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A new species of *Anchitherium* (Equidae: Anchitheriinae) from the Middle Miocene of Abocador de Can Mata (Vallès-Penedès Basin, NE Iberian Peninsula)

*Une nouvelle espèce d'*Anchitherium *(Equidae : Anchitheriinae) du Miocène Moyen de l'Abocador de Can Mata (Vallès-Penedès bassin, NE de la péninsule Ibérique)*

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ABSTRACT

Anchitherium nievei sp. nov. is erected on the basis of dentognathic remains from the late Aragonian (MN7+8, ca. 12.3–12.1 to 11.7–11.6 Ma, Middle Miocene) of three localities from the Abocador de Can Mata local stratigraphic series (els Hostalets de Pierola, Vallès-Penedès Basin, Catalonia, Spain). This taxon differs from endemic species of *Anchitherium* from the inner Iberian basins, most closely resembling *A. aurelianense*, *A. hippoides* and *A. steinheimense* by its marked brachyodonty and small dental size, although differing by dental proportions and several details of occlusal morphology. From a paleoenvironmental viewpoint, the presence of this taxon fits well with previous inferences that indicated a relatively closed and humid forested habitat, more similar to that of similarly aged French localities.

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RÉSUMÉ

Anchitherium nievei sp. nov. est érigé sur la base des restes dentognathiques de l'Aragonien supérieur (MN7+8, ca. 12,3–12,1 à 11,7–11,6 Ma, Miocène Moyen) de trois localités de la série stratigraphique locale de l'Abocador de Can Mata (els Hostalets de Pierola, bassin du Vallès-Penedès, Catalogne, Espagne). Ce taxon diffère des espèces endémiques d'*Anchitherium* des bassins ibériques intérieurs, ressemblant davantage à *A. aurelianense*, *A. hippoides* et *A. steinheimense* par sa brachyodontie marquée et sa petite taille dentaire, bien qu'en différant par les proportions dentaires et plusieurs détails de la morphologie occlusale. Du point de vue paléoenvironnemental, la présence de ce taxon correspond bien à des inférences précédentes qui indiquaient un habitat boisé, relativement fermé et humide, plus semblable à celui de localités françaises du même âge.

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1. Introduction

The genus *Anchitherium* von Meyer, 1834, dentally characterized by brachyodont and lophodont cheek-teeth without cement, is recorded in Europe from the MN3 (Early Miocene) up to the MN9 (Late Miocene), when it becomes extinct after a short coexistence with hipparionin horses (Daxner-Höck and Bernor, 2009; Kaiser, 2009; Rotgers and Alba, 2011). The taxonomy of *Anchitherium* is far from being settled. Leaving aside several endemic Iberian species (see below), two different European taxa are usually distinguished (either at the species or subspecies rank) from the widely-distributed *Anchitherium aurelianense* (Cuvier, 1825), which is the type species of the genus (Abusch-Siewert, 1983; Alberdi et al., 2004; Forstén, 1990; Güleç and Geraads, 2003; Miyata and Tomida, 2010): *A. hippoides* Lartet, 1851 and *A. steinheimense* Abusch-Siewert, 1983. The species status of *A. hippoides* is a matter of taxonomic opinion, having been considered both a synonym of the type species (Sánchez et al., 1998), a distinct subspecies (e.g., Abusch-Siewert, 1983; Alberdi et al., 2004) or a distinct species (Hernández Fernández et al., 2003; Salesa et al., 2011), although the latter view is favoured here. We provisionally also consider here *A. steinheimense* as a distinct species from both *A. aurelianense* and *A. hippoides*, since the former taxon differs in several regards from the type species, although additional comparisons would be required in other to confirm its distinct species (instead of subspecies) status as compared to *A. hippoides*.

The Iberian Peninsula records the highest diversity of the genus (Fig. 1). Thus, besides *A. aurelianense* and *A. hippoides* (Alberdi et al., 2004; Álvarez Sierra et al., 2003; Azanza et al., 2004; Hernández Fernández et al., 2003), the presence of some endemic species such as *A. ezquerrae* von Meyer, 1844 and *A. corcolense* Iñigo, 1997 is widely recognized (Abusch-Siewert, 1983; Alberdi and Rodríguez, 1999; Hernández Fernández et al., 2003; Iñigo, 1997; Sánchez et al., 1998); *A. sampelayoi* Villalta Comella and Crusafont Pairó, 1945 is not included here, because it was transferred to *Sinohippus* Zhai, 1962 by Salesa et al. (2004). Additional endemic Iberian species were erected by Sánchez et al. (1998): *A. castellanum* Sánchez, Salesa and Morales, 1998; *A. matritense* Sánchez, Salesa and Morales, 1998; *A. alberdiae* Sánchez, Salesa and Morales, 1998; *A. cursor* Sánchez, Salesa and Morales, 1998; *A. procerum* Sánchez, Salesa and Morales, 1998 (= *A. jaramense* Iñigo, 1998; Alberdi and Rodríguez, 1999; and Alberdi et al., 2004); and *A. parequinum* Sánchez, Salesa and Morales, 1998. Several authors (Alberdi and Rodríguez, 1999; Alberdi et al., 2004), who regard *A. hippoides* and *A. steinheimense* merely as species of *A. aurelianense*, have questioned the validity of many of the above-mentioned Iberian species (but see Salesa et al., 2011). It is however outside the scope of this paper to revise the taxonomy of *Anchitherium* in the Iberian Peninsula. Accordingly, the validity of most of the above-mentioned species is provisionally accepted here, except for *A. matritense*, which is considered a junior subjective synonym of *A. ezquerrae* (Alberdi and Rodríguez, 1999; contra Salesa et al., 2011).

In the Vallès-Penedès Basin (Catalonia, NE Iberian Peninsula), *Anchitherium* remains are quite scarce (Rotgers
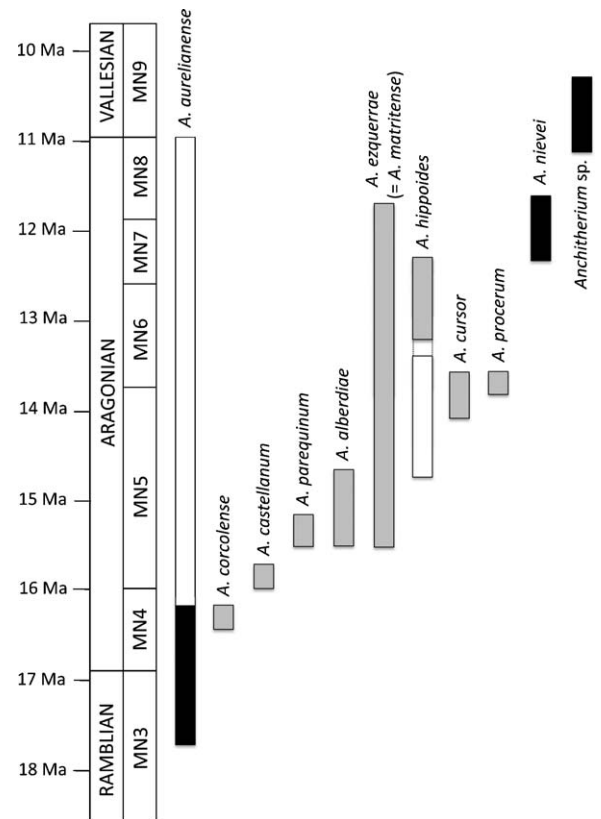

Fig. 1. Approximate chronological ranges of *Anchitherium* species from the Iberian Peninsula. Vallès-Penedès taxa are indicated in black, other Iberian taxa in grey, and the non-Iberian range of Iberian species is depicted in white. *Anchitherium* sp. corresponds to the localities of Castell de Barberà and Can Poncic in the Vallès-Penedès Basin. Stratigraphic ranges for endemic Iberian species are taken from Hernández Fernández et al. (2003), with minor modifications.

Fig. 1. Répartitions stratigraphiques approximatives des espèces d'*Anchitherium* de la Péninsule ibérique. Les taxons de Vallès-Penedès sont indiqués en noir, les autres taxons ibériques en gris, et le rang non ibérique des espèces ibériques en blanc. *Anchitherium* sp. correspond aux localités de Castell de Barberà et Can Poncic dans le bassin de Vallès-Penedès. Les extensions stratigraphiques pour les espèces endémiques ibériques sont issues d'Hernández Fernández et al. (2003), avec des modifications mineures.

and Alba, 2011), being recorded from the MN3 of Sant Andreu de la Barca (Sánchez et al., 1998), Costa Blanca 2 (Crusafont Pairó et al., 1968) and Molí Calopa (Crusafont et al., 1955), the MN4 of Sant Mamet (Golpe-Posse, 1974), Les Cases de la Valenciana (Sánchez et al., 1998) and Els Casots (MN4) (Rotgers and Alba, 2011), the MN7+8 of Hostalets Inferior (Rotgers and Alba, 2011), the MN8 or MN9 of Castell de Barberà (Rotgers and Alba, 2011), and the MN9 of Can Poncic I (Crusafont-Pairó and Golpe-Pose, 1974; Crusafont-Pairó, 1976; Sánchez et al., 1998). The MN3-MN4 remains from the Vallès-Penedès Basin are attributable to either *Anchitherium* sp. or *A. aurelianense*. Dental remains from Castell de Barberà (Crusafont-Pairó and Golpe-Pose, 1972, 1974) were originally ascribed to a distinct species, *A. osmundseni* Crusafont-Pairó and Golpe-Pose, 1974, on the basis of material that actually corresponds to the chalicotheriid *Anisodon grande* (de

Blainville, 1849) (Abusch-Siewert, 1983; Crusafont-Pairó, 1976; Forsten, 1991; Sánchez et al., 1998), although the former nominal taxon is not a nomen nudum (contra Sánchez et al., 1998), but rather a junior subjective synonym of the latter (Rotgers and Alba, 2011). In any case, the presence of *Anchitherium* sp. at Castell de Barberà can be verified on the basis of postcranial remains (Rotgers and Alba, 2011). The navicular of *Anchitherium* sp. from Can Poncic I, where *Hippotherium* is also recorded, would represent the youngest record of the former from the Vallès-Penedès Basin, being even younger (< 10.4 Ma) than other citations of both taxa from central Europe (Daxner-Höck and Bernor, 2009).

To sum up, until recently the scarce available remains indicated that *Anchitherium* dispersed into the Vallès-Penedès basin during the MN3 (Early Miocene), further persisting there until the MN9 (Late Vallesian, Late Miocene). However, no evidence was available as to whether which taxon was present there during the Aragonian (Middle Miocene), being merely recorded by some recently-reported but undescribed dentognathic material from Hostalets Inferior and several localities of the Abocador de Can Mata (ACM) series (Rotgers and Alba, 2011), which is here described and figured for the first time. The scarcity of the available remains is not attributable to low sampling effort, but to the rarity of this taxon in the Vallès-Penedès Basin thoughout all the Aragonian and Early Vallesian. The occlusal morphology of these remains is distinctive enough as to warrant the description of a new species, which most closely resembles on dental grounds the widely-distributed taxa *A. aurelianense* and *A. hippoides*, and thus has significant implications for the evolution and paleobiogeography of anchitheriines during the European Miocene.

2. Materials and methods

2.1. Abbreviations

Measurements: L, mesiodistal length; B, labiolingual breadth; L/B, length/breadth index.

Institutions and fossil collections: ICP, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona; IPS, collections from the ICP.

Fossil sites: ACM, local stratigraphic series of Abocador de Can Mata; BCV, sector of Barranc de Can Vila; BDA, sector of Bassa de Decantació d'Aigües Pluvials; C4-A, sector of Cell 4, subsector A; HI, Hostalets Inferior (Aragonian levels of els Hostalets de Pierola).

2.2. Nomenclature and measurements

Dental nomenclature follows Alberdi et al. (2004: Fig. 2). Standard dental measurements (L, B and L/B) were measured from original specimens and taken from the literature.

2.3. Studied material and comparative sample

The restricted sample of *Anchitherium* fossil remains described in this paper (including six cheek-teeth and several mandibular fragments from four different individuals) are housed at the ICP. The comparative sample includes material from other *Anchitherium* species of the Iberian Peninsula housed at the ICP, as well as data from other Iberian and European localities taken from the literature.

3. Age and geological context

The local series of ACM is located in the area of els Hostalets de Pierola (Vallès-Penedès Basin, Catalonia, Spain), which is characterized by thick Middle and Late Miocene sequences that correspond to marginal to distal facies of two coalescing alluvial fan systems (Alba et al., 2009; Moyà-Solà et al., 2009a). The ACM series includes more than 200 micro- and/or macromammal localities distributed along a 250 m-thick, Late Aragonian composite sequence (Alba et al., 2006a, 2009; Moyà-Solà et al., 2009a). On the basis of litho-, magneto- and biostratigraphic correlation (Moyà-Solà et al., 2009a; Alba et al., 2006b, 2009), an accurate dating of ACM localities and isolated fossil remains is possible (Casanovas-Vilar et al., 2011). Biostratigraphically (Alba et al., 2006b, 2009), the lower part of the series corresponds to the *Megacricetodon ibericus* + *Democricetodon larteti* local biozone, correlated to the MN7 sensu Mein and Ginsburg (2002), whereas the upper part of the series corresponds to the *M. ibericus* + *Democricetodon crusafonti* local biozone, correlated to the MN8 sensu Mein and Ginsburg, 2002, (Casanovas-Vilar et al., 2011). The *Anchitherium* remains described in this paper correspond to isolated finds from three ACM sectors (not from any of the formally-designated localities from the ACM series), with the following estimated ages: ca. 12.3–12.1 Ma (MN7) for *Anchitherium* remains from BDA; ca. 12.0–11.9 Ma (MN7 or MN8) for BCV; and 11.7 Ma (MN8) for C4-A. An isolated tooth from HI, recently found amongst the ICP collections (Rotgers and Alba, 2011) is also described; since stratigraphic provenance is not recorded, a greater range of age uncertainty (12.5–11.2 Ma, MN7+8) must be attributed to this specimen.

4. Systematic palaeontology

Order: PERISSODACTYLA Owen, 1848.
Family: EQUIDAE Gray, 1821.
Subfamily: ANCHITHERIINAE Leidy, 1869.
Genus *Anchitherium* von Meyer, 1834.
Anchitherium nievei sp. nov.
(Fig. 2)

Synonyms: *Anchitherium* sp. nov. in Alba et al. (2006a); *Anchitherium* sp. in Alba et al. (2006b, 2007, 2009); *Anchitherium* ssp. nov. in Rotgers and Alba (2011).

Holotype: IPS20433a–d, mandibular fragments (IPS20433d) with right m2 (IPS20433c: Fig. 2A–E) and m3 (IPS20433b: Fig. 2F–J), and left m3 (IPS20433a: Fig. 2K–O), of a single individual.

Paratypes: IPS41937 (Fig. 2P-T), left m3 from ACM/C4-A; IPS41989 (Fig. 2U-Y), right P2 from ACM/BCV.

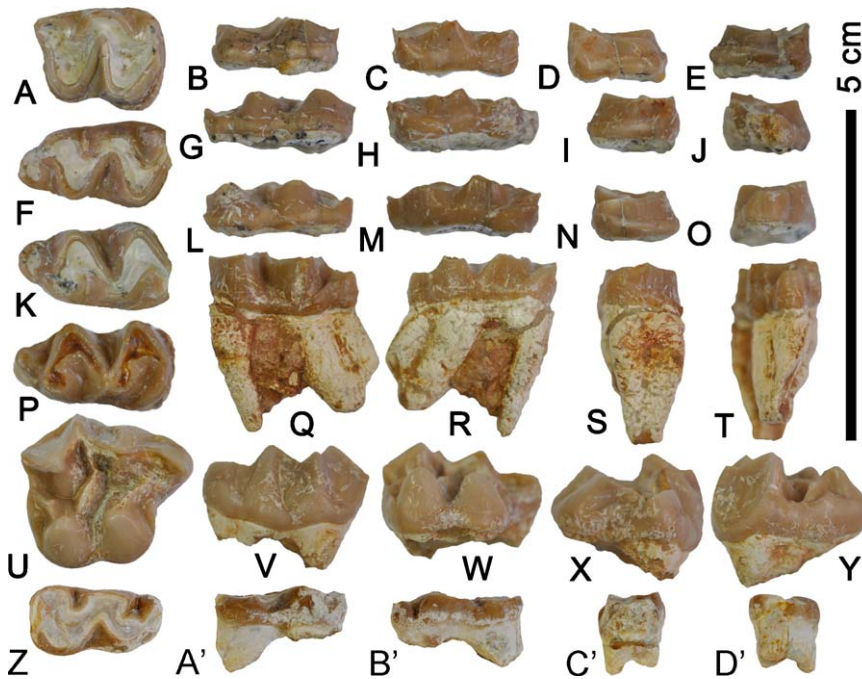**Type locality**: ACM/BDA (els Hostalets de Pierola, Catalonia, Spain).

Fig. 2. Dental remains of *Anchitherium nievei* sp. nov. from ACM (**A–Y**) and HI (**Z–D'**). **A–E**: right m2 IPS20433c (holotype): **A**: occlusal view; **B**: labial view; **C**: lingual view; **D**: mesial view; **E**: distal view. **F–J**: right m3 IPS20433b (holotype): **F**: occlusal view; **G**: labial view; **H**: lingual view; **I**: mesial view; **J**: distal view. **K–O**: left m3 IPS20433a (holotype): **K**: occlusal view; **L**: labial view; **M**: lingual view; **N**: mesial view; **O**: distal view. **P–T**: left m3 IPS41937 (paratype): **P**: occlusal view; **Q**: labial view; **R**: lingual view; **S**: mesial view; **T**: distal view. **U–Y**: right P2 IPS41989 (paratype): **U**: occlusal view; **V**: labial view; **W**: lingual view; **X**: mesial view; **Y**: distal view. **Z–D'**: right p2 IPS35041: **Z**: occlusal view; **A'**: labial view; **B'**: lingual view; **C'**: mesial view; **D'**: distal view.

Fig. 2. Restes dentaires d'*Anchitherium nievei* sp. nov. de l'ACM (**A–Y**) et HI (**Z–D'**). **A–E** : m2 droite IPS20433c (holotype) : **A** : vue occlusale ; **B** : vue labiale ; **C** : vue linguale ; **D** : vue mésiale ; **E** : vue distale. **F–J** : m3 droite IPS20433b (holotype) : **F** : vue occlusale ; **G** : vue labiale ; **H** : vue linguale ; **I** : vue mésiale ; **J** : vue distale. **K–O** : m3 gauche IPS20433a (holotype) : **K** : vue occlusale ; **L** : vue labiale ; **M** : vue linguale ; **N**, vue mésiale ; **O** : vue distale. **P–T** : m3 gauche IPS41937 (paratype) : **P** : vue occlusale ; **Q** : vue labiale ; **R** : vue linguale ; **S** : vue mésiale ; **T** : vue distale. **U–Y** : P2 droit IPS41989 (paratype) : **U** : vue occlusale ; **V** : vue labiale ; **W** : vue linguale ; **X** : vue mésiale ; **Y** : vue distale. **Z–D'** : p2 droit IPS35041 : **Z** : vue occlusale ; **A'** : vue labiale ; **B'** : vue linguale ; **C'** : vue mésiale ; **D'** : vue distale.

Diagnosis: *Anchitherium* with small dental size, very brachyodont teeth and broad cheek-teeth relative to length. P2 with a well-developed anterostyle; metacone more protruding than the paracone; protocone larger than the hypocone; protoloph and metaloph connected to the ectoloph merely due to wear; hypostyle connected to the hypocone; very small, style-like prefossette fold; little developed cingula (discontinuous labial one, vestigial lingual one, and mesial and distal absent). Lower molars with the distal lobe narrower than the mesial one; poorly-developed labial cingulid and no lingual cingulid; no stylids on the lingual valleys.

Differential diagnosis: The new species differs from *A. aurelianense* (the type species of the genus) by the relatively broader cheek-teeth; the P2 hypostyle connected to the hypocone; the presence of a prefossette fold in the P2; the lack of mesial and distal cingula, and the lack of a well-developed lingual cingulum in the P2; the lack of well-developed mesial, labial and distal cingulids in the lower molars; and the lack of styles on the lingual valleys of the lower molars. It differs from both *A. hippoides* and *A. steinheimense* by the relatively wider lower molars,

by the P2 hypostyle and hypocone being connected to one another merely due to wear, and by the lack of mesial and distal cingulids in the lower molars. It further differs from *A. hippoides* by the lack of mesial, distal and well-developed lingual cingula in the P2, and of labial cingulids in the lower molars; and from *A. steinheimense* by displaying the hypostyle connected to the hypocone in the P2. Finally, *A. nievei* differs from the remaining Iberian species of *Anchitherium* by the more marked brachyodonty, the smaller dental size but relatively broader lower molars, and other details of the occlusal morphology (see Discussion for further details).

Measurements: See Table 1.

Other referred material: IPS35041 (Fig. 2Z–D'), an isolated right p2 of unknown stratigraphic provenance from HI most likely belongs to the newly described species, on the basis of overall dental size and morphological congruence, as well as broadly similar age and geographic provenance. Nevertheless, due to the lack of an accurate dating and the impossiblity to directly compare it with *A. nievei* from ACM, this specimen is included in the hypodigm of the new species (see description in Results),

Table 1

Dental measurements of the holotype and paratypes of *Anchitherium nievei* sp. nov. from ACM.

Tableau 1

Mesures dentaires de l'holotype et des paratypes d'*Anchitherium nievei* sp. nov. de l'ACM.

Record No.	Locality andage	Tooth	L (mm)	B (mm)	L/B
IPS20433a (holotype)	ACM/BDA (12.3–12.1 Ma)	Left m3	21.8	13.3	1.64
IPS20433b (holotype)	ACM/BDA (12.3–12.1 Ma)	Right m3	21.7	13.1	1.66
IPS20433c (holotype)	ACM/BDA (12.3–12.1 Ma)	Right m2	18.8	15.3	1.23
IPS41937 (paratype)	ACM/C4-A (11.7 Ma)	leFt m3	21.3	12.0	1.78
IPS41989 (paratype)	ACM/BCV (12.0–11.9 Ma)	Right P2	23.1	21.8	1.06
IPS35041 (referred specimen)	HI (12.5–11.2 Ma)	Right p2	20.4	10.8	1.89

but not included in its diagnosis as part of its type material. See measurements in Table 1.

Geographic distribution: Exclusively known from the area of els Hostalets de Pierola (Vallès-Penedès Basin, NE Iberian Peninsula).

Chronostratigraphic range: Minimum from 12.1 up to 11.7 Ma (maximum from 12.3 to 11.6 Ma), corresponding to the MN7 and MN8 (Late Aragonian, Middle Miocene), on the basis of ACM material. It is not possible to precise the age of the isolated tooth from HI, other than attributing it to the MN7 or MN8.

Etymology: Species nomen dedicated to the late pale-ontologist Nieves López Martínez; derived as the genitive of "Nieves", considered a latinized personal name (in singular) and ascribed to the fifth declension, according to the rules of Latin grammar (International Commission on Zoological Nomenclature (ICZN), 1999: Article 31.1.1).

5. Results

5.1. Preservation and description

The holotype IPS20433 includes several uninformative mandibular fragments and three molar crowns, corresponding to the m2 (with an advanced degree of wear) and the two (right and left) m3 (with a somewhat less marked degree of wear). Two additional isolated teeth (paratypes) are available from ACM: IPS41937, an m3 crown with roots (showing a slight degree of wear); and IPS41989, a P2 crown (only very slightly worn).

All these cheek-teeth are very low-crowned and display a dental size overlapping with *A. aurelianense*. The P2 displays a subquadrangular occlusal contour, with a very protruding anterostyle on the mesiolabial corner of the crown, a biconvex lingual profile, a straight distal profile, and a W-shaped fold on the labial crown wall. The metacone is more protruding than the paracone, and the protocone is somewhat less peripheral than the similarly developed hypocone. The protoloph, which is unworn, does not connect to the ectoloph, and a considerable additional degree of wear would be required in order to do so. The metaloph displays a similar development and only minimally connects to the ectoloph, because the latter is worn to some degree. The prefossete fold is very small, merely consisting in a small style of enamel. The labial cingulum is not well developed and discontinuous (restricted to a small mesial portion between paracone and anterostyle, without reaching the distalmost portion of the crown, as

well as a somewhat longer portion from mesostyle to metastyle). The lingual cingulum is very poorly-developed, almost vestigial, being very restricted between the pro-tocone and hypocone. There are no mesial or distal cingula.

The available lower molars display a subrectangular occlusal profile (being longer than wide), the labial side of the crown being biconvex due to the presence of two distinct lobes, of which the mesial one is wider than the distal one (particularly in the m2). There is no lingual cingulid, whereas the labial cingulid is narrow and poorly developed (particularly between the mesial and distal lobes). The latter extends mesially until disappearing at about crown midline (being more marked in the m2 than in the m3), whereas distally it extends until crown midline in the m2, or until the distal lingual valley in the m3. Otherwise, there are no stylids on the lingual valleys of the lower molars. The m3 further differs from the m2 by being longer and relatively narrower, and further displaying a relatively small and rounded third lobe. The latter bears a distinct hypoconulid, lower than the remaining cuspids, and connected to the entoconid by a short crest.

Finally, the isolated p2 from HI referred to the newly described species preserves the complete crown and partially the fused roots of the distal lobe, whereas those from the mesial lobe are not preserved. This tooth is low-crowned and displays a small dental size, with a bilobulate occlusal profile (although the two lobes are united due to the advanced degree of wear), the mesial lobe being narrower than the distal one. There are no lingual, mesial or distal cingulids, whereas the labial one is only very slightly developed (almost imperceptible). Small and poorly-developed stylids are present on the distal lingual valley.

5.2. Morphometric comparisons

A. nievei most closely resembles in occlusal morphology and crown height the several brachyodont *Anchitherium* species that have been distinguished only as subspecies of *A. aurelianense* by other authors, although with significant proportional differences between them (Fig. 3). Thus, *A. hippoides* differs from *A. aurelianense* by the relatively broader P2 (Fig. 3A); the longer (although with some over-lap) and relatively broader m2 (Fig. 3B); and the longer (although with substantial overlap) and relatively slightly broader m3 (Fig. 3C). In turn, *A. steinheimense* displays a
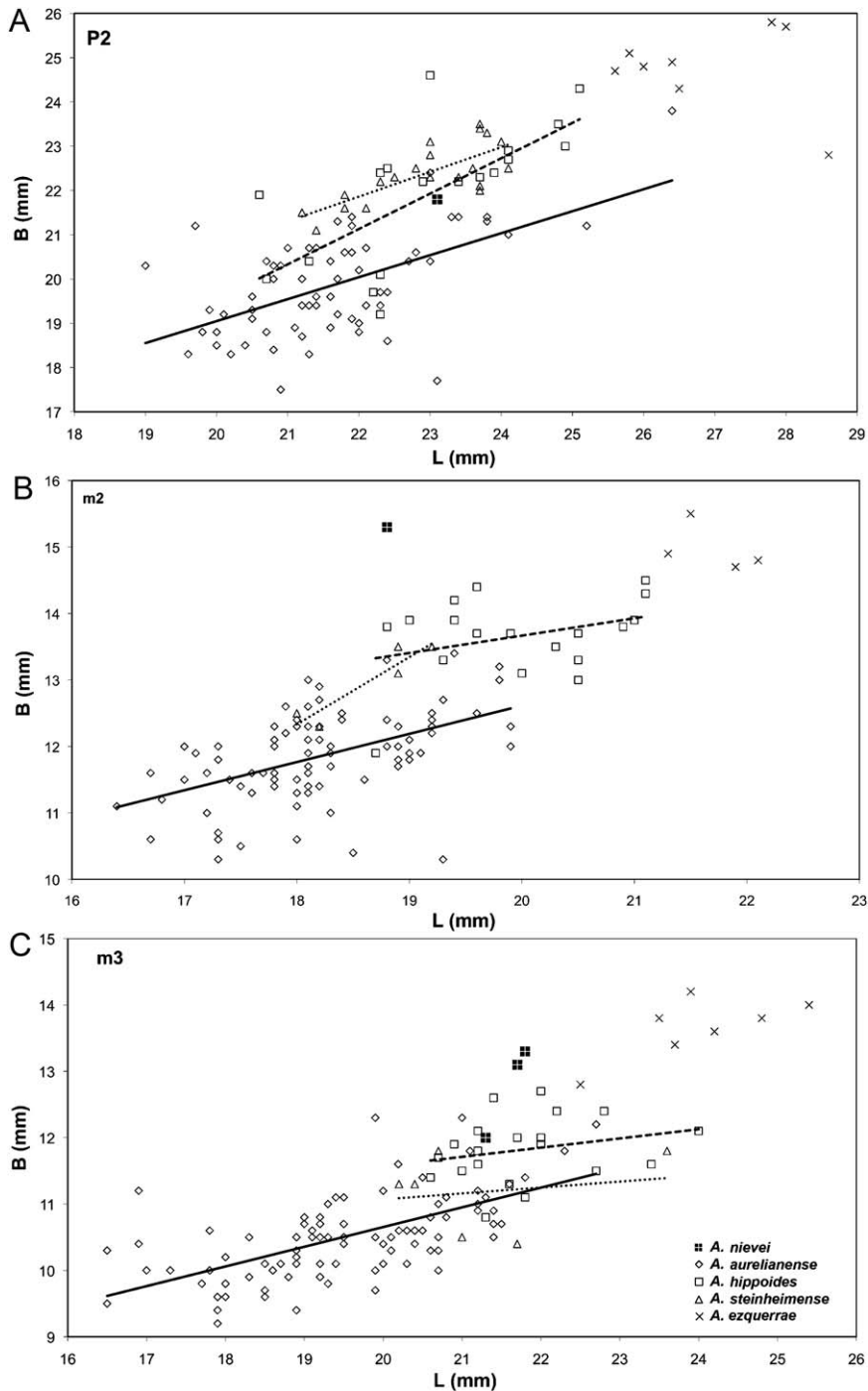
Fig. 3. Bivariate plots of labiolingual breadth (B) vs. mesiodistal length (L) of the cheek-teeth of *Anchitherium nievei* sp. nov. from ACM, as compared to the other brachyodont species of *Anchitherium*, as well as to *A. ezquerrae* as an example of a larger and hypsodont *Anchitherium* species. **A**: P2; **B**: m2; **C**: m3. The lines correspond to best-fit lines computed by means of linear regression (least-squares method), in order to show the main tendency of the several samples: continuous line, *A. aurelianense*; dashed line, *A. hippoides*; pointed line, *A steinheimense*. Drawn on the basis of own data as well as measurements taken from the literature (Abusch-Siewert, 1983; Alberdi et al., 2004).
Fig. 3. Graphiques à deux variables de largeur labiolinguale (B) vs. longueur mésiodistale (L) des dents de la joue de l'*Anchitherium nievei* sp. nov. de l'ACM, comparées à celles des autres espèces brachyodontes d'*Anchitherium*, ainsi que d'*A. ezquerrae,* à titre d'exemple d'une espèce plus grande et hypsodonte d'*Anchitherium*. **A** : P2 ; **B** : m2 ; **C** : m3. Les lignes correspondent à des lignes de meilleur ajustement, calculé par régression linéaire (méthode des moindres carrés), afin de montrer la tendance principale des différents échantillons : ligne continue, *A. aurelianense* ; ligne discontinue, *A. hippoides* ; ligne pointillée, *A. steinheimense*. Dessiné sur la base de données propres ainsi que de mesures prises dans la littérature (Abusch-Siewert, 1983 ; Alberdi et al., 2004).

P2 clearly broader than *A. aurelianense*, and even slightly so as compared to *A. hippoides* (although with substantial overlap) (Fig. 3A); a m2 intermediate in length and relative breadth between *A. aurelianense* and *A. hippoides* (Fig. 3B); and a m3 similar in length to *A. hippoides* but resembling *A. aurelianense* in relative breadth (Fig. 3C). The P2 of the new ACM species is more comparable to *A. hippoides* and *A. steinheimense*, i.e. slightly broader than in *A. aurelianense* (Fig. 3A), even though the considerable overlap and the small sample size preclude testing the significance of these differences. *A. nievei* further displays an m2 in the upper size range of *A. aurelianense* and *A. steinheimense*, and in the lower one of *A. hippoides*, although being clearly relatively wider than in all these other taxa (Fig. 3B and Table 2). Finally, the new species displays an m3 similar in length to *A. hippoides* and *A. steinheimense* (further overlapping with *A. aurelianense*), although clearly relatively broader, particularly as compared to *A. aurelianense* and *A. steinheimense* (Fig. 3C). When the m2 size and proportions are compared with other Iberian species of *Anchitherium* (Table 2), it can

be concluded that *A. nievei* clearly differs from them by displaying a shorter but relatively much broader m2 (with a LBI lower than in the remaining European *Anchitherium* taxa investigated).

6. Discussion

6.1. Comparisons with other taxa

A. nievei can be distinguished from other endemic Iberian *Anchitherium* spp. by the more marked brachyodonty, the smaller dental size but relatively broader lower molars, and other details of the occlusal morphology: from *A. corcolense* by the lower and discontinuous lingual cingulum of the P2, the lack of hypostyle-hypocone connection on the P2, the lack of lingual stylids on the distal valley of the m3, the rounder distal lobe of the m3, and the lower and shorter labial and lingual cingulids of the m3; from *A. ezquerrae* (= *A. matritense*) by the shorter prefossette fold, the lower lingual cingulum, the lack of mesial and distal cin-

Table 2
Descriptive statistics of dental measurements (L, B and L/B) of the m2 of *Anchitherium nievei* sp. nov. from ACM, as compared to other (sub)species of the same genus. Data taken from Sánchez et al. (1998), Iñigo (1997), and this study.
Tableau 2
Statistiques descriptives des mesures dentaires (L, B et L/B) de m2 d'*Anchitherium nievei* sp. nov. de l'ACM, par rapport aux autres (sous-)espèces du même genre. Données extraites de Sánchez et al. (1998), Iñigo (1997) et cette étude.

Site	Taxon	Variable	*n*	Mean	Variance	Range	
Alhambra (Spain)	*Anchitherium cursor*	L	9	22.04	1.891	19.34	24.18
		B	10	14.85	0.579	13.59	16.02
		L/B	9	1.48	0.006	1.36	1.60
Retama (Spain)	*Anchitherium castellanum*	L	7	21.51	3.507	19.67	24.83
		B	7	13.85	1.112	12.11	15.17
		L/B	7	1.56	0.035	1.34	1.81
Acacias (Spain)	*Anchitherium alberdiae*	L	7	21.23	0.823	19.46	22.07
		B	7	14.94	0.524	13.84	16.12
		L/B	7	1.42	0.004	1.34	1.51
Paracuellos V (Spain)	*Anchitherium procerum*	L	1	22.74	–	22.74	22.74
		B	1	16.61	–	16.61	16.61
		L/B	1	1.37	–	1.37	1.37
Puente Vallecas (Spain)	*Anchitherium ezquerrae*	L	11	21.64	1.879	19.88	24.33
		B	11	15.04	0.238	14.41	15.90
		L/B	11	1.44	0.010	1.32	1.66
Nombrevilla 1 (Spain)	*Sinohippus sampelayoi*	L	1	27.95	–	27.95	27.95
		B	1	19.13	–	19.13	19.13
		L/B	1	1.46	–	1.46	1.46
ACM (Spain)	*Anchitherium nievei*	L	1	18.80	–	18.80	18.80
		B	1	15.34	–	15.34	15.34
		L/B	1	1.23	–	1.23	1.23
Córcoles (Spain)	*Anchitherium corcolense*	L	30	22.05	1.04	19.5	23.2
		B	29	13.5	0.86	11.9	15.0
		L/B	–	–	–	–	–
France (several sites)	*Anchitherium aurelianense*	L	83	18.18	0.629	16.40	19.50
		B	83	11.84	0.463	10.30	13.40
		L/B	83	1.54	0.0004	1.39	1.87
France (several sites)	*Anchitherium hippoides*	L	19	19.78	0.596	17.70	21.10
		B	19	13.66	0.350	11.90	14.50
		L/B	19	1.46	0.005	1.36	1.58
Steinheim (Germany)	*Anchitherium steinheimense*	L	6	18.64	0.210	18.00	19.20
		B	6	12.98	0.250	12.30	13.50
		L/B	6	1.44	0.001	1.42	1.48

gula and the less developed labial cingulum in the P2; from *A. procerum* by the presence of a prefossette fold (albeit not very developed) in the P2, the presence of a distal cingulid in the m3, and the lack of stylids on the distal valley of the m2; from *A. alberdiae* by the presence of stylids on the distall valley of the m3; from *A. castellanum* by the presence of prefossette fold and the lack of lingual cingulum in the P2, and the lack of stylids on the distall valley of the m3; and from *A. cursor* by the larger prefossette fold and the lack of lingual cingulum in the P2, and the lack of stylids on the distall valley of the m3. Only *A. parequinum* (MN5 of Zaragoza) cannot be directly compared to the ACM taxon due to the lack of dental material in the former.

With regard to the remaining *Anchitherium* species, both *A. aurelianense* and *A. hippoides* are recorded in the Early and Middle Miocene (respectively) of the Iberian Peninsula. However, given the scarcity of the remains and the lack of published descriptions, the comparisons between *A. nievei* and these other species must rely on the much more abundant material from France. The dental size of the ACM species is more similar to these European taxa than to the endemic Iberian ones, although it can be clearly distinguished from the former on the basis of dental proportions. The details of the occlusal morphology further enable to distinguish the ACM remains from *A. aurelianense* and the roughly synchronous *A. hippoides* and *A. steinheimense* by a unique combination of features, as enumerated in the differential diagnosis. One of the most diagnostic features of the ACM taxon is that the ectoloph and metaloph of the P2 would become connected to the hypocone only by through very extensive dental wear, whereas other differences refer to the development of cingula and cingulids.

6.2. Paleoecological and evolutionary considerations

The new species *A. nievei*, recorded from the Late Aragonian (MN7+MN8), is roughly contemporaneous with *A. hippoides* from the Calatayud-Daroca Basin (Toril 3A and Nombrevilla 2; Álvarez Sierra et al., 2003; Azanza et al., 2004; Hernández Fernández et al., 2003), being only postdated in the Iberian Peninsula by the record of *Anchitherium* sp. from Castell de Barberà (MN8 or MN9) and especially Can Ponsic I (MN9), also from the Vallès-Penedès Basin. The lack of any record of *Anchitherium* in this basin during the MN5 and MN6, despite being recorded from several MN3 and MN4 localities, strikingly contrasts with the presence of several species throughout the whole Aragonian in the inner Iberian basins as well as in the rest of Europe, and is probably attributable to the scarcity of rich localities from this particular time interval at the Vallès-Penedès Basin. The genus *Anchitherium* displays a temporal trend towards size increase (Abusch-Siewert, 1983), in parallel to paleonvironmental changes. Climatic deterioration, and the associated increase of seasonability, resulted in more open habitats with a higher proportion of trophic resources with a high fibre content, which might have been the selection pressure that drove the size increase in the genus *Anchitherium* through the Middle Miocene (Forsten, 1991; Hernández Fernández et al., 2003). This would explain the prevalence of large-bodied and more hypsodont forms amongst the last-surviving anchitheri-

ines, particularly in the Iberian Peninsula, where trends towards increased occlusal area (Forsten, 1991) and hypsodonty (Eronen et al., 2010) have been detected. According to Sánchez et al. (1998), two different Iberian evolutionary lineages would have experienced this trend, beginning from a morphotype more similar to *A. aurelianense*, as an adaptation to more open environments with more abrasive vegetation.

This scenario is partly contradicted by the marked brachyodonty of the ACM *Anchitherium*, resembling the condition displayed by the earliest representatives of this genus in the Iberian Peninsula, together with the dispersal into Iberia during the late MN6 of *A. hippoides* (Hernández Fernández et al., 2003). Anchitheriines are considered inhabitants of subtropical to warm-temperate forests (Kaiser, 2009), displaying a browsing or mixed feeding niche (Eronen et al., 2010; Forsten, 1991; Kaiser, 2009), although the paleoecological implications of each *Anchitherium* species depend on its particular dental and postcranial features. On the basis of the small and low-crowned cheek-teeth of both *A. nievei* and *A. hippoides*, a closed forest environment can be inferred (Hernández Fernández et al., 2003). This agrees with the increase in humidity that had been previously detected in the Calatayud-Daroca Basin from the MN6 onwards (Van der Meulen and Daams, 1992), and which contrasts with the more arid conditions inferred from older Iberian localities (Hernández Fernández et al., 2003). In Toril 3A, a humidity peak is confirmed by dental microwear studies (DeMiguel et al., 2011), whereas in ACM this is confirmed by the presence of particular taxa linked to closed forest environments, such as primates (Alba et al., 2010; Moyà-Solà et al., 2004, 2009a,b). This further agrees with paleoenvironmental inferences based on the whole ACM fauna (Alba et al., 2006b, 2009, 2011; Casanovas-Vilar et al., 2008a,b), which is more similar to that from contemporaneous French and central European localities than to those from the inner Iberian basins (Casanovas-Vilar et al., 2008a), and which together with regional paleobotanical data agree with the presence of subtoprical to warm-temperate forest environments, although with a large proportion of deciduous taxa (Alba et al., 2009; Casanovas-Vilar et al., 2008a).

Throughout most of the Miocene, the Vallès-Penedès Basin apparently displayed more humid and forested conditions than most of the rest of the Iberian Peninsula (Casanovas-Vilar and Agustí, 2007; Casanovas-Vilar et al., 2008a, 2010), which would explain the presence of an *Anchitherium* species more closely related to French and European taxa than to endemic Iberian species. Given the scarcity of *Anchitherium* remains in the Catalan basins throughout all the Miocene, it is not possible to determine whether *A. nievei* represents an endemic evolutionary lineage, evolved in NE Iberian Peninsula from the earliest *A. aurelianense* that dispersed there by the Early Miocene, or whether it represents an independent later dispersal event from France, as suggested by the presence of *A. hippoides* in MN6 and other MN7+8 Iberian localities. The evolutionary and paleoecological implications of the presence of an endemic *Anchitherium* in the Vallès-Penedès Basin, contrasting with the presence of a more widely-distributed

species (*A. hippoides*) in other Iberian basins, should be subject to further research in the future when the available material of the latter taxon from Spanish localities is published in detail.

Finally, although the rarity of *Anchitherium* in the ACM series could be partly explained by taphonomic reasons – such as the lack of environments preferred by small and brachyodont anchitheriine species –, this explanation seems rather unlikely. Although very humid environments with small ponds and lakes would have been only occasionally developed in the area of els Hostalets – as suggested by the rarity of castorids (Casanovas-Vilar et al., 2008b) and tragulids (Alba et al., 2011) – *Anchitherium* is also rare (or even absent) at many other MN7+8 localities from the Vallès-Penedès Basin, such as Castell de Barberà, where beavers are particularly abundant (Casanovas-Vilar and Agustí, 2007). Alternatively, the rarity of *Anchitherium* in the Vallès-Penedès Basin, particularly during the Late Aragonian, might be related to the competence with the small-bodied, browsing rhino *Alicornops simorrense*, as previously suggested in order to explain the rarity of *A. hippoides* amongst Iberian faunas by Hernández Fernández et al. (2003). In the Vallès-Penedès Basin, *Al. simorrense* is more well represented than *Anchitherium* during the Late Aragonian and Vallesian (Cerdeño and Sánchez, 2000), albeit being more scarce than in other Iberian localities, further being recorded at the ACM series (Alba et al., 2006a, 2009), where it is more frequent (both in quantity of remains and stratigraphic occurrences) than *Anchitherium* (DMA, pers. obs.). Nevertheless, a quantitative assessment is precluded because the rhinocerotid remains from ACM are still unpublished and to a large extent remain to be prepared. Moreover, paleoecological and morphofunctional studies outside the scope of this paper would be required in order to test to what extent *Alicornops*, considered an inhabitant of open woodlands with lacustrine or marshy areas (Cerdeño and Sánchez, 2000), could have displayed similar ecological requirements than a brachyodont *Anchitherium* species such as *A. nievei*.

7. Summary and conclusions

A new species, *Anchitherium nievei* sp. nov., is described on the basis of dental remains from several localities of Abocador de Can Mata (MN7 and MN8, Late Aragonian, Middle Miocene), in els Hostalets de Pierola (Vallès-Penedès Basin, Catalonia, Spain). Although the lack of postcranial material precludes a more extensive comparison between the new species and previously-recognized taxa, the dental morphology and proportions of the new species show that it clearly differs from endemic Iberian species of *Anchitherium*, showing its closest affinities with *A. aurelianense*, *A. hippoides* and *A. steinheimense*, given its small size and marked brachyodonty. Dental size, proportions and occlusal morphology further enable to distinguish the new taxon from the latter species, as detailed in the differential diagnosis, thereby justifying the erection of a new species. From a paleoenvironmental viewpoint, the presence of a small-bodied and brachyodont anchitheriine at ACM fits well with previous paleoecolog-

ical inferences based on the rest of the fauna, indicating the presence of relatively closed and humid forested environments, more similar to those of Late Aragonian French localities than to those from the inner Iberian basins.

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