), Puente de Vallecas (MNCN, IPS), Elgg (PIMUZ), Paşalar (PDTFAU, PIMUZ) and Le Fousseret (MNHN). *Parachleuastochoerus steinheimensis* is from La Grive (old collections in MGL) and Channay (data from Ginsburg, 1987).

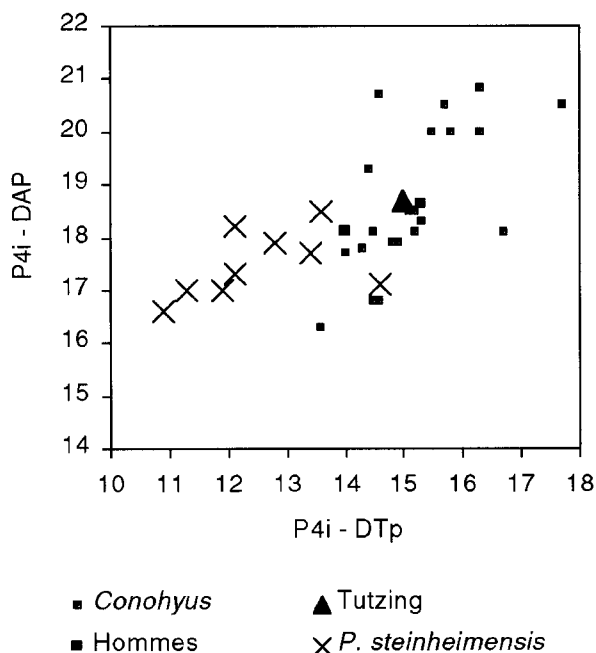


Fig. 7.—Bivariate plot (DAP against DT) of the P_4 of *Conohyus* and *Parachleuastochoerus steinheimensis*. *Conohyus* from Göriach (SLJG, NMW; data given by Van der Made, 1998), Puente de Vallecas (MNCN), Elgg (NMB), Tutzing (NMB), St. Oswald (SLJG), Paşalar (PDTFAU, PIMUZ), Le Fousseret (MNHN), Haute Garonne (MGPU SB), Mira (IPS) and Fonte do Pinheiro (LM). *Parachleuastochoerus steinheimensis* is from La Grive (old collections in MGL). Data from Channay from Ginsburg (1987).

Thenius (1952) assigned two fragmentary teeth from Neudorf Sandberg to *Conohyus simorrensis simorrensis* and a complete molar to *Hyotherium soemmeringi*, but did not give any measurements. There is probably only one species, either belonging to *Conohyus* or to *Parachleuastochoerus*, but with the data available, it is not possible to decide.

Van der Made (1990a, 1997) listed four localities as possibly having *Conohyus*. These localities remain problematic. In one of them, Can Ponsic II, there are two M^3 that are too large for most of the suids that are known from MN9 and too small for *Hippopotamodon antiquus*, but might fit the large MN9 *Conohyus*. However no *Conohyus* M^3 are known from MN9, so this possibility cannot be confirmed. The citation from La Ciesma is based on a single molar.

Conclusions

The suid material from Alhambra is assigned to *Conohyus simorrensis*. This new record from MN6 fills a gap in the Spanish record of the genus, where it is now known from late MN5 (or zone E) to MN9. The Spanish record shows that *Conohyus* became larger, with relatively larger posterior molars and with reduced premolars. This evolution

must have occurred in a large area that extends from western Europe to Anatolia, because the lineage is also recorded with different ages and evolutionary levels from France, Austria and Anatolia.

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