Presence of the Asian horse *Sinohippus* in the Miocene of Europe

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The Anchitheriinae are a group of browsing horses with a widespread distribution throughout the Miocene. The subfamily includes the genera *Hypohippus*, *Megahippus*, *Kalobatippus*, *Anchitherium*, and *Sinohippus*. In the present paper we compare the remains of a giant anchitherine from the Spanish site of Nombrevilla-1, "*Anchitherium" sampelayoi,* with other species of *Anchitherium* from Europe, the North American genera *Megahippus* and *Hypohippus*, and the Asian genus *Sinohippus.* These comparisons allow us to suggest the inclusion of this large Spanish browsing horse in the Asian genus *Sinohippus,* rather than in *Anchitherium*. This proposal is made on the basis of some morphological traits from the upper cheek teeth of the Nombrevilla-1 fossils, and their large size, which clearly is outside the range of all other known European *Anchitherium*.

Key words: Mammalia, Anchitheriinae, *Anchitherium*, *Sinohippus*, browsers, Miocene, Spain.

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Introduction

The Anchitheriinae are an extinct subfamily of Equidae with a widespread distribution throughout the Miocene. They are considered as browsing horses that probably occupied forested habitats (Forstén 1991). The genera *Hypohippus* and *Megahippus* were large-sized horses known from the Early to Late Miocene faunas of North America (MacFadden 1998), whereas the medium-sized *Kalobatippus* is restricted to the Early Miocene of North America (MacFadden 1998). The genus *Anchitherium*, of medium size, is known from the Early to the Late Miocene of Eurasia and North America (Forstén 1990, 1991; Sánchez et al. 1998; Tleuberdina and Forstén 2001) and *Sinohippus* is only known in the Vallesian and maybe in the Turolian (Late Miocene) of China and Mongolia (Forstén 1982; McKenna and Bell 1997; Qiu 1990; Zhai and Cai 1984). *Sinohippus* has not been considered in most of the studies about the Anchitheriinae due to the scarcity of its fossil remains and doubts about its systematic value.

The genus *Anchitherium* is the best-known member of the subfamily Anchitheriinae. It has its first occurrence in the fossil record in the Late Ramblian (Early Miocene) of Wintershof-West (Germany) (Bruijn et al. 1992) and Chilleurs and Neuville (France) (Abusch-Siewert 1983), both in the zone MN 3 (Early Miocene, 20 Ma). The first record in the Iberian Peninsula is from Agreda (province of Soria, Spain; MN 3) (Sánchez et al. 1998). Thereafter, this genus becomes a typical component in the mammalian Iberian faunas until the Early Vallesian (MN 9, 11 Ma), when it becomes extinct. At the same time, the North American tridactyl equid *Hipparion* Christol, 1832, arrives in Eurasia (Alberdi 1989; Bernor et al. 1980, 1988, 1996; Sondaar and Staesche 1978; Falbusch 1976). However, it seems that these two genera coexisted for a short time, because they have been discovered associated in several sites including Nombrevilla-1 (Spain) (Villalta and Crusafont 1945), Doué-la-Fontaine and Soblay (France) (Ginsburg et al. 1979; Sondaar 1971), Holzmannsdorfberg (Austria) (Mottl 1970), Uçak (Turkey) (Ozansoy 1969), and Gaiselberg (Austria) (Thenius 1950). Some of these latest *Anchitherium* were similar in size to previous populations, whereas others, such as the Soblay, Doué-la-Fontaine, Eçme-Akçaköi (Sondaar and Staesche 1975) and Nombrevilla-1 specimens, could be considered as giant Anchitheriinae. These large forms appeared suddenly in the fossil record, without a clear connection with previous species. The presence at the same time of typical medium-sized *Anchitherium* and giant anchitherines could suggest an external origin for the latter. Unfortunately, these large forms are mainly known from some upper and lower cheek teeth, and there are few postcranial remains. Villalta and Crusafont (1945) studied the material from Nombrevilla-1 and they created a new species, *Anchitherium sampelayoi*, for this unexpected giant Spanish Vallesian anchitherine.

Sánchez et al. (1998) proposed a hypothesis to explain the evolution of *Anchitherium* in the Iberian Peninsula: they identified two successive radiations, with relatively high species diversity. One of these lineages was present in the Early and Middle Aragonian (Early Miocene), whereas the other was restricted to the Middle and Late Aragonian (Middle

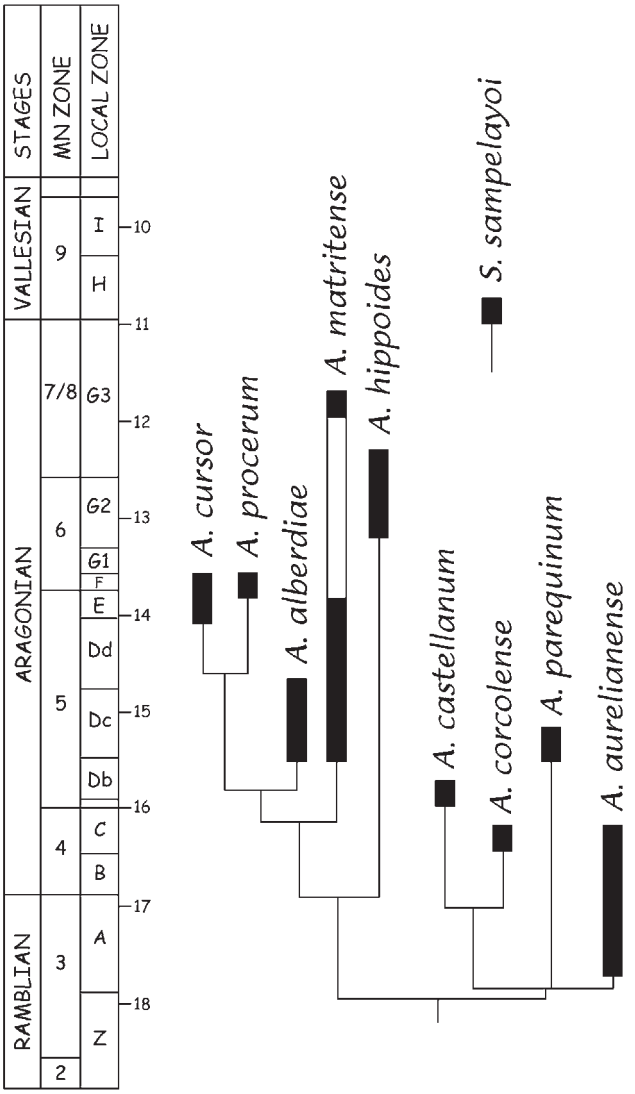

Fig. 1. Cladogram proposed by Sánchez et al. (1998) for the Iberian Anchitheriinae, showing the relationships between the two lineages of *Anchitherium*. Abbreviations: A., *Anchitherium*; S., *Sinohippus*.

Miocene) (Sánchez et al. 1998). "*Anchitherium sampelayoi*" could not be included in either of these two lineages because of the lack of skeletal remains (Fig. 1). In both groups an increase of the relative size of cheek teeth took place, perhaps related to the climate aridity of the Middle Aragonian (Alcalá et al. 2000; Calvo et al. 1993; Daams et al. 1988; Forstén 1991) or more probably to the appearance of thermal seasonality (Hernández Fernández et al. 2003). Nevertheless, these species do not show an increase in body size throughout their temporal distribution, and species with different masses have been found together in some fossil sites of different ages (Forstén 1991; Sánchez et al. 1998).

Anchitherium sampelayoi was accepted as a valid species, but its systematic position was uncertain because it was only known from very scarce dental material, being its postcranial skeleton absent in the Nombrevilla-1 sample. However, the dentition of this species is so large compared with other *Anchitherium* species (Sánchez et al. 1998), that the postcranial skeleton would be probably gigantic for this genus. Other Anchitheriinae, as some species of the North American genera *Hypohippus* and *Megahippus*, and the Asian genus *Sinohippus*, have dentitions with similar size and morphology, and they are the largest species among the Anchitheriinae.

Materials and methods

The dental remains of Nombrevilla-1 have been compared with the fossils of *Sinohippus* (Forstén 1982) and the two North American giant anchitherines *Hypohippus* and *Megahippus* from the Vertebrate Paleontology Collections of the AMNH. We chose the species *H. giganteus*, from Xmas Quarry (Middle Clarendonian, Late Miocene, Nebraska) (Alroy 2002), and *M. matthewi* from the Ash Hollow Formation, Cap Rock Member (Early Clarendonian, Middle Miocene, Nebraska) (Janis et al. 1998), because they are very well represented.

Nomenclature and metrical parameters of teeth follow Sánchez et al. (1998).

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; IGME, Instituto Geológico y Minero de España, Madrid, Spain; IPS, Institut Paleontologic "Miquel Crusafont", Sabadell, Spain; MLS, Museo "La Salle", Teruel, Spain; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain.

Systematic palaeontology

Class Mammalia Linnaeus, 1758
Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Subfamily Anchitheriinae Leidy, 1869
Genus *Sinohippus* Zhai, 1962
Sinohippus sampelayoi (Villalta and Crusafont, 1945).

Figs. 1–4.

Synonyms: *Anchitherium sampelayoi* Villalta and Crusafont, 1945: figs. 1–4; *Anchitherium ezquerrae sampelayoi* Abusch-Siewert, 1983: pl. 3: 2.

Holotype: IGME 1175M (Fig. 2), Right hemimandible with p2, d2, p3, d3, p4, d4, m1, m2, and m3 (see Villalta and Crusafont 1945: figs. 1–3).

Paratype: IPS-70, Fragment of left hemimandible with d2 and d3 (see Villalta and Crusafont 1945: fig. 4).

Other material examined: IPS-2001, fragment of hemimandible with p4, m1 and m2 (Fig. 3). There is a cast of an unpublished fragment of maxilla with P3 and P4 (Fig. 4), deposited in the MNCN, which give the only information about the upper dentition of this species; the original specimen belongs to MLS.

Type locality: Nombrevilla-1 (Calatayud-Daroca Basin, province of Zaragoza, Spain).

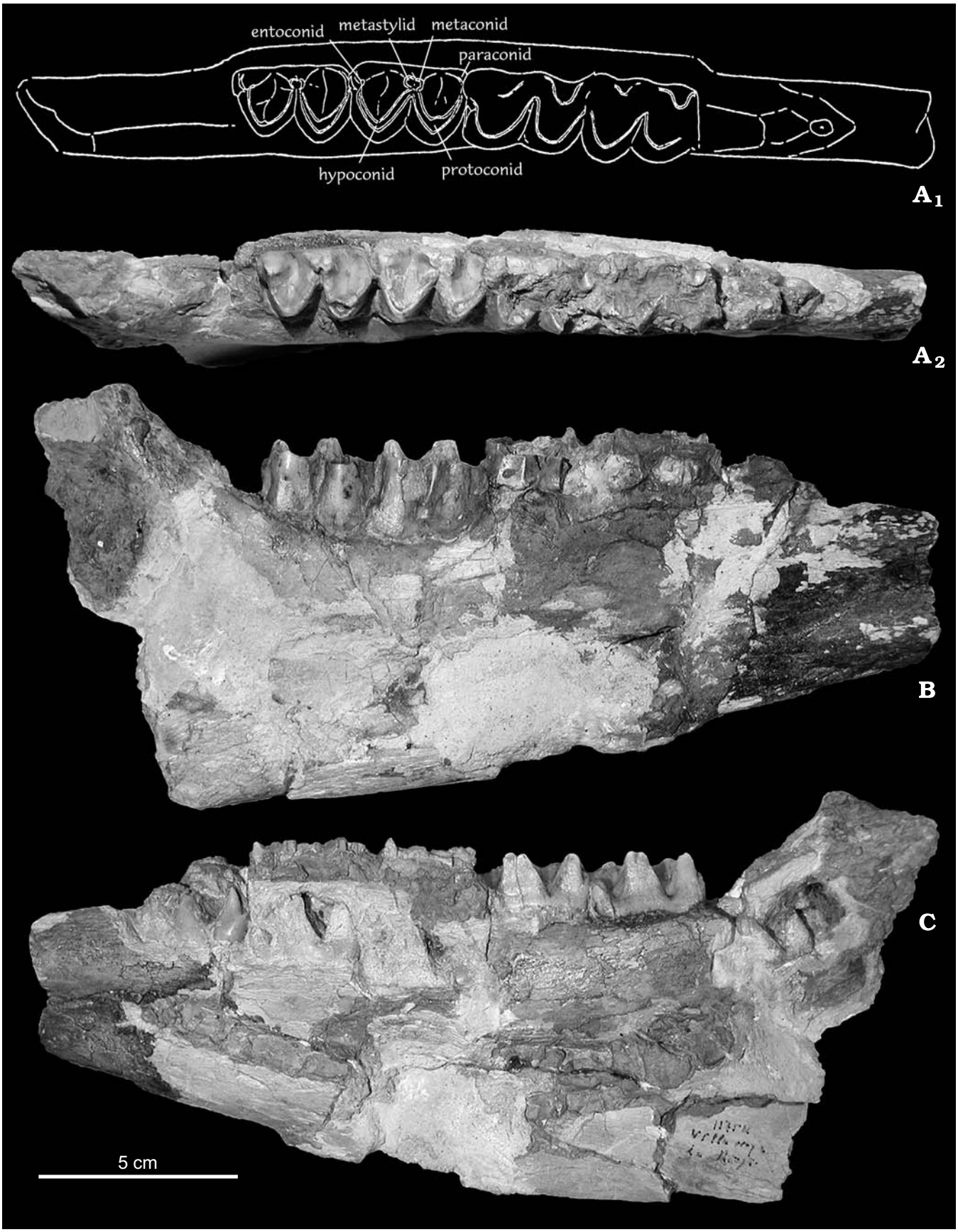

Fig. 2. *Sinohippus sampelayoi*, IGME 1175M, holotype. Fragment of right hemimandible with p2, d2, p3, d3, p4, d4, m1, m2, and m3. In occlusal (**A**), buccal (**B**), and lingual (**C**) views.

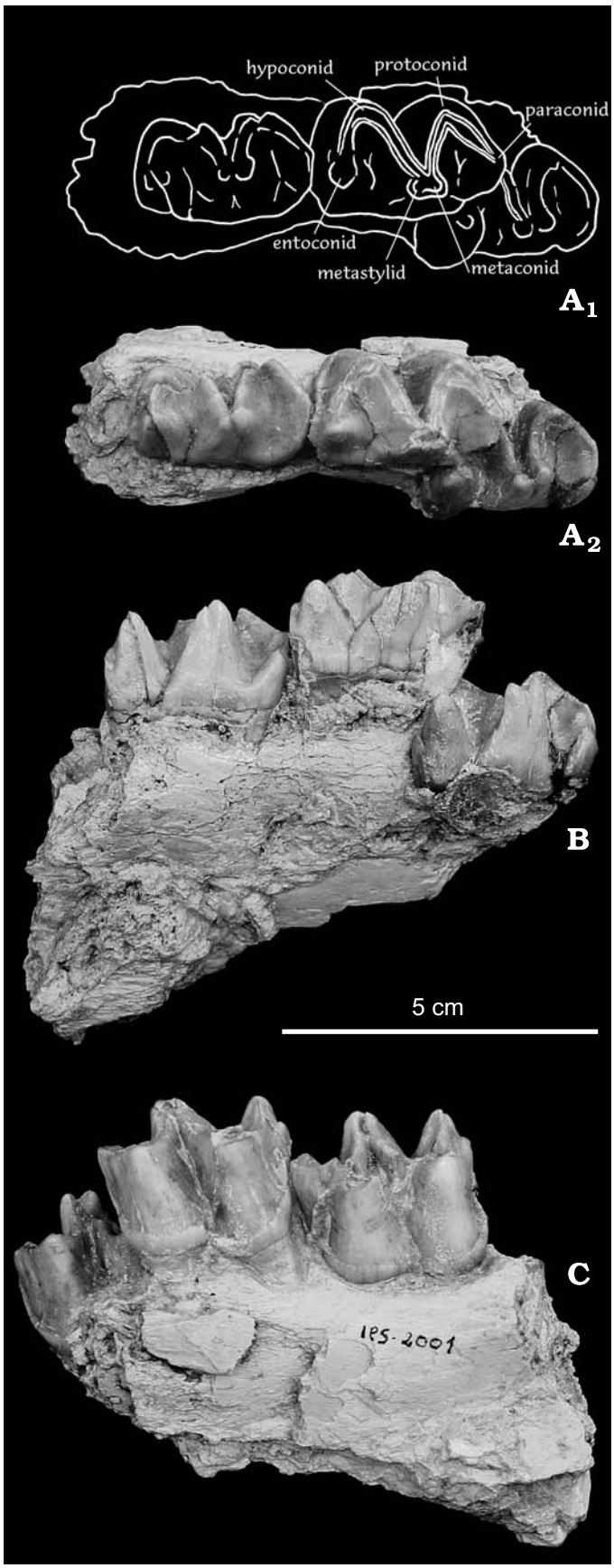

Fig. 3. *Sinohippus sampelayoi*, IPS 2001. Fragment of left hemimandible with p4, m1 and m2. In occlusal (**A**), lingual (**B**), and buccal (**C**) views.

Age: Early Vallesian (basal Late Miocene) (zone MN 9 of Mein 1975).

Other localities: Soblay and Doué-la-Fontaine (France), and Eçme-Akçaköi (Turkey).

Diagnosis.—In Villalta and Crusafont (1945: 78): "terminal, derived *Anchitherium* of large size, with marked tendency to hypsodonty, basal cingulum almost obsolete, mainly in the juvenile teeth; more evident homeodonty than in the primitive forms, milk teeth highly reduced, special shape of d2"; additionally: upper premolars with marked buccal cingulum and absence of lingual cingulum, hypostyle without connection with the metalophe, and absence of crochet.

Discussion

The Anchitheriinae fossil material from Nombrevilla-1, Doué-la-Fontaine, Soblay and Eçme-Akçaköi clearly shows a larger size than any other fossil remains known in Europe for this group (Forstén 1982; Sánchez et al. 1998; Sondaar 1971; Villalta and Crusafont 1945), and it is very similar, in size and morphology, to the gigantic genera *Sinohippus*, *Megahippus,* and *Hypohippus*. The dentition of the Anchitheriinae is very primitive and conservative within the Equidae, and there are few morphological differences between the included genera (Evander 1989; Forstén 1973, 1982; MacFadden 1998; Sánchez et al. 1998). Consequently, the separation between species of similar dental size can be very difficult if there are no postcranial elements or complete skulls available.

The last species of *Anchitherium* present in the European record do not show an increase in dental size compared with the previous populations of this genus, so there is no possible relationship between these last survivors and *S. sampelayoi* (Fig. 5). It is very interesting that the dental remains of *Anchitherium* from Nombrevilla-2, only slightly older than Nombrevilla-1, have the expected size of an anchitherine of this period, showing no evidence of the beginning of an increase in the size of this element. The other European populations of *Anchitherium* do not show any trace of size increase (Sanchez et al. 1998).

Remains of big anchitherines present in the Vallesian sites of Eçme Akçaköy, Inönü-I and Çanakale-Alcitepe (Turkey) and Soblay (France) (Forstén 1990; Sondaar 1971; Sondaar and Staesche 1975) of similar age to Nombrevilla-1, would represent the same form. There is another large anchitherine in the Late Miocene (Vallesian age, MN 9 to 10) of Shansi (China) (Forstén 1982, 1991), described as *A. zittelli* by Schlosser (1903) and included in *Hypohippus* by Osborn (1918). Zhai (1962) created the new genus *Sinohippus* for this species, and Abusch-Siewert (1983) included it in the genus *Anchitherium*. The equid from Shansi is very similar to the species from Nombrevilla-1, although it can be distinguished from the Spanish form by its lower crowned cheek teeth and a clearly developed lingual cingulum in the lower cheek teeth. These differences could be considered to be of

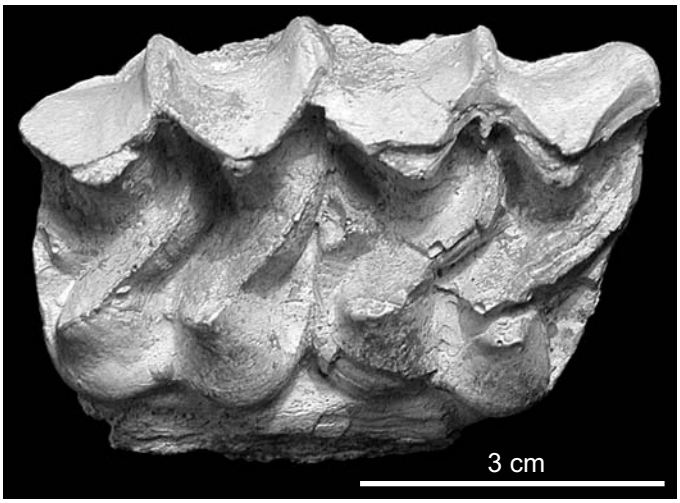

Fig. 4. *Sinohippus sampelayoi*, MNCN 50110. Occlusal view of fragment of right maxilla with P3–P4.

species level significance, and both forms should be placed in the genus *Sinohippus*.

Fig. 6 shows the great size difference in the dentition of the European anchitherines and the American species *Hypohippus giganteus* and *Megahippus matthewi*. It can also be seen that the anchitherine from Nombrevilla-1 has larger cheek teeth than the European *Anchitherium*, and only slightly smaller cheek teeth than *Hypohippus* and *Megahippus*. Most of the North American species of the genus *Hypohippus*, such as *H. affinis* Leidy, 1858, *H. equinus* (Scott, 1893), *H. osborni* Gidley, 1907, and *H. nevadensis* Merriam, 1913 are smaller and earlier (Middle Miocene). Only *H. giganteus* and *M. matthewi*, from Late Miocene, are similar sized animals to *Sinohippus*. The second lower deciduous and permanent premolars of the Nombrevilla-1 species are very short in relation to the other lower teeth, as Villalta and Crusafont (1945) noted. The available remains from Shansi (one p2, d2, p3, and m1) have similar proportions to the Spanish form, with larger size than the European *Anchitherium*, and a relatively short p2 and d2 (Forstén 1982). This relative reduction of p2 and d2 is not present in *Hypohippus* and *Megahippus*.

As we have stressed, the dental morphology of the Anchitheriinae is very conservative (Abusch-Siewert 1983; Forstén 1973, 1982; Sánchez et al. 1998) so this reduction in the premolars from Nombrevilla-1 and Shansi is sufficient to distinguish between the North American and Eurasian giant Anchitheriinae. In the Iberian anchitherines, Sánchez et al. (1998) described an increase in relative dental size in some species, and percentage differences in the presence of some features on the occlusal surface. The fossil material from Nombrevilla-1 is very scarce, so it is impossible to make a quantitative study; nevertheless, its large size makes evident that this species is different from any other Anchitheriinae known in the European fossil record, and very similar to *Sinohippus zitelli* from China and Mongolia.

Hypohippus and *Megahippus* can be distinguished by some morphological traits, such as the presence of a continuous lingual cingulum in the upper cheek teeth, which is present in *Megahippus* and absent in *Hypohippus* (Osborn 1918; Mawby 1968; MacFadden 1982). The upper premolars of *S. sampelayoi* from Nombrevilla-1, and *S. zitteli* lack the cingulum (Fig. 4), so these species are more similar to *Hypohippus* than to *Megahippus*. Nevertheless, *Sinohippus* can be clearly distinguished from *Hypohippus* in the development of the preorbital fossa, without sharp anterior boundaries that are present in *Hypohippus* and *Megahippus* (Forstén 1982). In that character *Sinohippus* resembles the Old World *Anchitherium*, and that suggests a phylogenetic relationship between these two genera, as pointed out by MacFadden (1998).

In our opinion, the anchitherine fossils from Nombrevilla-1 are more closely related to *Sinohippus* than to the European *Anchitherium*, and we identify them as *Sinohippus sampelayoi*. This assignment to the Asian genus is justified by the size of the dental remains of this species, which are larger than that of any other species of European *Anchitherium*, and by the morphological features in the cheek teeth, such as absence of a lingual cingulum in the upper cheek teeth and relatively high crown and absence of lingual cingulum in the lower cheek teeth. In addition to this, *S. sampelayoi* can be distinguished from the other Iberian anchitherines and the smaller species of *Hypohippus* by its larger dental size, by a d2 with protolophid-paralophid reduced in width, and a relative shorter p2 (Villalta and

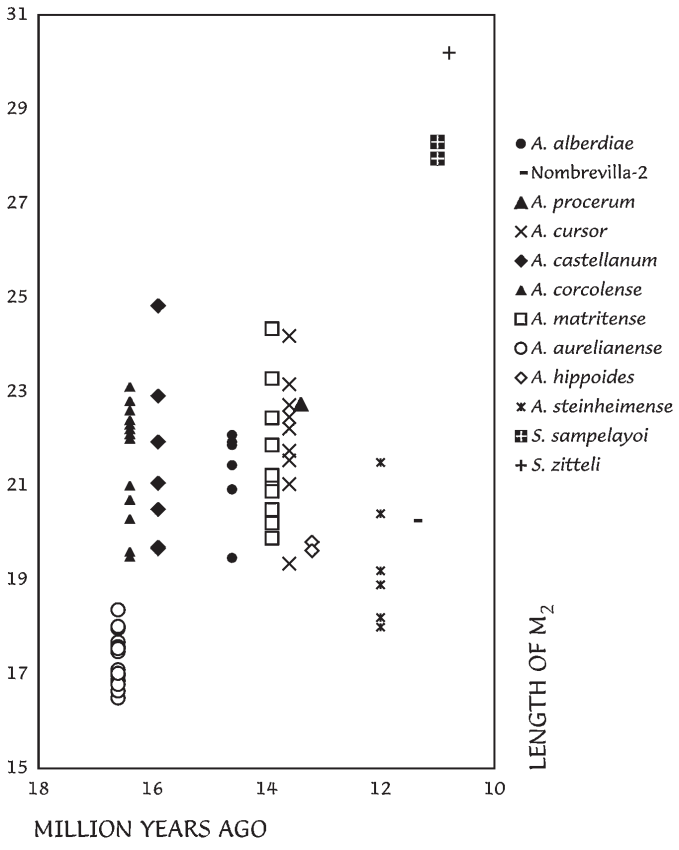

Fig. 5. Comparison in the size of m2 in the genera *Anchitherium* and *Sinohippus* along their distribution in the Eurasian record. Abbreviations: A., *Anchitherium*; S., *Sinohippus*.

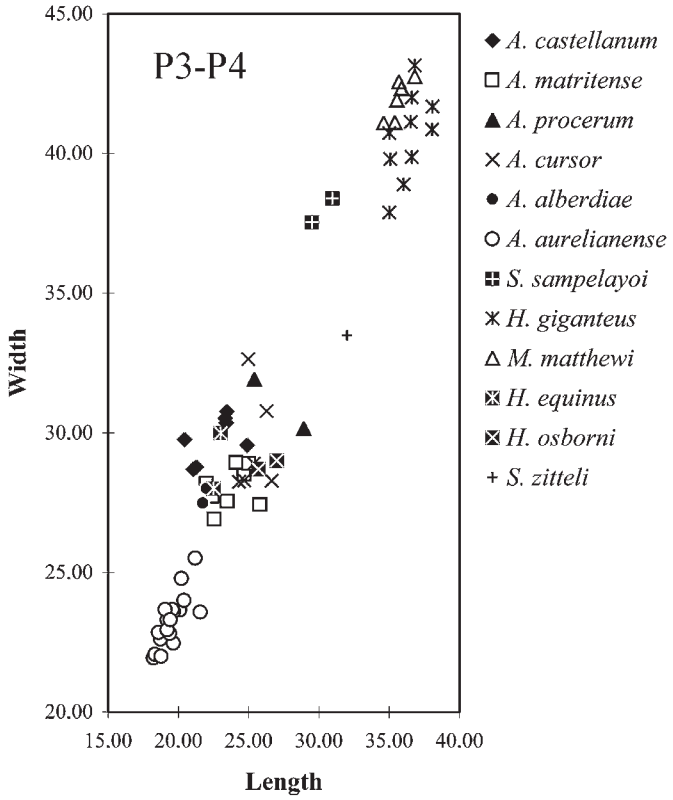

Fig. 6. Relationship between length and width of P3–P4 in different European species of *Anchitherium* and the giant anchitheres. Abbreviations: A., *Anchitherium*; H., *Hypohippus*; M., *Megahippus*; S., *Sinohippus*.

Crusafont 1945). This reduction in the size of d2 and p2 can be also observed in the other species of *Sinohippus*, *S. zitelli* from East Asia.

Palaeobiogeographical and palaeoecological implications

Two equid migrations have been classically recognized in the European Miocene: *Anchitherium* in the early Aragonian (Early Miocene), and *Hipparion* at the beginning of the Vallesian (Late Miocene) (Alberdi 1989; Alberdi and Bonadonna 1990; Morales et al. 1999). The sudden appearance of *Sinohippus* in the European faunas supports the hypothesis that this animal was part of the immigration event from eastern Asia, in which the genus *Hipparion* was also included. Despite its great size, this giant anchitherine would be more related to the Eurasian *Anchitherium*, than to the North American genera *Hypohippus* and *Megahippus*.

Sinohippus fossils are not very abundant in the fossil record, whereas *Hipparion* remains are common in Upper Miocene–Pliocene fossil sites. This fact could reflect differences in their ecological preferences. It is possible that the new climate conditions of the Eurasian ecosystems, more arid than in the Middle Miocene (Alberdi and Bonadonna 1990; Alcalá et al. 2000; Bernor et al. 1990; Calvo et al. 1993; Forstén 1991; Salesa et al. 2001), were not the preferred habitat for a giant browser such as *Sinohippus*, which was more closely restricted to the more forested habitats, and so this animal became a rare component in the mammalian faunas. Hernández Fernández et al. (2003) identified the biome of Nombrevilla-1 as a savannah, which could then explain the scarcity of *S. sampelayoi* in this fossil community.

Because the last European species of *Anchitherium* are medium-sized horses, it is difficult to find a link between them and *S. sampelayoi*. This species could be a giant descendant of some population of Asian *Anchitherium* that showed a rapid increase in size. *S. zitteli* shows an increase in size in relation to *S. sampelayoi*, which would be a parallel tendency to the North American genera *Hypohippus* and *Megahippus*, as Forstén (1982) has pointed out.

Sinohippus sampelayoi would have been a very rare component of the Vallesian faunas, in the same way that the larger *Sinohippus zitteli* from the Upper Miocene of China and Mongolia, probably inhabiting the more forested areas (Viret 1945). These giant forms would have remained in Eurasia for a short time, and they are not recorded at the end of the Late Miocene. The changes in the climatic conditions, which started in the Middle Miocene, probably favoured the more cursorial and hypsodont equids such as *Hipparion*, that crossed Beringia at that time from North America, reaching the Iberian Peninsula around 11 million years ago (at the beginning of the zone MN 9). The giant browsing equid *Sinohippus* was able to follow the same route into Europe in that dispersal event, reaching the Iberian Peninsula and Turkey, but probably with a duration too short to have been registered more widely in the fossil faunas.

Final remarks

The inclusion of "*Anchitherium*" *sampelayoi* in the Asian genus *Sinohippus* changes the traditional point of view about the evolution of the subfamily Anchitheriinae in Eurasia. Until now, it was assumed that the North American branch of this subfamily had a successful evolutionary history, with at least three different genera (*Anchitherium*, *Hypohippus*, and *Megahippus*), whereas there was a very different situation in Eurasia. There, *Anchitherium* remained as the only known Anchitheriinae, except for the giant species *Sinohippus zitelli* from China, which was of unclear origin. In the new scenario, an Asian species of *Anchitherium* evolved into the genus *Sinohippus*, reaching the Iberian Peninsula at least at the beginning of the Vallesian age, 11 Ma.

In our scheme, the taxonomic diversity of the European branch of Anchitheriinae increases at the end of its biochronological range, with the presence of a giant form, *Sinohippus*. This anchitherine could have been widely distributed all over Eurasia, although it presence in the fossil samples is very scarce, probably reflecting its ecological preferences as a forest giant browser.

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