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

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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, Miocene, 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 Herráiz and Susana Consuegra (Herráiz et al., 2000).

The fossils were found arcosandy clays, corresponding to the middle levels of the Unidad Superior (upper unit) of the Madrid basin (Peláez-Campo- manes 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

Ophisaurs sp.

Chelonia indet.

Aves

Aves indet.

Mammalia

Soricinae indet.

Galerix sp.

Pseudaelurus quadridentatus

Hemicyoninae indet.

Lagopsis verus

Democricetodon darocensis

Megacricetodon gersii

Megacricetodon raifeli

Armantomys tricristatus

Heteroxerus rubricati

Heteroxerus grivensis

Gomphotherium angustidens

Anchitherium cursor

Alicornops simorrensis

Conohyus simorrensis

Hispanomeryx aragonensis

Heteropox moralesi

Bovidae indet.

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Conohyus is a suid with enlarged premolars, which is typical for the Tetracodonotinae, 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 Tetracodonotinae 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 diameter or length.
- DT = transverse diameter 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:
- IGGL = Institut für Geowissenschaften / Geologie der Montan Universität Leoben.
- IPS = Institut Paleontologic M. Crusafont, Sabadell.
- IPUW = Institut für Paläontologie der Universität, Wien.
- MGL = Muséum Guimet, Lyon.
- MGPUBS = Museo di Geologia e Paleontologia, Università degli Studi di Bologna.
- MPZ = Museo Paleontológico de la Universidad de Zaragoza.
- MTA = Maden Tektik ve Arama (geological survey of Turkey, Ankara).
- NMB = Naturhistorisches Museum Basel.
- PDTPAU = Paleontolojiyi, Dil ve Tarih Cografya Facultesi, Ankara Universitesi.
- PIMUZ = Paläontologisches Institut und Museum der Universität, Zürich.
- SLG = Steiermärkisches Landesmuseum Joanneum, Graz.
- UCM = Université Claude Bernard, Lyon.

**Fig. 1.**—Bivariate plot of the P3 of *Conohyus* and *Parachaeochoerus steinheimensis*. Length (DAP) against width (DT). *Conohyus* from Görriach (SLG, NMW; data given by Van der Made, 1998), Puente de Vallclos (cast in MNHN), Villefranche d’Asturac (cast in MNHN), Pauzal (PDTPAU), Klein Hadersdorf (IPUW), Mira (IPS), St. Gaudens? (cast in MGPUBS), Fonte do Pinheiro (LM), Hommes (Ginsburg, 1989) and Alhambra (MNHN). *Parachaeochoerus steinheimensis* is from La Grive (old collections in MGL).

**Description**

*Family Suidae Gray, 1821*

*Subfamily TETRACODONOTINAE Lydekker, 1876*

*Tribe NYANZACHOERIN Van der Made, 1999*

*Genus Conohyus* Pilgrim, 1926

Species *Conohyus simorrensis* (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 Túneles, a name initially applied for the locality.)
Description and comparison

The P₃ (Plate 1, fig. 3) is a massive tooth with a high protoconid and protopre- and protoanteristids 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 Parachaeolastacochoerus 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 Parachaeolastacochoerus steinheimensis or of the M₂ of the latest Aragonian and Vallesian Conohyus. Because of the tendencies in Conohyus in increase in the size of the posterior
Plate 1.—(1) Tu863, left M₂: a) anterior view, b) buccal view, c) occlusal view, stereopair, d) lingual view, e) posterior view. (2) right M₂: a) lingual view, b) occlusal view, stereopair, c) buccal view. (3) Tu534, right P₃: a) lingual view, b) occlusal view, c) buccal view.
THE PIG *CONOHYUS SIMORRENSES* FROM THE UPPER ARAGONIAN

**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 Milva (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 Pašalar
5 Pero Filho

**MN7+8 / zone G**
1 El Buste
2 Mira
3 Le Fousseret
4 Klein Eisenbach
4 Urlau, Tutzling (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 P1 from Alhambra, it is more likely, that the molars are M1 than M2. The M2 tend to have relatively thicker enamel than M1, and absolutely much thicker enamel (Van der Made, 1996). However, in the specimen 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 M1 and M2, 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 M2 of *Conohyus simorrensis* (fig. 3).

**Discussion**

As appears from the description, the material from Alhambra fits best *Conohyus simorrensis* and in particular the early, but not very early stages. Alhambra is placed in MN6, or zone F, what is consistent with the apparent 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 *Parachleuastachoerus steinheimensis*. Length (DAP) against width (DT). *Conohyus* from Görlich (SLJG, IPUW; data given by Van der Made, 1998), Urlau (SMNS), Elgg (PIMUZ), Au (SLJG), Payalar (PIMUZ) and Mira (IPS). *Parachleuastachoerus steinheimensis* is from La Grive (old collections in MGL) and Lublé (data from Ginsburg, 1987).

*Conohyus* 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 *Parachleuastachoerus*, with two lineages and three species (Van der Made, 1990b, 1999). The *Conohyus* lineage starts with *C. simorrensis*, which evolved into the larger *C. giganteus* (= *C. ebroensis*). *Parachleuastachoerus* has one lineage of small size (*P. huenermanni - P. crusafontii*) and one of larger size (*P. steinheimensis*). *Conohyus simorrensis* and *Parachleuasta-

*steinheimensis* are of similar size, differing mainly in the relative size of their premolars, those of *Parachleuastachoerus* being smaller. Till relatively recently, *P. steinheimensis* was not considered to be a different species, or a subspecies of *C. simorrensis* (eg. Hünermann, 1968; Thenuis, 1952, 1956; Ginsburg, 1980), but Chen (1984) proved them to be different species, and Fortelius et al. (1996) transferred "*Conohyus* steinheimensis" to *Parachleuastachoerus*. 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 Urlau 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 Mottil (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 simorrense*. We do not know this material; it might belong to *Conohyus* or to *Parachleuastachoerus steinheimensis*.

A specimen from Nuri Yaman might represent *Conohyus* or *Sivachoerus* (Van der Made & Tuna, 1999).
### Table 1. — European and Anatolian localities with Conohus.

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

Ginsburg (1977) described teeth from three localities in the Faluns de Toraine and assigned them to *Conohus simorrensis*, and believed them to be of a “faun” 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 “faun à Arca” (MN9). The P₃ from Hommes is much larger than that of *P. steinheimensis* and is even large for *Conohus* (Fig. 1). The P₃ from Fonte do Pinheiro (MN9) are small (Van de 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 P₃ from Lublé is narrow, is out of the known range for *Conohus* and within that of *Parach-
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 M3 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* M3 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 linkage is also recorded with different ages and evolutionary levels from France, Austria and Anatolia.

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References


Made, J. van der and Ribot, F. (1999). Additional hominoid material from the Miocene of Spain and remarks


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