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## New remains of *Dorcatherium crassum* (Artiodactyla: Tragulidae) from the Early Miocene (MN4) of Els Casots (Subirats, Vallès–Penedès Basin)



### *Nouveaux restes de Dorcatherium crassum (Artiodactyla : Tragulidae) du Miocène inférieur (MN4) de Els Casots (Subirats, bassin de Vallès–Penedès)*

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## ABSTRACT

New tragulid dental remains from the late Early Miocene (16.5–16.3 Ma, MN4) locality of Els Casots (Vallès–Penedès Basin, Catalonia, Spain) are described. This sample fits well, both in size and occlusal morphology, with the material of *Dorcatherium crassum* from the type locality (Sansan, France; MN6). We therefore attribute the tragulid from Els Casots to this species, also in agreement with its known chronostratigraphic range throughout Europe (MN4–MN6) and the previous records of this species from other MN4 localities of the Vallès–Penedès Basin. The described remains – which include the postcanine lower deciduous and permanent dentition, as well as several upper cheek teeth – constitute the most complete sample of *D. crassum* from the Iberian Peninsula. The presence of this species at Els Casots is consistent with the lacustrine depositional environment inferred from sedimentological evidence and associated fauna, and further confirms the nearby presence of densely forested environments with a humid climate with low seasonality.

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## R É S U M É

De nouveaux restes dentaires d'un Tragulidé de la localité de la fin du Miocène inférieur (16,5 à 16,3 Ma, MN4) d'Els Casots (bassin de Vallès–Penedès, Catalogne, Espagne) sont décrits ici. Cet échantillon correspond bien, en termes de taille et de morphologie occlusale, au matériau de *Dorcatherium crassum* de la localité type (Sansan, France; MN6). Nous attribuons donc le Tragulidé d'Els Casots à cette espèce, également d'après sa répartition chronostratigraphique connue dans toute l'Europe (MN4–MN6) et des enregistrements antérieurs de cette espèce dans d'autres localités du MN4 du bassin de Vallès–Penedès.

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Les restes décrits – qui comprennent la dentition postcanine inférieure de lait et permanente, ainsi que plusieurs dents jugales supérieures permanentes – constituent l'échantillon le plus complet de *D. crassum* de la péninsule Ibérique. La présence de cette espèce à Els Casots est compatible avec le milieu de dépôt lacustre déduit des caractéristiques sédimentologiques et de la faune associée; elle confirme aussi la présence, à proximité, d'environnements à forêt dense, témoins d'un climat humide et d'une saisonnalité peu marquée.

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## 1. Introduction

### 1.1. Els Casots

The site of Els Casots was discovered in 1989 and excavated between 1989 and 1994, leading to the recovery of abundant vertebrate fossil remains – including fishes, amphibians, reptiles, birds and both small and large mammals (Moyà Solà and Rius Font, 1993; see Casanovas-Vilar et al., 2011a, for the most updated faunal list of the site). Moyà Solà and Rius Font (1993) provided a general overview of the large mammalian fauna from the site, whereas Agustí and Llenas (1993) reported a preliminary faunal list of the micromammals. Subsequently, only the sciurid and cricetodontid rodents (Aldana Carrasco, 1991, 1992; Ginestí, 2008), the equids (Rotgers and Alba, 2011) and some artiodactyls (Duranthon et al., 1995; Pickford and Moyà Solà, 1994, 1995; van der Made, 1997) have been studied in further detail.

The artiodactyl remains from Els Casots have significantly contributed to the knowledge on late Early Miocene faunas from Iberia. Pickford and Moyà Solà (1994) reported a very complete palaeochoerid cranium, which was subsequently attributed to *Taucanamo primum* by van der Made (1997). Pickford and Moyà Solà (1995) also described a new suid genus and species, *Eurolistriodon adelli*, on the basis of the material from this locality (see also Orliac, 2006). Finally, Duranthon et al. (1995) erected a new genus and species of palaeomyricid, *Ampelomyx ginsburgi*, partially on the basis of material from this site. Apart from these studies, a large portion of the mammalian fauna from Els Casots still remains unpublished. With regard to tragulids, Casanovas-Vilar et al. (2011a, fig. 3.2), Alba et al. (2011, p. 138) and Rössner and Heissig (2013, online resource 2) reported the presence of *Dorcatherium crassum* (Lartet, 1851) in Els Casots, but did not describe the material or justified such a taxonomic attribution. Here we describe and figure all the available tragulid remains from Els Casots and justify its attribution to this species on the basis of comparisons with material from the type locality (Sansan, France; Morales et al., 2012).

### 1.2. Tragulids

Tragulids constitute a clade of small-bodied ruminants with no cranial appendages, and a bunoselenodont to selenodont dentition with large male upper canines. Besides these primitive features, tragulids are characterized by a single main synapomorphy, i.e., the presence of an M-structure in the lower molars (for a review of this

family, see Rössner, 2007). Tragulids occupy a basalmost position among crown ruminants (Hassanin and Douzery, 2003), which coupled with their primitive morphology and physiology has led several researchers to consider them as living fossils (Janis, 1984; Rössner, 2007). Although extant tragulids (mouse deer or chevrotains) display a disjunct distribution in Southeastern Asia as well as western and central Africa, fossil representatives of this family were much more widely distributed across Africa and Eurasia (Rössner, 2007). All European and many African fossil tragulids are referred to the genus *Dorcatherium* (Fig. 1), which includes bunoselenodont to selenodont species that mainly differ in body size, some postcranial adaptations and several occlusal details (Morales et al., 2012; Rössner, 2007; Sánchez et al., 2010). First recorded from the Early Miocene of Africa (Pickford, 2001; Whitworth, 1958), *Dorcatherium* apparently dispersed into Eurasia through the *Gomphotherium*-landbridge by the latest Early Miocene (Sánchez et al., 2010), being recorded then in Europe and slightly later (by the Middle Miocene) in Asia (Rössner, 2007; Sánchez et al., 2010).

The alpha-taxonomy of *Dorcatherium* needs revision, because the morphological disparity of the species currently lumped into that genus suggests that several evolutionary lineages might be included and that, as currently defined, it might be paraphyletic (Rössner, 2007; Rössner and Heissig, 2013; Sánchez et al., 2010). The following European species of *Dorcatherium* are currently distinguished (Alba et al., 2011; Rössner, 2007, 2010; Rössner and Heissig, 2013): *D. crassum* (Lartet, 1851), from the Early to Middle Miocene (MN4–MN6); *D. guntianum*



Fig. 1. Life reconstruction of an adult male of the genus *Dorcatherium*. Artwork by Mauricio Antón.

Fig. 1. Reconstitution d'un animal vivant, mâle adulte du genre *Dorcatherium*. Dessin par Mauricio Antón.

von Meyer, 1846, from the Early to Middle Miocene (MN4–MN7+8); *D. vindebonense* von Meyer, 1846, from the Middle Miocene (MN5–MN6); *D. peneckeii* (Hofmann, 1893), also from the Middle Miocene (MN5 to MN6); *D. nauii* Kaup, 1833, from the Middle to Late Miocene (MN7+8–MN11); *D. jourdani* (Depéret, 1887), from the Late Miocene (MN11/12); *D. puyhauberti* Arambourg and Piveteau, 1929, also from the Late Miocene (MN11/12); and *D. bulgaricum* Bakalov and Nikolov, 1962, probably from the Pliocene. The remains of *D. crassum* described in this paper represent the largest known sample of *D. crassum* from the Iberian Peninsula, and one of the oldest samples of *Dorcatherium* across Europe.

## 2. Age and geological background

The site of Els Casots is situated 600 m north of the farmhouse of Cal Sutxet (Subirats, Catalonia, Spain), in the southern margin of the Vallès-Penedès Basin (Casanovas-Vilar et al., 2011a; Fig. 2). The fossils were recovered from several different facies of palustrine to lacustrine deposits (see Casanovas-Vilar et al., 2011a, fig. 2, for additional details). These sediments overlie the Mesozoic substrate (Casanovas-Vilar et al., 2011a, b) and correspond to a small paleolake (ca. 500 × 100 m in size; Moyà Solà and Rius Font, 1993). Given the lack of magnetostratigraphic data, the dating of the site relies on litho- and biostratigraphic evidence (Casanovas-Vilar et al., 2011a). In particular, the lacustrine system from Els Casots is integrated in the Detritic-Carbonated Unit of Subirats (Casanovas-Vilar et al., 2011a, b), which is Burdigalian in age (Cabrera et al., 1991; de Gibert and Casanovas-Vilar, 2011). The micromammal remains further enable us to correlate Els Casots with the local biozone C of the Calatayud-Daroca Basin (MN4, Early Aragonian), with an estimated age of 16.5–16.3 Ma (Casanovas-Vilar et al., 2011a, b).

## 3. Materials and methods

### 3.1. Abbreviations

**Measurements:** MD, mesiodistal length (in mm); BL, labiolingual breadth (in mm).

**Institutions and fossil collections:** ICP, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Cerdanyola del Vallès (Catalonia, Spain); IPS, acronym of the ICP collections (former Institut de Paleontologia M. Crusafont); MNHN, Muséum national d'Histoire naturelle, Paris (France).

### 3.2. Studied material and comparative sample

The fossil remains described in this paper (Table 1) are housed at the ICP. The comparative sample includes dentognathic remains of *D. crassum* from Sansan, housed at the MNHN (see list of material in Morales et al., 2012, p. 229), as well as material of *D. nauii* from Iberian localities (mainly from the Vallès-Penedès Basin; see Alba et al., 2011, p. 137–138). Dental measurements (MD and BL) for *Dorcatherium* species from Europe were also taken from the literature (Alba et al., 2011; Antunes et al., 1994; Czyżewski

**Table 1**

List of specimens of *Dorcatherium crassum* from Els Casots described in this paper.

**Tableau 1**

Liste des spécimens de *Dorcatherium crassum* d'Els Casots décrits dans ce travail.

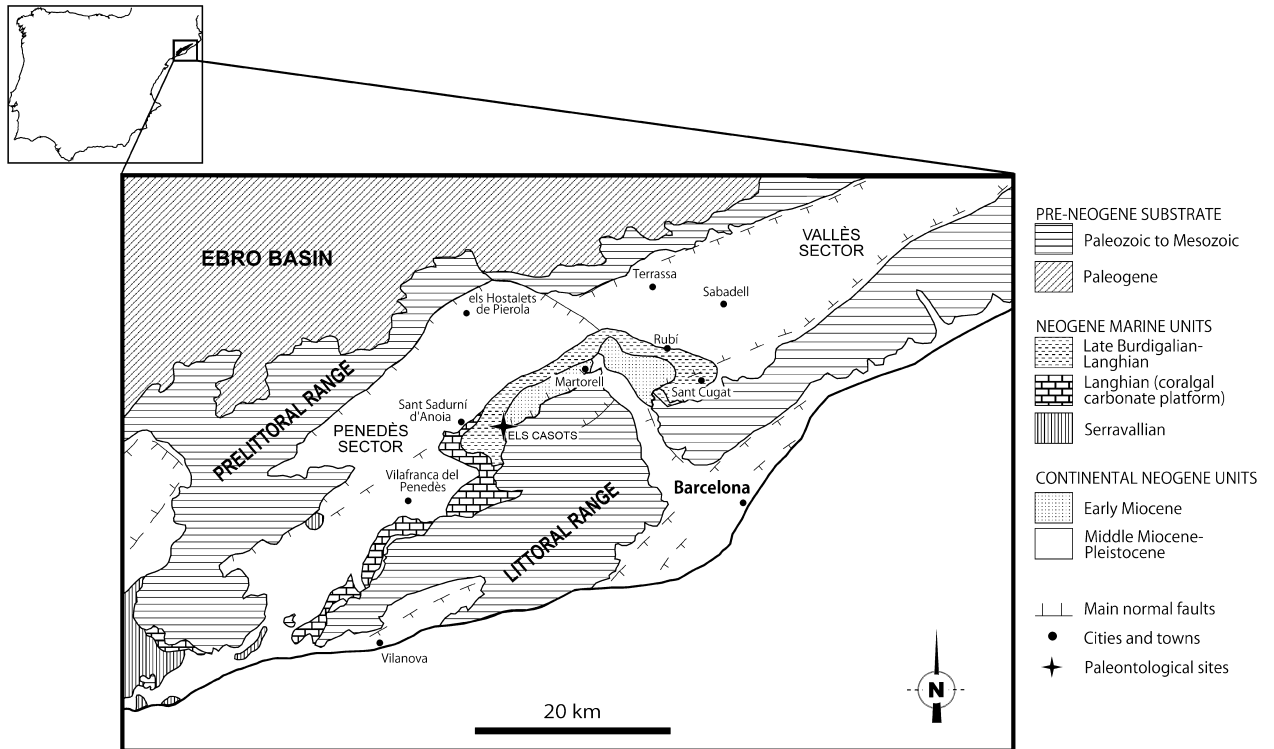
Catalogue No.	Description	Figure
IPS24106	Right mandibular corpus with dp1–m1 series (m2 erupting in crypt)	Fig. 4A
IPS24607	Right mandibular corpus with p1–m3 series (m1 broken)	Fig. 5B
IPS24753a	Right maxillary fragment with P4–M3 and associated five lower incisors	Fig. 6A
IPS24753b	Left mandibular fragment with p3–p4	Fig. 5C
IPS24753c	Left mandibular fragment with m1–m3	Fig. 5D
IPS24757	Left mandibular fragment with dp3–m2	Fig. 4D
IPS24758	Right mandibular fragment with dp1–m2	Fig. 4B
IPS57512	Left mandibular corpus with dp2–m2	Fig. 4C
IPS57513	Right mandibular fragment with dp4–m2 and distal lobe of dp3	Fig. 5A
IPS63879	Right unerupted germ of M3	Fig. 6B

and Stefaniak, 1994; Fahlbusch, 1985; Ginsburg and Bulot, 1987; Hillenbrand et al., 2009; Kaup, 1839; Montoya and Morales, 2004; Morales and Soria, 1981; Morales et al., 2012; Mottl, 1961, 1966; Moyà-Solà, 1979a; Rössner and Heissig, 2013; Sach, 1999), in order to construct bivariate plots of dental proportions.

### 3.3. Dental nomenclature

Providing references for the dental nomenclature employed in any descriptive study is important for avoiding misunderstanding (Bärnmann and Rössner, 2011). As in Alba et al. (2011), the nomenclature used in this paper generally follows Gentry et al. (1999, fig. 23.1), although with some exceptions and also substituting the terms anterior/posterior by mesial/distal (following the recommendation by Smith and Dodson, 2003). This terminology, which is illustrated in Fig. 3, differs in some other regards from that employed by other authors (e.g., Sánchez and Morales, 2008, fig. 3; after Azanza, 2000) and also from the new terms more recently suggested by Bärnmann and Rössner (2011, figs. 2–3), especially regarding the names of the premolar cusps and crests. Although we understand the need to homologize dental terminology in ruminants, the nomenclature recommended by Bärnmann and Rössner (2011) sometimes departs from the more general terms employed for mammals in general. The latter are favored here on the basis of spatial analogy – i.e., without implying homology between premolar and molar crests and cusps, or between different mammalian orders.

Following Gentry et al. (1999), “hypocone” is therefore used instead of “metaconule” (e.g., Bärnmann and Rössner, 2011) for the distolingual cone of upper molars, with concomitant changes in the associated crests (e.g., “prehypocrista” instead of “premetaconule-crista”). In contrast, the lingual cone of the upper premolars is termed “protocone” (following Hamilton, 1973) instead of “hypocone” (Gentry et al., 1999). With regard to the accessory crest that is present distally from the protocone in the upper molars

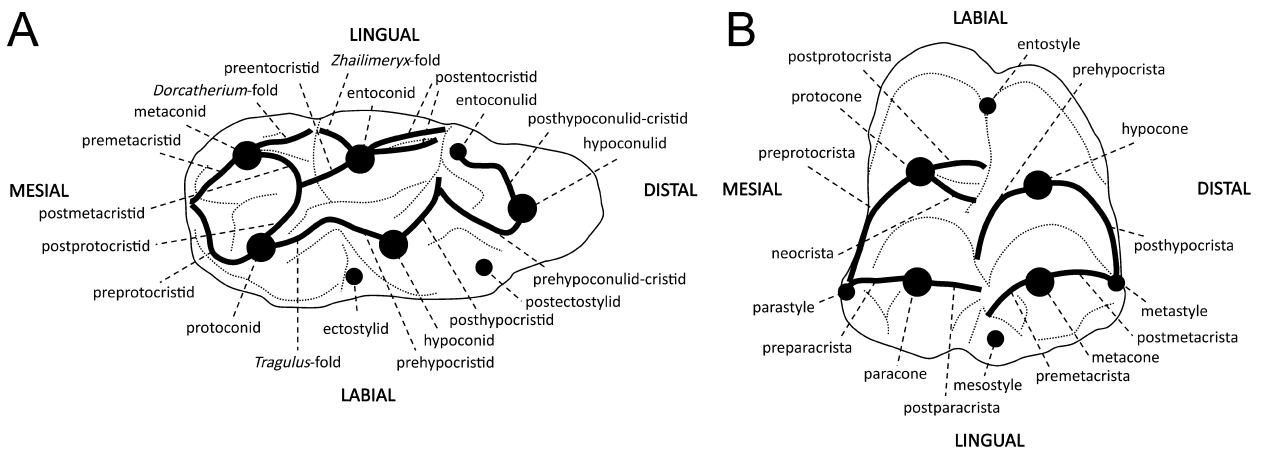


**Fig. 2.** Schematic geological map of the Vallès-Penedès Basin, showing the main geological units as well as the situation of Els Casots. Modified from an original kindly provided by Isaac Casanovas-Vilar and Àngel H. Luján.

**Fig. 2.** Carte géologique schématique du bassin de Vallès-Penedès, montrant les principales unités géologiques ainsi que la situation d'Els Casots. Modifié à partir d'un original aimablement fourni par Isaac Casanovas-Vilar et Àngel H. Luján.

of cervoids and tragulids, “neocrista” is employed instead of “central fold” (Azanza, 2000) or “internal postprotocrista” (Bärmann and Rössner, 2011). Finally, regarding the particularly complex crest pattern (M-structure) present on the distal slope of the trigonid in tragulids, following

Sánchez et al. (2010, fig. 4; see also Sánchez et al., 2011; Alba et al., 2011; Morales et al., 2012) “*Dorcattherium*-fold” is employed for the cristid running distolingually from the metaconid (“external postmetacristid” of Bärmann and Rössner, 2011), whereas “*Tragulus*-fold” is preferred



**Fig. 3.** Dental nomenclature employed in this paper, illustrated in schematic drawings of lower and upper third molars of *Dorcattherium crassum* from Els Casots: **A**, left m3 (IPS24753c); **B**, right M3 (IPS63879). Cones/-ids are depicted by circles, cristae/-ids by thick lines, and grooves and cingula by dotted lines.

**Fig. 3.** Nomenclature dentaire utilisée dans cet article, illustrée dans les schémas des troisièmes molaires, inférieure et supérieure de *Dorcattherium crassum* d'Els Casots: **A**, m3 gauche (IPS24753c); **B**, M3 droite (IPS63879). Les cônes/-ids son représentés par des cercles, les cristae/-ides par des lignes épaisses, et les sillons et cingulums par des lignes pointillées.

over “*Palaeomeryx*-fold” (“external postprotocristid” of [Bärmann and Rössner, 2011](#)) for referring to the cristid running distolabially from the protoconid in tragulids. For the sake of clarity, it is also necessary to specify that the term “cleft” refers to indentations or depressions on the labial/lingual crown walls, that the term “notch” refers to vertical incisions on the crown occlusal profile in labial/lingual views, and that occlusal valleys or fossae are referred to as “fossettes/-ids”.

#### 4. Systematic paleontology

Class: MAMMALIA [Linnaeus, 1758](#)  
 Order: ARTIODACTYLA [Owen, 1848](#)  
 Suborder: RUMINANTIA [Scopoli, 1777](#)  
 Infraorder: TRAGULINA [Flower, 1883](#)  
 Family: TRAGULIDAE [Milne Edwards, 1864](#)  
 Genus *Dorcatherium* [Kaup, 1833](#)  
*Dorcatherium crassum* ([Lartet, 1851](#))  
 (Figs. 4–6)

**Neotype:** Left hemimandible with p2–m3 (MNHN Sa 9950), designated by [Morales et al. \(2012, figs. 1–3\)](#).

**Type locality:** Sansan (MN6, Middle Miocene; Gers, France).

**Studied material:** See [Table 1](#).

**Measurements:** See [Table 2](#) for measurements of the described material, and [Fig. 7](#) for dental proportions compared to European tragulid species (including *D. crassum* from the type locality).

##### 4.1. Description

**Lower dentition:** All the deciduous lower premolars can be described on the basis of several juvenile specimens. IPS24106 ([Fig. 4A](#)) and IPS24758 ([Fig. 4B](#)) preserve the whole lower deciduous (dp1–dp4) series, whereas IPS57512 ([Fig. 4C](#)) displays the dp2–dp4 row, and IPS24757 ([Fig. 4D](#)) and IPS57513 ([Fig. 5A](#)) have the dp3–dp4 portion (although it is too worn in IPS24757 and damaged in IPS57513). The length of the lower deciduous premolar row (dp2–dp4) is 35.9 mm in IPS24106, 35.5 mm in IPS24758 and 34.4 mm in IPS57512.

The dp1 is present in all the juvenile specimens that preserve the appropriate region of the mandible: IPS24106 ([Fig. 4A](#)) and IPS24758 ([Fig. 4B](#)); its presence can be also inferred for IPS57512 ([Fig. 4C](#)), in which the distal portion of its alveolus, filled with sediment, is preserved. It is a short, unicuspid and uniradicated tooth, similar in morphology and dimensions to the p1 (see below). The dp1 is not followed by any conspicuous diastema, merely being separated from the dp2 by a space of 1–2 mm.

The dp2 and dp3 are tricuspid, and similar in size and occlusal morphology to the p2 and p3 (see below), respectively, although with some differences. The deciduous ones, in particular, are slightly more labiolingually compressed and lower-crowned than the permanent corresponding premolars. Moreover, the former also show more clearly double cristids on the distal slopes of the protoconid and hypoconid—this is best ascertained in

**Table 2**

Dental measurements of *Dorcatherium crassum* from Els Casots.

**Tableau 2**

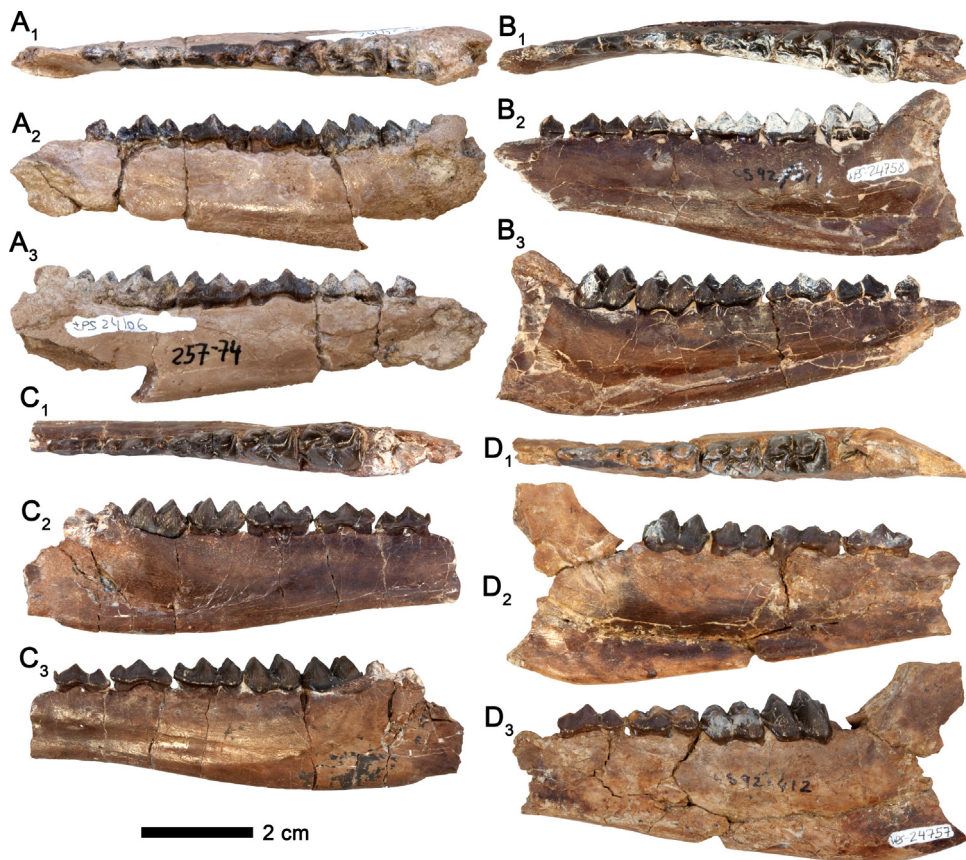
Mesures dentaires de *Dorcatherium crassum* d’Els Casots.

Tooth	Side	Catalogue No.	MD	BL
dp1	Right	IPS24106	5.3	3.0
dp1	Right	IPS24758	5.1	2.7
dp2	Right	IPS24106	11.6	3.9
dp2	Right	IPS24758	10.7	3.1
dp2	Left	IPS57512	10.5	3.1
dp3	Right	IPS24106	11.9	4.0
dp3	Left	IPS24757	12.7	4.0
dp3	Right	IPS24758	12.0	3.3
dp3	Left	IPS57512	11.6	3.5
dp4	Right	IPS57513	12.4	6.1
dp4	Right	IPS24106	12.3	6.4
dp4	Left	IPS24757	13.0	6.0
dp4	Right	IPS24758	12.4	5.8
dp4	Left	IPS57512	12.8	5.9
P4	Right	IPS24753a	9.0	9.6
M1	Right	IPS24753a	10.4	11.4
M2	Right	IPS24753a	12.6	13.5
M3	Right	IPS24753a	12.5	–
M3	Right	IPS63879	13.2	15.8
p1	Right	IPS24607	4.7	2.6
p2	Right	IPS24607	11.3	4.0
p3	Right	IPS24607	11.7	4.2
p3	Left	IPS24753b	12.6	4.5
p4	Right	IPS24607	11.3	5.6
p4	Left	IPS24753b	11.8	5.7
m1	Right	IPS57513	11.5	7.7
m1	Right	IPS24106	10.8	7.5
m1	Left	IPS24753c	11.7	7.0
m1	Left	IPS24757	11.1	7.6
m1	Right	IPS24758	10.2	7.2
m1	Left	IPS57512	10.6	7.3
m2	Right	IPS24607	10.9	8.9
m2	Right	IPS57513	12.1	8.7
m2	Left	IPS24753c	11.8	9.0
m2	Left	IPS24757	12.4	8.6
m2	Right	IPS24758	11.6	8.1
m2	Left	IPS57512	12.1	8.3
m3	Right	IPS24607	17.9	8.8
m3	Left	IPS24753c	17.5	8.5

MD: mesiodistal length (in mm); BL: labiolingual breadth (in mm).

IPS57512 ([Fig. 4C](#)) and IPS24758 ([Fig. 4B](#)). Moreover, the dp2 is generally shorter than the p2 and, unlike the latter, displays a comparatively reduced protoconulid, as well as a preprotocristid that is longer than the distal cristid of the protoconid. There is some variation in dp2 occlusal morphology, with that of IPS24106 ([Fig. 4A](#)) displaying a larger and more distinct protoconulid and a shorter preprotocristid—thereby resembling in these regards a p2, from which it differs by being lower-crowned.

The dp4 is molariform, although trilobulated, and longer and more labiolingually compressed than the permanent molars. The central and the distal lobes resemble a permanent molar in occlusal morphology (see below). With regard to the mesial lobe, in the less worn specimen (IPS57512; [Fig. 4C](#)), a distinct and relatively large paraconid can be discerned close to the mesiolingual corner of the crown, whereas a much reduced and slightly more distally-positioned cusp (protoconulid) is present on the labial side. Both the very short preparacristid and the slightly longer preprotoconulid-cristid merge close to the mesial-most portion of the crown. The postparacristid and



**Fig. 4.** (Color online). Lower dentognathic remains of *Dorcatherium crassum* from Els Casots. **A**, IPS24106, right dp1–m1 (m2 in crypt), in occlusal (A<sub>1</sub>), lingual (A<sub>2</sub>) and labial (A<sub>3</sub>) views; **B**, IPS24758, right dp1–m2, in occlusal (B<sub>1</sub>), lingual (B<sub>2</sub>) and labial (B<sub>3</sub>) views; **C**, IPS57512, left dp2–m2, in occlusal (C<sub>1</sub>), lingual (C<sub>2</sub>) and labial (C<sub>3</sub>) views; **D**, IPS24757, left dp3–m2, in occlusal (D<sub>1</sub>), lingual (D<sub>2</sub>) and labial (D<sub>3</sub>) views.

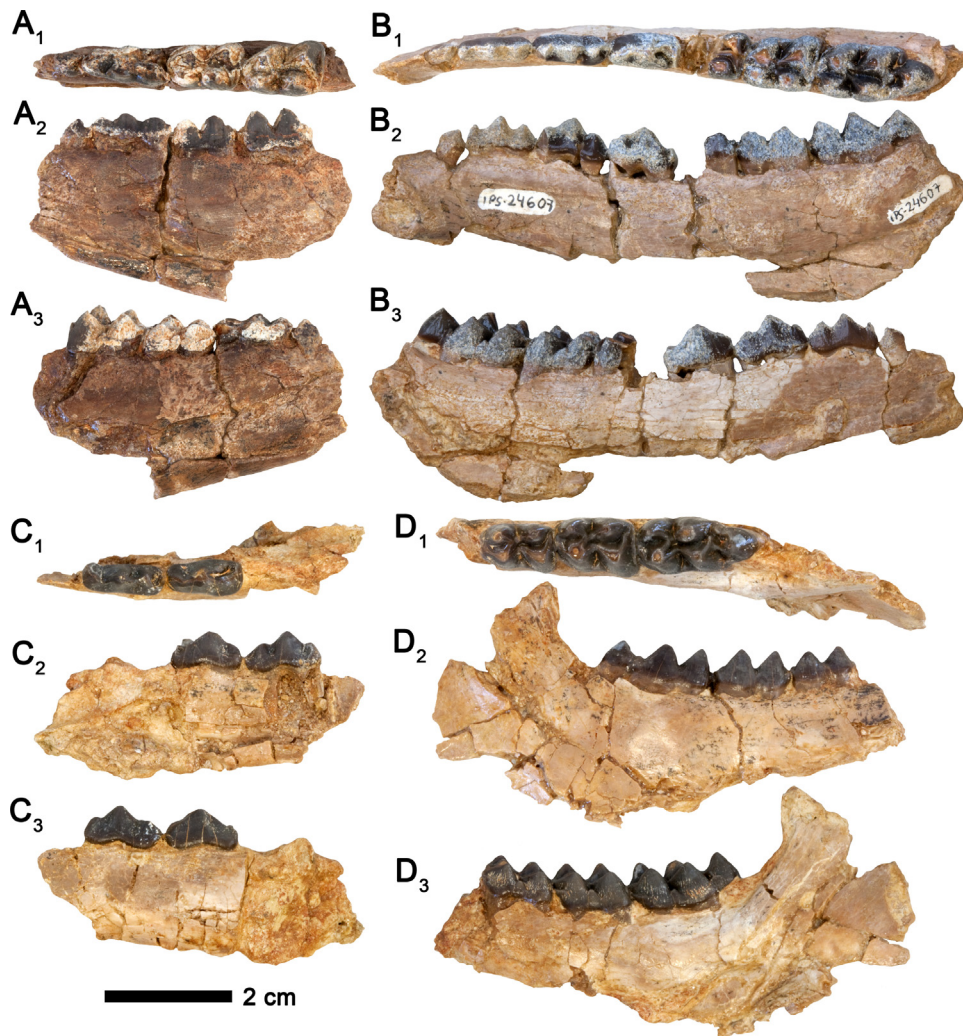
**Fig. 4.** (Couleur en ligne). Restes dentognathiques inférieures de *Dorcatherium crassum* d'Els Casots. **A**, IPS24106, dp1–m1 (m2 dans la cavité) droites, en vues occlusale (A<sub>1</sub>), linguale (A<sub>2</sub>) et labiale (A<sub>3</sub>); **B**, IPS24758, dp1–m2, droites, en vues occlusale (B<sub>1</sub>), linguale (B<sub>2</sub>) et labiale (B<sub>3</sub>); **C**, IPS57512, dp2–m2 gauches, en vues occlusale (C<sub>1</sub>), linguale (C<sub>2</sub>) et labiale (C<sub>3</sub>); **D**, IPS24757, dp3–m2 gauches, en vues occlusale (D<sub>1</sub>), linguale (D<sub>2</sub>) et labiale (D<sub>3</sub>).

postprotoconulid-cristid (respectively directed towards the steeper premetacristid and preprotocristid) are much longer than the former and show an incipient development of double cristids. On the central lobe, the cristids on the distal slope of the trigonid are clearly double, constituting a well-developed M-structure (with *Dorcatherium*- and *Tragulid*-folds) analogous to that of the permanent molars. A double crest pattern is much reduced in the entoconid, whereas the hypoconid is clearly selenodont, as in the permanent molars. There are narrow but distinct mesial and distal cingulids; the former extends labially to the very weak (almost non-existent) ectostylid; the distal cingulid is also prolonged labially beyond the small, but much more distinct, postectostylid.

With regard to the lower permanent dentition, it is preserved in several partial hemimandibles. The whole postcanine dentition (including the p1) is preserved in the adult specimen IPS24607 (Fig. 5B), although the m1 is broken. With regard to the premolars, the morphology of the p3 and p4 can be also described on the basis of IPS24753b (Fig. 5C). The length of the premolar row (only considering the p2–p4 series) is 34.3 mm in IPS24607 (Fig. 5B).

The p1 is thus present in the only adult specimen (IPS24607) that preserves the appropriate region of the mandible (Fig. 5B). This tooth is rather short, labiolingually compressed, unicuspid and uniradicated. Its single cuspid is acuminate and slightly tilted distalwards, and possesses two mesiodistally-aligned cristids: the preprotocristid, which is convex in labial/lingual view; and the somewhat shorter and concave postprotocristid. The labial wall of the p1 is uniformly convex, whereas the lingual one displays two (mesial and distal) loosely-defined and shallow clefts. The p1 is followed by the p2 without any diastema.

The p2 and p3, much longer than the p1, are very labiolingually compressed (slightly more so on the mesial than on the distal portion of the crown) and have a trenchant appearance. These teeth are quite similar to one another, although the p3 is slightly longer and to some extent broader than the p2. Unlike the p1, both the p2 and the p3 are tricuspid, with the central cusp (protoconid) being higher (more so in the p3) than both the distal cusp (hypoconid) and, especially, the mesial one (protoconulid); no lingual cusp is present. The three



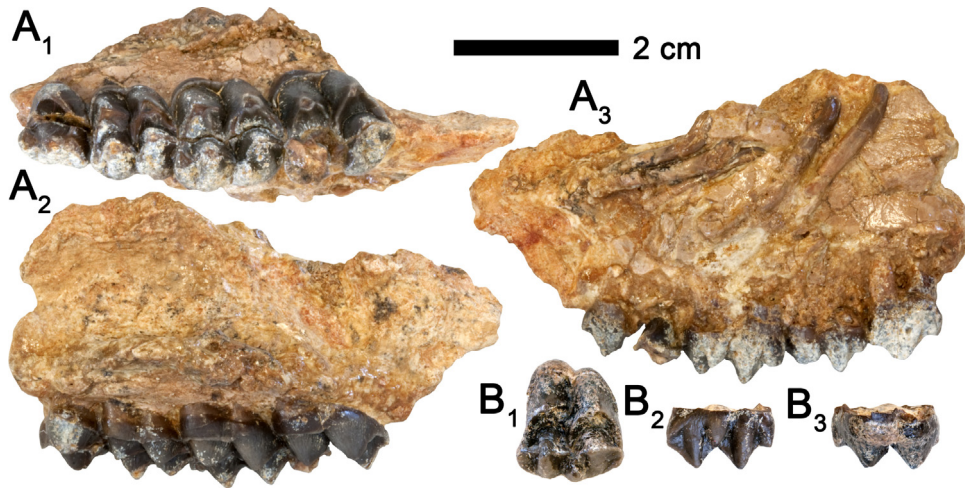
**Fig. 5.** (Color online). Lower dentognathic remains of *Dorcatherium crassum* from Els Casots. **A**, IPS57513, right dp4–m2, in occlusal (A<sub>1</sub>), lingual (A<sub>2</sub>) and labial (A<sub>3</sub>) views; **B**, IPS24607, right p1–m3, in occlusal (B<sub>1</sub>), lingual (B<sub>2</sub>) and labial (B<sub>3</sub>) views; **C**, IPS24753b, left p3–p4, in occlusal (C<sub>1</sub>), lingual (C<sub>2</sub>) and labial (C<sub>3</sub>) views; **D**, IPS24753c, left m1–m3, in occlusal (D<sub>1</sub>), lingual (D<sub>2</sub>) and labial (D<sub>3</sub>) views.

**Fig. 5.** (Couleur en ligne). Restes dentognathiques inférieurs de *Dorcatherium crassum* d'Els Casots. **A**, IPS57513, dp4–m2 droites, en vues occlusale (A<sub>1</sub>), linguale (A<sub>2</sub>) et labiale (A<sub>3</sub>); **B**, IPS24607, p1–m3 droites, en vues occlusale (B<sub>1</sub>), linguale (B<sub>2</sub>) et labiale (B<sub>3</sub>); **C**, IPS24753b, p3–p4 gauches, en vues occlusale (C<sub>1</sub>), linguale (C<sub>2</sub>) et labiale (C<sub>3</sub>); **D**, IPS24753c, m1–m3 gauches, en vues occlusale (D<sub>1</sub>), linguale (D<sub>2</sub>) et labiale (D<sub>3</sub>).

cusps of the p2 and p3 are mesiodistally aligned, and well distinct from one another in labial/lingual view. The protoconulid, better developed in the p3 than in the p2, possesses poorly-defined associated crests. The protoconid, in contrast, displays well-developed mesial and distal crests of similar length. Whereas the mesial one (preprotocristid) is clearly single, the distal one is partially divided by a distolingually-directed vertical groove, indicating an incipient development of a double cristid (although the distolingual one is much shorter and indistinct than the more mesiodistally-aligned cristid). The hypoconid is intermediate in size between the protoconid and the protoconulid; the former shows a mesiodistally-aligned and short prehypocristid, as well as a much longer posthypocristid. The latter originates from the distolabial aspect of the hypoconid, but abruptly curves until ending

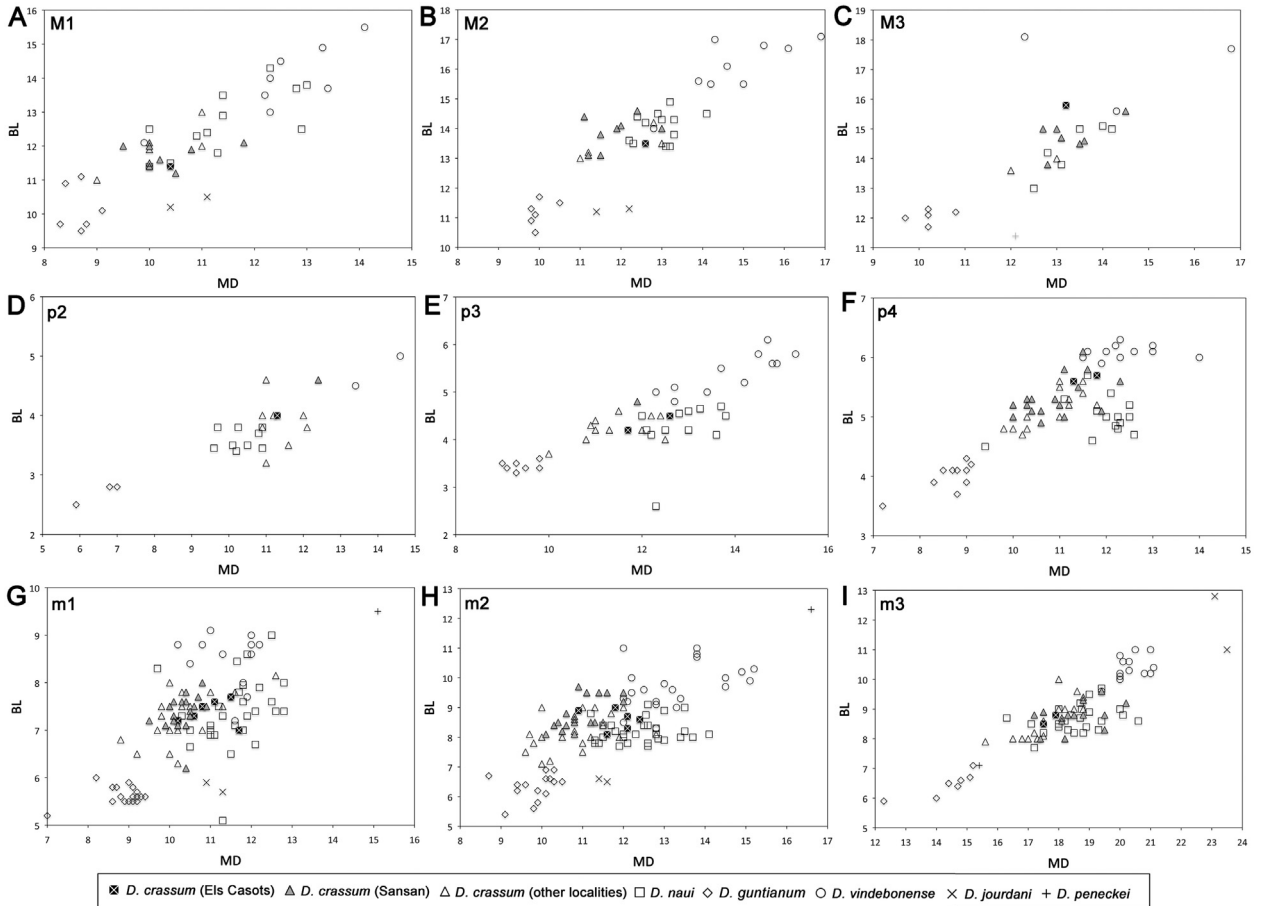
at the distolingual corner of the crown, thereby distally enclosing the very restricted (groove-like) and obliquely-oriented distal fossettid. The labial crown wall is almost continuous, except for a shallow and little distinct distal cleft in the p3 (almost non-existent in the p2). In contrast, on the lingual crown wall the conids are much more distinct due to the presence of deeper and more distinct mesial and distal clefts. No distinct cingulids are present.

The p4 is slightly shorter in absolute terms and clearly broader in relative terms than the two preceding premolars, from which it further differs by a more triangular shape in labial view (with less distinct protoconulid and hypoconid). Like in the p2 and p3, no lingual cusps are present. From the apex of the narrow and acuminate protoconid, a single preprotocristid descends mesially towards the poorly-developed protoconulid. The latter, which also



**Fig. 6.** (Color online). Upper dentognathic remains of *Dorcatherium crassum* from Els Casots. **A**, IPS24753a, right P4–M3, in occlusal (A<sub>1</sub>), lingual (A<sub>2</sub>) and labial (A<sub>3</sub>) views; **B**, IPS63879, right M3, in occlusal (B<sub>1</sub>), labial (B<sub>2</sub>) and lingual (B<sub>3</sub>) views.

**Fig. 6.** (Couleur en ligne). Restes dentognathiques supérieurs de *Dorcatherium crassum* d'Els Casots. **A**, IPS24753a, P4–M3 droites, en vues occlusale (A<sub>1</sub>), linguale (A<sub>2</sub>) et labiale (A<sub>3</sub>); **B**, IPS63879, M3 droite, en vues occlusale (B<sub>1</sub>), labiale (B<sub>2</sub>) et linguale (B<sub>3</sub>).



**Fig. 7.** Dental proportions (labiolingual breadth vs. mesiodistal length) of *Dorcatherium crassum* from Els Casots, compared to *Dorcatherium* species from other European localities: **A**, M1; **B**, M2; **C**, M3; **D**, p2; **E**, p3; **F**, p4; **G**, m1; **H**, m2; **I**, m3. See [Material and Methods](#) for data sources.

**Fig. 7.** Proportions dentaires (largeur labiolinguale vs. longueur mésiodistale) de *Dorcatherium crassum* d'Els Casots, comparées à celles des espèces de *Dorcatherium* d'autres localités européennes: **A**, M1; **B**, M2; **C**, M3; **D**, p2; **E**, p3; **F**, p4; **G**, m1; **H**, m2; **I**, m3. Voir le paragraphe [Matériel et Méthodes](#) pour les sources des données.



possesses a single and short cristid of mesiolingual direction (preparacristid), is more or less distinct due to the presence of a subtle notch (discernible in labial view, when not eroded by wear) as well as a shallow mesial lingual cleft. As in the lower molars, two clearly distinct cristids originate distally from the tip of the p4 protoconid: the relatively long and obliquely-aligned postprotocristid, which ends close to the distolingual corner of the crown; and a longer and more distally-directed cristid, which ends in a small and little conspicuous hypoconid with no distinct prehypocristid. The hypoconid is centrally situated at the distal-most portion of the crown. The two distal cristids of the protoconid delimit a relatively deep but narrow fossettid, which is much longer than in the preceding premolars. This fossettid is distally enclosed by the hypoconid as well as by the short and lingually-directed posthypocristid. The end of the latter is however separated from that of the postprotocristid by a groove-like prolongation of the distal fossettid on the lingual crown wall. A relatively marked but narrow lingual cleft is present at about the level where the more labial distal crest of the protoconid originates. Unlike in the preceding premolars, very faint mesiolabial and mesiolingual cingulids – the latter observable only in IPS24753b (Fig. 5C) – are present.

The lower molars show a bunoselenodont occlusal morphology, with relatively low crowns and pyramidal cusps with a not very marked occlusal relief; the labial walls are rugose. The length of the molar row is 39.6 mm in IPS24607 (Fig. 5B) and 40.4 mm in IPS24753c (Fig. 5D), which are the only adult specimens preserving the whole molars series. The morphology of the m1 and/or m2 can be also ascertained in several juvenile individuals: IPS24106 (Fig. 4A), IPS24757 (Fig. 4D), IPS24758 (Fig. 4B), IPS57512 (Fig. 4C) and IPS57513 (Fig. 5A). The m1 and m2 display a subrectangular occlusal profile with two distinct lobes (separated by a deep and wide labial cleft and a narrower, shallower and groove-like lingual one), whereas the m3 is more elongate and markedly oval (distally tapering) with three distinct lobes.

The morphology of the m1 and m2 can be best studied in the juvenile specimens IPS24758 (Fig. 4B) and IPS57512 (Fig. 4C), due to their good state of preservation coupled with their slight degree of wear. The m1 and m2 display a similar occlusal morphology, with the distal lobe being broader than the mesial one; the m1 is however smaller and relatively narrower than the m2 – especially at the mesial lobe, so that the protoconid and metaconid are closer to one another. The protoconid shows a long preprotocristid that curves along the mesial-most end of the crown, until merging with the shorter and straighter premetacristid. The distal slope of the trigonid has a well-developed M-structure. The *Tragulus*-fold is directed towards the prehypocristid, whereas the postprotocristid, more obliquely aligned, runs until merging with the postmetacristid close to the distal end of the latter (more mesially than the level of the lingual cleft). Besides the postmetacristid, the metaconid displays a more lingual cristid (*Dorcatherium*-fold), of similar length than the former, and directed towards the metaconid (from which it is separated by the lingual cleft). The conical entoconid shows two mesial cristids of moderate length,

which are situated opposite to the distal cristids of the metaconid. The more lingual accessory cristid (i.e., a rudimentary *Zhailimeryx*-fold) is directed to (but does not contact with) the *Dorcatherium*-fold; the more labial preentocristid, in turn, is directed towards the distal end of the postmetacristid. The postentocristid is also double – i.e., it displays a deep and narrow incision along its midline, being composed of two twinned cristids, which end at the distolingual corner of the crown. The hypoconid is more selenodont than the remaining cusps; the prehypocristid is single and short, like the markedly posthypocristid, which is much longer than the former. The posthypocristid extends until close to the distolingual portion of the crown, somewhat distally from the base of the entoconid, without reaching the ends of the double postentocristid. There are marked mesial and distal cingulids, as well as an ectostylid of moderate size (slightly more reduced in the m2 than in the m1), but no distinct labial cingulid.

The m3 has two main lobes (mesial and central) that are similar in occlusal morphology to the two lobes of the preceding molars, as well as a distal, hypoconulid-bearing lobe, which is narrower than the former. This third lobe, which is centrally situated and aligned with the major mesiodistal axis of the crown, is separated from the central lobe by a wide and deep labial cleft as well as by a much less marked and groove-like lingual cleft. The hypoconulid is well developed (only subequal to the remaining cusps). Unlike in the preceding molars, the posthypocristid shows at about its mid-length a distal bifurcation directed to the mesial end of the prehypocristid-cristid. The posthypocristid-cristid is similarly curved but longer than the prehypocristid-cristid; the former ends, without connecting to the posthypocristid, close to the postentocristid, where it constitutes a cuspid-like thickening that might be interpreted as a vestigial entoconulid. Like the preceding molars, the m3 displays a marked mesial cingulid, as well as a distinct ectostylid that is however slightly smaller than in the preceding molars. Unlike in the latter, the m3 shows around the base of the hypoconid a poorly-defined labial cingulid, which runs from the ectostylid to the weakly-developed postectostylid.

**Upper dentition:** No upper deciduous teeth are preserved in the sample from Els Casots. With regard to the upper permanent teeth, they are represented by a P4–M3 row (IPS24753a; Fig. 6A), with a moderate degree of wear but slightly damaged P4 and M3, as well as by an isolated unerupted germ of M3 (IPS63879; Fig. 6B). The upper molar series is 34.0 mm in length (IPS24753a; Fig. 6A). All the upper cheek teeth are brachyodont and not markedly selenodont.

The P4 shows a triangular occlusal outline that is slightly broader than long. It displays a single and large labial cusp (paracone) that is somewhat tilted distalwards, so that the preparacrista is slightly longer than the postparacrista. The latter ends in a poorly defined metastyle, whereas the parastyle at the end of the preparacrista is comparatively more developed. The fossette is quite restricted and broader than long. The protocone is pyramidal and more selenodont than the paracone; the preprotocrista joins the parastyle, whereas the postprotocrista ends distally

from the paracone base close to the beginning of the post-paracrista. There is a narrow but distinct lingual cingulum.

The molars show a subquadrangular occlusal outline with four distinct cusps, being slightly broader than long. The M1 is markedly smaller than the M2 and M3; the latter, in turn, is similar in length to the M2, but is relatively broader and has a more retracted distal lobe. The paracone is very voluminous and robust – discounting an attribution to contemporaneous cervids, such as *Procervulus* or *Dicrocerus* – and higher than the remaining cusps. The paracone has a marked labial pillar (especially in the M2 and M3), and its associated crests (preparacrista and postparacrista) are short and low. The preparacrista ends in a well-developed parastyle. The mesostyle is large and well individualized, markedly protruding from the rest of the labial crown wall. The metacone is only subequal in size to the paracone, but slightly less peripheral, clearly more labiolingually compressed, and with a less protruding labial pillar (although distinct, except in the M1). Compared to the crests of the paracone, both the premetacrista and the postmetacrista are slightly longer; the latter ends in a weak metastyle. A moderately-developed labial cingulum is present distally around the base of the metacone, at least in the M3 (it cannot be properly ascertained in the preceding molars). The protocone is pyramidal. The pre-protocrista is very long, joining the parastyle. Distally from the protocone there are two distinct crests (which can be best appreciated in the two M3s, due to their lesser degree of wear): a short postprotocrista, which is distally directed and ends at the transverse groove separating the bases of protocone and metacone; and a distolabially-directed neocrista. The latter crest originates distally (IPS24753a; Fig. 6A) or distolabially (IPS63879; Fig. 6B) from the protocone, and ends at the above-mentioned groove close to the end of the prehypocrista and the base of the paracone. The hypocone, slightly more peripherally situated than the protocone (except in IPS63879), is semicircular, with the posthypocrista joining the poorly-constituted metastyle, and the prehypocrista ending between the bases of the protocone and the metacone (close to the end of the postparacrista). A strong lingual cingulum is present along the base of the protocone. This cingulum is weaker and more irregularly developed distally around the base of the hypocone, being continuous until the distal aspect of the hypocone (the M3 IPS63879 and the M1 of IPS24753a) or interrupted at about its mid-length (in the M2 and M3 of IPS24753a). The entostyle is moderate in size, just representing a triangular thickening of the lingual cingulum. The enamel on the lingual wall is rugose.

#### 4.2. Dental size and proportions

The dental size of the *Dorcatherium* sample from Els Casots (Table 2) corresponds to a medium-sized tragulid, which enables discounting an attribution to other European species except *D. crassum* and the type species of the genus, *D. nauti* (Fig. 7; see also Alba et al., 2011; Morales et al., 2012; Rössner, 2010; Rössner and Heissig, 2013, online resource 1). The teeth of both species are on average larger than those of *D. guntianum* and smaller than those of *D. vindebonense* (Fig. 7).

*Dorcatherium nauti* tends to display on average slightly larger upper and lower cheek teeth than *D. crassum* (Fig. 7) in absolute terms, with the exception of the p2 (Fig. 7D). In relative terms, the p4 tends to be relatively broader in *D. crassum* (Fig. 7F). There is however a considerable overlap in occlusal dimensions between the two species – especially when the sample of *D. crassum* from Sandelzhausen is taken into account (see Rössner, 2010). Taken as a whole, the premolar row (p2–p4) in *D. crassum* is shorter relative to the molar series than in *D. nauti* from the Vallesian (Morales et al., 2012) – the exception being the late Aragonian *D. nauti meini* Alba et al., 2011. In the single specimen from Els Casots in which this relationship can be computed (IPS24607), the premolar row is shorter than the molar row (87%). This specimen therefore differs in this regard from *D. nauti nauti* (99%, N=2; Morales et al., 2012) and falls instead within the range of variation of *D. crassum* from Sansan (89%, range 84–94%, N=7; data taken from Morales et al., 2012, fig. 85) – although it is also similar to the paratype of *D. nauti meini* IPS4422 (85%; Alba et al., 2011).

Overall, the *Dorcatherium* sample from Els Casots is metrically quite similar to that of *D. crassum* from the type locality (Fig. 7). However, given that these two species largely overlap in dental size and proportions (Fig. 7), an attribution to either of them is not warranted solely on metrical grounds (Alba et al., 2011).

## 5. Discussion

### 5.1. Taxonomic attribution

In the past, some authors (e.g., Gentry et al., 1999; Hofmann, 1893; Hünermann, 1983. Rüttimeyer, 1883. Schlosser, 1886) considered *D. crassum* to be a junior synonym of the type species of the genus, *D. nauti*. This purported synonymy stemmed from the assumption of a consistent molar morphology as well as a too heavy reliance on the supposed lack of p1 in *D. crassum* (Ginsburg, 1967; Ginsburg and Bulot, 1987), when in fact the presence of this tooth is variable in populations of both *D. crassum* (Fahlbusch, 1985; Filhol, 1891; Ginsburg, 1967; Morales et al., 2012; Rössner, 2010; this study) and *D. nauti* (Alba et al., 2011; Moyà-Solà, 1979a). The latter fact, together with the above-mentioned general similarities in dental size, led Gentry et al. (1999) to provisionally accept the synonymy between the two species – in spite of the distinct occlusal features that had been already noted by some previous authors (Mottl, 1961, 1966; Moyà-Solà, 1979a; Stromer, 1928). Currently, it is well established that *D. crassum* is a distinct species, on the basis of dental (Alba et al., 2011; Hillenbrand et al., 2009; Morales et al., 2012; Rössner, 2007, 2010; Sánchez et al., 2011) as well as postcranial (Alba et al., 2011; Hillenbrand et al., 2009; Morales et al., 2003, 2012; Sánchez et al., 2011) differences.

The tragulid sample from Els Casots can be readily attributed to *D. crassum* based on its brachyodont dental morphology – differing from the less bunoselenodont and higher-crowned cheek-teeth with more marked occlusal relief of *D. nauti* (Alba et al., 2011; Hillenbrand et al., 2009; Morales et al., 2012). An attribution of the sample from Els

Casots to *D. crassum* instead of *D. nauti* is further confirmed by additional occlusal details shown by the former (Alba et al., 2011; Morales et al., 2012; Mottl, 1961; Rinnert, 1956; Rössner, 2010; Sánchez et al., 2011): the better-developed *Dorcatherium*-fold; the more reduced postentocristid; the mesiodistally-aligned third lobe of the m3; and the size and morphology of the premolars, including the longer p2 but shorter p3 and p4, the clearly tricuspid (instead of bicuspid) p2 and p3 with a more reduced distolingual portion, and the shorter premolar (p2–p4) row relative to the molar one.

In these and other regards, the dental morphology of the sample from Els Casots is very similar to that from the type locality of *D. crassum* (Sansan, France; see Morales et al., 2012), including the degree of dental brachyodonty. However, a few minor differences must be noted:

- all the specimens from Els Casots that are complete enough preserve the p1, whereas the latter is only rarely present in the population from Sansan;
- in the upper molars from Els Casots, the protocone shows two distal cristae (a distally-directed postprotocrista and a more distolabially-directed neocrista). In contrast, in the larger sample of *D. crassum* from Sansan there is generally a single and more distally-directed (lingually-situated) postprotocrista – and when present in some molars, the development of the two cristae is less marked than in the specimens from Els Casots;
- in all the lower molars from Els Casots, both the preentocristid and postentocristid are double, whereas in *D. crassum* from Sansan this feature is variable, and the more labial mesial cristid can be very weakly expressed (even absent) in some specimens;
- the cristids of the protoconulid of the p2 and, especially, the p3 are poorly developed and hardly observable in the material from Els Casots, whereas in *D. crassum* from Sansan, although variable, such cristids are always well distinct and even very strong in some specimens (MNHN Sa 9950 and MNHN Sa 1022).

The above-mentioned differences are relatively minor and, most likely, they simply reflect intraspecific variability.

## 5.2. Biostratigraphy

Whereas *Dorcatherium nauti* is recorded from the late Middle Miocene (early MN7+8) onwards (see Alba et al., 2011, and references therein; Gross et al., 2011; Rössner and Heissig, 2013), *D. crassum* is recorded from the latest Early Miocene (MN4) to the Middle Miocene (MN6), being distributed in central, western and southwestern Europe (Morales et al., 2012; Rössner and Heissig, 2013; Rössner, 2010). The latter species is best documented from the MN6 of Sansan in France (Morales et al., 2012) and the MN5 of Sandelzhausen in Germany (Rössner, 2010), although its biostratigraphic range extends back to the MN4. In the Iberian Peninsula, the biostratigraphic range of *D. crassum* is more restricted than in the rest of Europe, being recorded in several MN4 to MN5 localities of both Portugal and Spain (Antunes et al., 1994, and references therein; Golpe-Posse, 1974; Iñigo and Cerdeño, 1997).

Before excavations at Els Casots were performed, in the Vallès-Penedès Basin *D. crassum* had been only reported from the MN4 localities of Can Canals and El Canyet (Golpe-Posse, 1974), on the basis of scarce material that remains undescribed (Moyà-Solà, 1979b). In spite of being similarly correlated to the Aragonian local biozone C, the above-mentioned Vallès-Penedès localities are slightly younger than Els Casots – because they correspond to the Upper Detritic Unit (UDU), whereas Els Casots belongs instead to the Detritic-Carbonated Unit of the Lower Continental Complexes of the Vallès-Penedès Basin (Casanovas-Vilar et al., 2011b). The material described here allows us to conclusively confirm the presence of *D. crassum* in the Vallès-Penedès Basin, and further provides details on the dental morphology of one of the oldest European populations of this species.

It has been recently shown that the genus *Dorcatherium* is likely to be diphyletic, with two different lineages (one bunoselenodont and the other selenodont) having dispersed more or less simultaneously into Europe by the Early Miocene (MN4) and subsequently diversified in this continent (Rössner and Heissig, 2013). *D. crassum* is the oldest – and presumably most plesiomorphic – representative of the European lineage of bunoselenodont *Dorcatherium* (Rössner and Heissig, 2013). As noted by the latter authors, many previous studies on European *Dorcatherium* species suffer from insufficient descriptive details and/or figures, thereby hindering the scrutiny of the identifications (although with notable exceptions, e.g. Alba et al., 2011; Morales et al., 2012; Rössner, 2010). The detailed descriptions and figures provided in this paper therefore represent an important addition to the knowledge of earliest European representatives of the genus *Dorcatherium*, since the site of Els Casots (MN4) is much older than the type locality of Sansan (France) – which is the reference site for the MN6 (Ginsburg and Bulot, 2000; Sen and Ginsburg, 2000) – although this does not necessarily imply that the former sample displays a more primitive dental morphology (except perhaps for the retention of the p1).

## 5.3. Paleoenvironmental implications

Extant tragulids live in the undergrowth of tropical rain forests from Africa and Southeast Asia in wet and densely-covered areas in which fruits are available at least nine months per year, and the African water chevrotain (*Hyemoschus*) is particularly aquaphilous and only inhabits areas with low seasonality and at least 1,500 mm of average annual rainfall (Dubost, 1975, 1978). *Hyemoschus* is an extraordinary diver, which usually lives within 250 m from water masses and resorts to aquatic escape behavior (Dubost, 1978). Recently, this behavior has been also reported for the Asian genus *Tragulus*, suggesting that aquatic habits might be ancestral for the whole family (Meijaard et al., 2010).

It is generally thought that the habitat of *Dorcatherium* was most similar to that of *Hyemoschus* (Alba et al., 2011; Köhler, 1993; Pickford et al., 2004; Rössner, 2004, 2007, 2010), being tightly and almost exclusively associated with limnofluvial deposits (Rössner and Heissig, 2013), and thereby indicative at the very least of wet

and densely-forested environments, probably with masses of water nearby. The fusion of the ectomesocuneiform with the cubonavicular in *D. crassum*, as in other extinct *Dorcatherium* and extant tragulids (Morales et al., 2012; Moyà-Solà, 1979a), indicates an inability to zigzag at full speed (Leinders and Sondaar, 1974) and might be interpreted as an adaptation for running straight to dive into the water in order to escape predators (Moyà-Solà, 1979a), as in extant tragulids (Dubost, 1978; Meijaard et al., 2010). Moreover, European species of *Dorcatherium* more closely resemble *Hyemoschus* than extant Asian tragulids in several anatomical postcranial features, such as the more robust limbs, the better developed lateral metapodials, and the different type of fusion of the central metatarsals (Milne Edwards, 1864; Morales et al., 2012; Rössner, 2007; Zittel, 1925).

Given the above-mentioned evidence, the presence of *D. crassum* at Els Casots fits very well with the inferred lacustrine depositional environment (Casanovas-Vilar et al., 2011a; Moyà Solà and Rius Font, 1993), and is further indicative of the nearby presence of densely-forested areas and a humid and warm climate with low seasonality. Moreover, such a paleoenvironmental reconstruction agrees with the occurrence of aquatic vertebrates (fishes and crocodylians) at the site, together with that of potentially aquaphilous large mammals (e.g., some rhinocerotids) and other taxa characteristic of forested humid environments, such as the suoid *Taucanamo* and the cervoid *Lagomeryx* (see Casanovas-Vilar et al., 2011a, and references therein). In contrast, the presence of certain glirids of arid affinities (*Simplomys* and *Pseudodryomys*) and terrestrial sciurids (*Heteroxerus*), together with the scarcity of glirids with more forested affinities and the lack of castorids, suggest that more open and non-inundated environments must have been also present relatively close to the site (Casanovas-Vilar et al., 2011a).

## 6. Summary and conclusions

We describe and figure new fossil remains of *D. crassum* from the Early Miocene site of Els Casots, in the Vallès-Penedès Basin (NE Iberian Peninsula). The reported specimens, mostly including mandibular fragments of juvenile and adult individuals, show close metrical and morphologic similarities with those from Sansan (the type locality of *D. crassum*). This fact enables a straightforward assignment to the latter species—in spite of minor differences, merely attributable to intraspecific variability. The sample from Els Casots therefore constitutes the most complete sample of *D. crassum* thus far described from the Iberian Peninsula. With an estimated age of 16.5–16.3 Ma, the remains from Els Casots confirm the presence of *D. crassum* in the late Early Miocene (MN4) of the Iberian Peninsula, in agreement with the chronostratigraphic range of this species elsewhere in Europe (MN4–MN6). Moreover, the described remains represent one of the most complete samples of the earliest representatives of the bunoselenodont *Dorcatherium* lineage from Europe thus far described. Finally, the occurrence of this traguid species at Els Casots fits well with the lacustrine environment inferred for this

site from sedimentologic evidence, and also supports the reconstruction of a densely-forested paleoenvironment with a humid and warm climate with low seasonality.

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