



The Record of *Prodeinotherium* in the Iberian Peninsula: New Data from the Vallès-Penedès Basin

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Abstract

Deinotheres (Proboscidea, Deinotheriidae) are a clade of non-elephantiform proboscideans that originated in Africa and dispersed into Eurasia by the early Miocene. In Europe, deinotheres are first recorded in Greece during MN3, although they did not become a common faunal element throughout Europe until MN4. Early Miocene (MN3–MN4) deinotheres remains from Europe are generally assigned to a different species (*Prodeinotherium cuvieri*) than those from the early middle Miocene (*Prodeinotherium bavaricum*; MN5–MN6). In the Vallès-Penedès Basin (NE Iberian Peninsula), *Prodeinotherium* remains are very scarce and largely remain unpublished. To clarify their taxonomic assignment, we describe the available material and compare it with that from elsewhere in Europe. Based on size and a few diagnostic occlusal details, we tentatively recognize both *Prodeinotherium* cf. *P. cuvieri* and *Prodeinotherium* cf. *P. bavaricum* in the basin. Although all the studied sites had previously been correlated to MN4, the recognition of *P.* cf. *P. bavaricum* at els Casots and les Escletxes is consistent with ongoing litho- and magnetostratigraphic studies suggesting a slightly younger age for these sites. The lack of *Prodeinotherium* remains in older (MN3) localities from the Vallès-Penedès Basin, where *Gomphotherium* is already recorded, further supports the view that deinotheres dispersed into Western Europe somewhat later than gomphotheres.

Keywords Proboscidea · Deinotheriidae · *Prodeinotherium cuvieri* · *Prodeinotherium bavaricum* · Miocene · Europe

Abbreviations

CHE	Chevilly
ICP	Institut Català de Paleontologia Miquel Crusafont, Sabadell, Barcelona, Spain
IPS	Acronym of the ICP collections (for the former ‘Institut de Paleontologia de Sabadell’).
BL	Buccolingual
BLI	Breadth/length index
L	Left
MD	Mesiodistal
R	Right

Introduction

The Genus *Prodeinotherium*

Deinotheres (family Deinotheriidae) are a clade of non-elephantiform proboscideans characterized by a single pair of downwardly-recurved tusks and a lophodont cheek tooth morphology (Osborn 1936; Bergounioux and Crouzel 1962a; Harris 1973, 1978; Göhlich 1999; Sanders et al. 2010). Like proboscideans as a whole, deinotheres originated in Africa, where two subfamilies are distinguished (Sanders et al. 2004, 2010): the plesiomorphic and small Chilgatheriinae, with a single monotypic genus (*Chilgatherium* Sanders et al., 2004) from the late Oligocene of East Africa; and the larger and more derived Deinotheriinae, from the late Oligocene to early Pleistocene of Africa and the early to late Miocene of Eurasia, represented by several species.

The number of distinct deinotheriine genera is still a matter of debate. Some recent authors (Böhme et al. 2012; Pickford and Pourabrishami 2013) still distinguish a single genus (*Deinotherium* Kaup, 1829), but most other authors (e.g., Harris 1973, 1978; Gasparik 1993, 2001; Göhlich

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1999; Huttunen 2002a,b, 2004; Huttunen and Göhlich 2002; Duranthon et al. 2007; Markov 2008; Rasmussen and Gutierrez 2009; Sanders et al. 2010; Aiglstorfer et al. 2014; Konidaris et al. 2017; Alba et al. 2020) distinguish the smaller *Prodeinotherium* Éhik, 1930 (late Oligocene to early middle Miocene; but see Qiu et al. 2007 for a report of *Prodeinotherium* from the late Miocene of China) from the larger *Deinotherium* s.s. (late middle to late Miocene). The distinction between the two genera has been supported on dental, cranial, and postcranial features (Harris 1973, 1978; Huttunen 2002a, 2004; Sanders et al. 2010). According to Harris (1973, 1978), purported dental diagnostic features (other than size) between the two genera would include the more reduced postmetaloph ornamentation in M2 and M3, the presence of mesostyles in P3 and P4, and the longer and more recurved tusks in *Deinotherium* as compared with *Prodeinotherium*. Together with the more numerous cranial and postcranial differences noted by Harris (1973, 1978), the aforementioned dental features have been accepted as diagnostic by many (e.g., Huttunen 2002a; Sanders et al. 2010) but not all subsequent researchers. In particular, Ginsburg and Chevrier (2001) noted that mesostyle development and postmetaloph ornamentation are too variable and inconsistent to distinguish the two genera, while purported differences in tusk shape and some cranial features would not hold when the European material is considered. An in-depth joint taxonomic revision of African, European, and Asian deinotheriid species would be required to re-evaluate the diagnostic features between the two genera, together with a rigorous cladistic analysis to further confirm that *Deinotherium* is monophyletic (instead of polyphyletic). Pending such studies, both taxonomic views seem reasonable, but given the undisputed differences in multiple postcranial features (Harris 1973, 1978; Huttunen 2004), we tentatively follow most recent authors (e.g., Konidaris et al. 2017; Alba et al. 2020) in recognizing *Prodeinotherium* as a distinct genus.

Deinotheriids are first recorded in the late Oligocene of Africa by *Chilgatherium* at 28–27 Ma and subsequently by *Prodeinotherium* sp. at 27.5–24.0 Ma (Sanders et al. 2004, 2010; Rasmussen and Gutierrez 2009), being only later recorded in Eurasia. The dispersal of proboscideans into Eurasia was once considered a single biochronological event in the framework of multiple intercontinental dispersal events that took place coinciding with the closure of the Tethys Seaway and the emergence of a terrestrial corridor (the so-called *Gomphotherium* Landbridge) in the current Middle East ca. 19 Ma, due to the collision of the Afro-Arabian and Eurasian plates (Rögl 1999; Harzhauser et al. 2007; Sen 2013). However, the formation of this landbridge was a multi-episodic phenomenon (e.g., Harzhauser et al. 2007), with several proboscidean lineages apparently having dispersed out of Africa at different times. Currently available data indicate that deinotheriids are first recorded in Asia than

in Europe. In particular, *Prodeinotherium* is first recorded by the earliest Miocene (~22.5 Ma) in the Bugti area of Pakistan (Métais et al. 2009; Antoine et al. 2013), and only later recorded in eastern Europe (MN3, early Miocene; Koufos et al. 2003). Subsequently, this genus was present throughout most of the European Miocene from MN4 onward until it was replaced by *Deinotherium* (Göhlich 1999; Sanders et al. 2010; Konidaris et al. 2017).

European Species of *Prodeinotherium*

Some authors recognized a single valid species of *Prodeinotherium* in Europe (Bergounioux and Crouzel 1962a; Göhlich 1999; Huttunen 2002a,b, 2004; Huttunen and Göhlich 2002), but most current authors (Ginsburg and Chevrier 2001; Böhme et al. 2012; Pickford and Pourabrishami 2013; Aiglstorfer et al. 2014; Konidaris et al. 2017) distinguish *Prodeinotherium cuvieri* (Kaup, 1832) from *Prodeinotherium bavaricum* (von Meyer, 1831).

Prodeinotherium cuvieri was originally described as *Dinotherium Cuvieri* Kaup, 1832 by Kaup (1832: 14–16) after Cuvier (1822: pl. IV figs. 1, 2, 5, pl. VII fig. 2, pl. VIII figs. 1, 3, 4). The type locality of *P. cuvieri* is customarily considered Chevilly (MN4, France; Ginsburg and Chevrier 2001; Huttunen 2002a, b), even though no holotype or type locality was mentioned in the original description by Kaup (1832), who referred to specimens figured by Cuvier (1822) from Chevilly and other localities. Lartet (1859: pl. XIII fig. 2C') figured an m1 from Chevilly that he asserted came from the mandible “that has become the type of *D. Cuvieri*”, and Mayet (1908) also considered that a fragmentary mandible from Chevilly (Mayet 1908: pl. VIII figs. 3–4) was the type of the species. Most recently, Huttunen (2002a, b) considered this specimen (CHE.13) as the lectotype. However, given that it was not mentioned by Cuvier (1822) or Kaup (1832), we concur with Ginsburg and Chevrier (2001) that only the three isolated teeth from Chevilly figured by Cuvier (1822: pl. IV figs. 1, 2, 5)—respectively, an m2 (CHE.19), an M3 (CHE.22), and a dp4 (CHE.20)—should be considered syntypes.

Prodeinotherium bavaricum was originally erected as *Dinotherium Bavaricum* von Meyer, 1831, by von Meyer (1831: 297), although the species was not described until somewhat later (von Meyer 1833: pls. XXXIV figs. 12–15, XXXVI figs. 10–11, 16–17) based on material from Gmünd (currently Georgensgmünd, Germany, MN5). Von Meyer (1833) included the material from Chevilly in his newly erected species, whereas in contrast Depéret (1887) considered that the latter (whose authorship he dated to 1832) was a junior subjective synonym of *D. cuvieri*. Other authors (e.g., Lartet 1859; Mayet 1908, 1909) subsequently distinguished the two species but assigned to them specimens from overlapping time ranges—contrasting with the non-overlapping chronostratigraphic distribution currently recognized for

them (see below). Although Lartet (1859) and Mayet (1908) mentioned distinguishing features between the two species, most of them have not withstood more recent scrutiny, even by authors who consider them distinct (Ginsburg and Chevrier 2001). This has led some authors to synonymize them, in which case *P. bavaricum* must take priority (Huttunen 2002a, b; contra Depéret 1887).

Two additional nominal species of *Prodeinotherium* from Europe were considered junior subjective synonyms of *P. bavaricum* by Huttunen (2002a, b): *Prodeinotherium hungaricum* Éhik, 1930, and *Prodeinotherium petenyii* Vörös, 1989. Ginsburg and Chevrier (2001) similarly considered *P. hungaricum* as a junior synonym of *P. bavaricum*, while Gasparik (1993, 2001) considered *P. petenyii* as a junior synonym of *P. hungaricum*, which he considered as a valid species. Given their small size and the MN4 age of the type material of both *P. petenyii* and *P. hungaricum*, here we consider that both nominal species are junior subjective synonyms of *P. cuvieri* instead of *P. bavaricum*.

Although *P. bavaricum* has sometimes been reported to coexist with *Deinotherium* during the middle Miocene (Bergounioux and Crouzel 1962b; Ginsburg and Chevrier 2001; Duranthon et al. 2007), this has been questioned or attributed to mixing of reworked faunas by more recent authors (Böhme et al. 2012; Pickford and Pourabrishami 2013; Konidaris et al. 2017). According to Konidaris et al. (2017), *P. cuvieri* is recorded during the early Miocene (MN3–MN4) and *P. bavaricum* during the middle Miocene (MN5–MN6).

***Prodeinotherium* in the Iberian Peninsula**

Prodeinotherium remains are not abundantly represented in the Iberian Peninsula, at least according to the literature. All the remains reported by Bergounioux and Crouzel (1962b) in their review of Spanish deinotheres belong to *Deinotherium*, except for a few remains from the Vallès-Penedès Basin (see below). Azanza et al. (1993) reported a maxillary fragment with P4–M3 from Artesilla (MN4, Calatayud-Teruel Basin, Spain), which is correlated to local subzone Ca, with an estimated age of 16.5 Ma (Van der Meulen et al. 2012). In turn, Antunes and Ginsburg (2003) reviewed the deinotheres from Portugal and reported 15 dentognathic specimens that they assigned to *Deinotherium bavaricum*. Most of the material derives from localities (Quinta das Pedreiras and Quinta da Barbacena) correlated to Tagus Basin Unit Va2 (MN4; Antunes 1996; Antunes and Ginsburg 2003; The NOW Community 2020). A tusk fragment from Quinta Grande (lower part of Unit Vb) and a mandible from Quintanelas (upper part of Unit Vb, based on Chelas 2) were correlated by Antunes and Ginsburg (2003) to MN5, but the former is more likely MN4 (The NOW Community 2020) whereas the latter might be MN4 or MN5. In light of the MN4 age for some of these

sites, it is surprising that Antunes and Ginsburg (2003) assigned all the material to *D. bavaricum*, given that Ginsburg and Chevrier (2001) had distinguished the MN4 material from France as *D. cuvieri*. The latter was considered a synonym of *D. bavaricum* by Ginsburg in Antunes and Ginsburg (2003: 176)—which did not cite Ginsburg and Chevrier (2001). Given the arguments above, on biochronological grounds we consider that most (if not all) of the Portuguese material reported by Antunes and Ginsburg (2003) might belong to *P. cuvieri*—although this cannot be adequately ascertained based on the information provided by the authors.

In the Vallès-Penedès Basin, the taxonomic allocation of deinotheres remains, which are scarce and mostly consist of fragmentary remains, is currently unclear. Solé Sabarís (1936) attributed an upper premolar from Can Corró (Caldes de Montbui) to *Deinotherium giganteum* Kaup, 1829, but the specimen was subsequently assigned to *D. bavaricum* by Crusafont and Truyols (1954). The latter authors also reported *D. cuvieri* from Can Mas, and Crusafont et al. (1955) briefly described a lower molar fragment of *D. cuvieri* from les Escletxes (el Papiol). In turn, Bergounioux and Crouzel (1962b) assigned a partial m3 from Can Mas, seven teeth from les Escletxes del Papiol, and a dp4 from Can Canals to *D. bavaricum* (as they considered *D. cuvieri* was merely a synonym). Finally, the record of deinotheres at els Casots and el Canyet was first reported by Moyà Solà and Rius Font (1993) and Casanovas-Vilar et al. (2011b), respectively, but their species ascription remains to be determined. In summary, although part of the *Prodeinotherium* material from the Vallès-Penedès Basin has previously been reported, it has never been figured or described in detail. Here we describe the available material and compare it with *Prodeinotherium* from elsewhere in Europe, to clarify its taxonomic identity.

Age and Geological Background

The Vallès-Penedès Basin (NE Iberian Peninsula) has yielded a rich fossil record of terrestrial vertebrates from the early to the late Miocene (Agustí et al. 1985; Casanovas-Vilar et al. 2016a, b). Early Miocene (Burdigalian, MN3–MN4) fossil sites are located in facies associated with small-range alluvial fan systems and lacustrine systems, the latter having delivered the richest fossil localities (Casanovas-Vilar et al. 2016a). Eustatic changes during the mid-Miocene Climatic Optimum led to three different marine transgressions (late Burdigalian, Langhian, and early Serravallian), and continental sedimentation was not fully re-established until later in the Serravallian (Casanovas-Vilar et al. 2016a).

The *Prodeinotherium* remains from the Vallès-Penedès Basin come from various sites (Fig. 1) in the municipalities of el Papiol (Can Mas, les Escletxes, and prob-

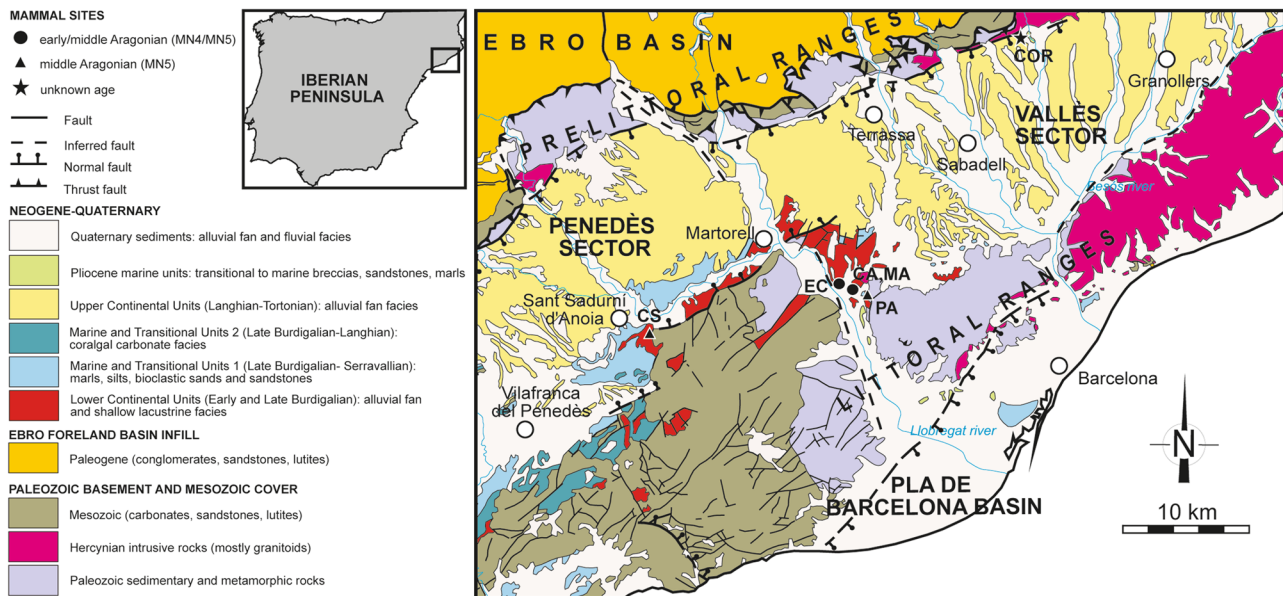


Fig. 1 Schematic geological map of the Vallès-Penedès Basin indicating the location of the localities that have yielded *Prodeinotherium* remains. Modified from Casanovas-Vilar et al. (2016b: fig. 1).

Abbreviations: CA = Can Canals; COR = Can Corró; CS = els Casots; EC = el Canyet; MA = Can Mas; PA = les Escletxes del Papiol

ably Can Canals), Castellbisbal (el Canyet), Subirats (els Casots), and Caldes de Montbui (Can Corró). Except for the last (whose age is unknown), all these sites have classically been correlated to MN4 (Agustí et al. 1985; Casanovas-Vilar et al. 2011a,b, 2016b). However, ongoing analysis of recently gathered litho-, bio-, and magnetostratigraphic data (Casanovas-Vilar et al. 2019; Jovells-Vaqué and Casanovas-Vilar in press; Jovells-Vaqué et al. 2017, 2019) preliminarily indicates that els Casots and especially les Escletxes are younger. Depending on the criteria used to define the MN4/MN5 boundary, these sites can be correlated to the uppermost MN4 or lowermost MN5. This boundary is commonly defined by the extinction of the eomyid *Ligerimys* Stehlin and Schaub, 1951 (e.g., Mein 1999; Kälin and Kempf 2009; Van der Meulen et al. 2012), which turns out to be a diachronous event in Western Europe, with the last Iberian species *Ligerimys ellipticus* Daams, 1976, surviving for about 0.5 Myr more than the last central European species, *Ligerimys florancei* Stehlin and Schaub, 1951 (see Van der Meulen et al. 2012). However, Van der Meulen et al. (2012) noted that the last occurrence of *L. florancei* in both areas is approximately simultaneous, so that Hilgen et al. (2012) redefined the boundary using this event and placed it at 16.4 Ma. This implies that many sites traditionally placed within MN4 (such as those belonging to Aragonian subzone Cb) are to be correlated to the earliest MN5.

Therefore, els Casots, which has only delivered scarce remains of *L. ellipticus*, is correlated to the MN5 with an estimated age of ca. 16 Ma (authors' unpublished data).

Ligerimys ellipticus is absent from les Escletxes, thus favoring a correlation with middle Aragonian zone D (Da?), early MN5 (see Van der Meulen et al. 2012). The younger age of this site is confirmed by its stratigraphical position, between a coquina layer and a carbonate reef platform, both assigned to the Langhian (early middle Miocene; Permanyer 1990). The age of Can Canals, Can Mas, and el Canyet is difficult to constrain as they have delivered very few or no small mammal remains at all. These sites are geographically very close to les Escletxes and belong to the same alluvial unit, which is certainly below the mentioned Langhian coquina layer and several meters above Molí Calopa, a classical MN3 site (Crusafont et al. 1955; see also Casanovas-Vilar et al. 2011b, 2016b). Therefore, their age may range between MN4 or early MN5. The scarce rodent remains recovered at el Canyet include the cricetid *Democricetodon hispanicus* (Agustí 1981; Jovells-Vaqué and Casanovas-Vilar in press), which rules out an age older than MN4.

Materials and Methods

The studied materials include 18 teeth housed at the ICP. The Can Corró specimen was not studied but included in the comparisons based on published data (Solé Sabarís 1936). Dental terminology generally follows Pickford and Pourabrishami (2013: figs. 2-3). Dental measurements of MD length and BL breadth were taken to the nearest 0.1 mm, and crown proportions were assessed by means

of the BLI (computed as BL breadth/MD length \times 100), bivariate plots of BL breadth vs. MD length, and box-and-whisker plots. The comparative sample includes figured specimens of *Prodeinotherium* from Europe (Table S1). For metrical analyses of the tooth loci recorded at the Vallès-Penedès Basin, given the potential confusion between *Prodeinotherium* and *Deinotherium* in MN6 (see above), we restricted the comparative sample to measurements of MN4 *P. cuvieri* and MN5 *P. bavaricum* from Europe taken from the literature (Éhik 1930; Vörös 1989; Azanza et al. 1993; Gasparik 1993; Ginsburg and Chevrier 2001; Sach and Heizmann 2001; Huttunen 2002b; Huttunen and Göhlich 2002; Antunes and Ginsburg 2003; Pickford and Pourabrishami 2013). Statistical comparisons between the two samples were done by means of t and Mann–Whitney tests using PAST (Hammer et al. 2001), and comparisons of Vallès-Penedès fossils with these samples were performed using z-scores.

Data availability All data generated during this study are included in this published article and its supplementary information files. The dataset of published measurements analyzed during the current study is available from the corresponding author on request.

Systematic Paleontology

Order Proboscidea Illiger, 1811

Family Deinotheriidae Bonaparte, 1841

Genus *Prodeinotherium* Éhik, 1930

Type species *Prodeinotherium hungaricum* Éhik, 1930, here considered a subjective junior synonym of *Prodeinotherium cuvieri* (Kaup, 1832)—see SOM S1.

Remarks The genus *Prodeinotherium* was originally erected as *Prodinothierium* Éhik, 1930, following Kaup's (1832) unjustified amendment of the original spelling of the type genus of the family (*Deinotherium* Kaup, 1829) as "*Dinothierium*," which was reinstated by Osborn (1936). On this basis, Harris (1973) emended the original spelling of "*Prodinothierium*" into *Prodeinotherium*. Such an emendation was indeed unjustified at the time—as it did not fit into any of the categories that would deem it incorrect according to the Code (ICZN 1999: Article 32). However, given that it has been in prevailing usage since Harris' (1973) emended diagnosis of the genus, currently it must be considered justified and is therefore adopted here, in agreement with other authors. The type species of the genus is *Prodeinotherium hungaricum* Éhik, 1930, generally considered a junior subjective synonym of one of the other species of the genus

(e.g., Huttunen 2002a; Pickford and Pourabrishami 2013; Konidaris et al. 2017; but see Gasparik 1993, 2001; Markov 2008).

Prodeinotherium cf. *P. cuvieri* (Kaup, 1832)

Fig. 2M, O, Q

Material Three lower molars from el Canyet, Castellbisbal (see Table 1 for measurements and further details).

Description The lower molars display a typical deinotheriid morphology, with a trilophodont m1 (Fig. 2M) and bilophodont m2 (Fig. 2O) and m3 (Fig. 2Q)—although only the distal half of the last tooth is preserved. The fragmentary m2 crown displays a long and marked prehypocristid that almost reaches the metalophid, and a very protruding distal cingulid. The m3 talonid is very large, distally protruding, and buccally tilted.

Remarks The m1 morphology is consistent with both *P. cuvieri* and *P. bavaricum* (Table S1), whose proportions

Table 1 List of *Prodeinotherium* cheek teeth from the Vallès-Penedès Basin with measurements (in mm). Parentheses indicate that measurements are estimated due to minor damage. Abbreviations: MD = mesiodistal length (mm); BL = buccolingual breadth (mm); BLI = breadth/length index (%), computed as BL / MD \times 100. Actual measured values for IPS10480 are MD = 66.0 mm and BL = 63.5 mm. IPS12712 is labeled as coming from Can Mas, but most likely this is the same specimen as reported by Bergounioux and Crouzel (1962b) from Can Canals. IPS12708 was identified as an M1 by Bergounioux and Crouzel (1962b). Actual measurement for IPS12713 is BL = 40.5 mm. Data for Can Corró were taken from Solé Sabarís (1936)

Catalog No	Locality	Tooth	MD	BL	BLI
IPS10480	els Casots	L M2	(66.0)	(63.5)	(96.2)
IPS10481	els Casots	L P3	54.1	50.3	93.0
IPS10482	els Casots	R m3	—	> 46.5	—
IPS10483	els Casots	R DP3	(35.8)	29.9	(83.5)
IPS10533	els Casots	R P3	53.4	(52.3)	(97.9)
IPS12695	el Canyet	R m3	—	> 50.0	—
IPS12696	el Canyet	R m1	(60.0)	(44.0)	(73.3)
IPS12697	el Canyet	R m2	(59.6)	(49.0)	(82.2)
IPS12711	Can Mas	R M1?	> 50.4	—	—
IPS12712	Can Canals?	L dp4	—	27.6	—
IPS12719	Can Mas	R m3	—	(55.0)	—
IPS12708	les Escletxes	R M3	> 46.7	(66.3)	—
IPS12709	les Escletxes	L p3	(42.0)	(33.0)	(78.6)
IPS12710	les Escletxes	R p3	(42.1)	> 30.0	—
IPS12713	les Escletxes	L m1	—	(44.0)	—
IPS12714	les Escletxes	R p4	47.0	> 39.0	—
IPS12715	les Escletxes	R P3	> 48.0	(48.0)	—
IPS12718	les Escletxes	L M2?	—	> 49.2	—
No number	Can Corró	L P3	54.0	52.0	96.3

Fig. 2 *Prodeinotherium* cheek teeth from the Vallès-Penedès Basin housed at the ICP: *Prodeinotherium* sp. from Can Canals? (A) and Can Mas (F, P); *P. cf. P. bavaricum* from els Casots (B, D–E, G, R) and les Escletxes (C, H–L, N); *P. cf. P. cuvieri* from el Canyet (M, O, Q). **A.** IPS12712, L dp4. **B.** IPS10483, R DP3. **C.** IPS12715, R P3. **D.** IPS10481, L P3. **E.** IPS10533 R P3. **F.** IPS12711, R M1. **G.** IPS10480, L M2. **H.** IPS12718, L M2. **I.** IPS12708, R M3. **J.** IPS12709, L p3. **K.** IPS12710, R p3. **L.** IPS12714, R p4. **M.** IPS12696, R m1. **N.** IPS12713, L m2 (digitally reconstructed, see Fig. S1). **O.** IPS12697, R m2. **P.** IPS12719, R m3. **Q.** IPS12695, R m3. **R.** IPS10482, R m3



appear similarly variable and largely overlap among the two species (Figs. 3D and 4G; Tables S2–S4)—but see below for comparisons with the m1 from les Escletxes. The size and proportions of the m2 also fit well with both species (Figs. 3E and 4H; Table S4), which largely overlap and display no significant differences for this tooth (Tables S2–S3). However, the great distal projection of the distal cingulid in the el Canyet m2 most closely resembles some specimens of *P. cuvieri*, being more projecting than others and, particularly, of *P. bavaricum* (Table S1), where the cingulid is closer to the hypolophid. The large talonid of the m3 from el Canyet also more closely resembles specimens of *P. cuvieri* than *P. bavaricum*, although this feature is somewhat variable in both species (Table S1).

Prodeinotherium cf. *P. bavaricum* (von Meyer, 1831)
Fig. 2B–E, G–L, N, R

Material Seven cheek teeth (probably belonging to the same individual) from les Escletxes del Papiol, el Papiol; and four permanent cheek teeth and a deciduous premolar

from els Casots, Subirats (see Table 1 for measurements and further details).

Description The DP3 from els Casots (Fig. 2B), which only lacks a small distal portion of the crown, is bilophodont and displays a vaguely figure-eight-shaped, very waisted contour (especially buccally) that is longer than broad, and broadest distally. The well-developed mesial cingulum is buccally flanked by a distinct parastyle, much larger than the mesiolingually located protostyle. The short postproto-crista shapes a slightly acute angle with the preprotocrista. The extensive central valley is lingually open, with a poorly defined lingual cingulum. Buccally, the ectoflexus is very marked, and the fine and low postparacrista and premetacrista do not constitute a conspicuous ectoloph; there is a small cusplule-like enamel thickening buccally to the end of the postparacrista. The short and steep postmetacrista is directed toward the damaged distal cingulum.

Based on their similar morphology and wear, the two P3 from els Casots (Fig. 2D–E) might belong to the same individual. They display a subsquare contour (slightly larger than

broad), a slightly oblique mesial margin, and an indistinct ectoflexus. The protoloph is continuous (although the preprotocrista is not well defined close to the paracone), whereas the metaloph is discontinuous (because the posthypocrista does not surpass crown midline); the distally-oriented postparacrista is very short. The two lingual cusps are conical (not buccolingually compressed); the hypocone is more peripheral than the protocone. These cusps are separated by a deep transverse groove that opens into a V-shaped lingual notch, which is flanked by a moderately developed lingual cingulum. The mesial cingulum is well developed but there is no distinct parastyle, whereas the distal cingulum is poorly developed; the ectoloph ends in an indistinct metastyle that barely protrudes distally. The worn and partial P3 from les Esclatxes (Fig. 2C), as far as it can be ascertained due to incomplete preservation, resembles the specimens from els Casots, except for the somewhat more convex distal profile.

The partial M2 from els Casots (Fig. 2G) displays a non-tapering subsquare occlusal profile (minimally longer than broad), with two distally concave transverse lochs. The mesial and distal cingula are well developed, but the distal one is much narrower. The transverse valley is ample and buccally displays no entostyle. The postmetacrista is continuous with a faint convolute located on the buccal side of the crown. In turn, two partial upper molars from les Esclatxes probably correspond to an M2 distobuccal crown fragment (Fig. 2H) and an M3 crown only lacking its mesialmost portion (Fig. 1I). The former specimen displays a less restricted median transverse valley than the latter, whereas the M3 displays a distally tapering contour (the metaloph is buccally more restricted than the protoloph). In both specimens, and unlike in the M2 from els Casots, the postmetacrista ends close to a marked (even if buccolingually narrow) convolute, which is close to the crown midline, just mesial to the marked distal cingulum.

The two p3s (probably antimeres) from les Esclatxes (Fig. 2J–K) display a subtriangular (longer than broad) and mesially tapering contour, but their damaged condition precludes assessing several occlusal details. The ectoflexid is slightly obliquely oriented and appears continuous between protoconid and hypoconid. The metaconid (partially preserved in the left specimen) is well separated from the protoconid, but due to damage it cannot be ascertained if these cusps were linked by a short transverse crest or whether a mesial tubercle (paraconid) was present. The median valley displays no secondary cusps or cristids, and the entoconid is buccolingually compressed and located very peripherally. The p4 from les Esclatxes (Fig. 2L) displays a subrectangular (longer than wide) contour, but the extent of the mesial valley and of the mesial cingulid cannot be assessed due to damage. The postprotocristid and prehypocristid constitute a continuous ectolophid that separates the median valley from the wide buccal notch, but the buccal cingulid cannot

be ascertained. The distal cingulid is relatively well developed. The lower molars are only represented by a partial and digitally ‘restored’ specimen from les Esclatxes (Fig. 2N), identified as an m1 due to its trilophodont occlusal pattern, as well as an m3 distal fragment from els Casots (Fig. 2R). The latter displays a buccally tilted and moderately developed talonid.

Remarks The DP3 shows similar size and proportions to the few available specimens of *P. cuvieri* and, especially, *P. bavaricum* (Figs. 3F and 4F), and merely differs from the figured specimens of the latter species (Table S1) by the more pronounced interlophid waisting of the crown.

The described P3s fit well with the morphology of *Prodeinotherium*—peripheral hypocone, indistinct ectoflexus, weakly developed parastyle and metastyle, and mesial cingulum more marked than the distal—but show no particular similarities with either *P. cuvieri* or *P. bavaricum* (Table S1). The upper premolar from Can Corró, originally described as a P4 (Solé Sabarís 1936: fig. p. 84), is best identified as a P3 given its occlusal morphology and proportions, and resembles the els Casots specimens, except for the better developed lingual cingulum. *Prodeinotherium bavaricum* displays on average significantly longer P3s than *P. cuvieri* (Tables S2–S4), and the measurements for MD length of all the Vallès-Penedès specimens (Figs. 3A and 4A) rule out an assignment to the latter species (Table S4).

The M2? fragment from les Esclatxes is not very informative but displays a similar distal crown morphology to the M3 from the same locality. The latter tooth was identified as an M1 by Bergounioux and Crouzel (1962b), but the development of the crown behind the distal lophid and the width of the metaloph (only subequal to the protoloph) is characteristic of an M3. The morphology of the els Casots M2 is consistent with that of both *Prodeinotherium* species (Table S1). *Prodeinotherium bavaricum* significantly differs from *P. cuvieri* by displaying on average absolutely longer and relatively narrower M2 (Tables S2–S3), and the dimensions of the els Casots specimen fit better with *P. bavaricum* (Figs. 3B and 4B), although the z-score does not reject an attribution to either species (Table S4). The morphology and BL breadth (Fig. 4C) of the M3 from les Esclatxes is also compatible with both species (Tables S1–S4), which do not display significant differences in this regard.

As far as it can be ascertained due to damage, the two p3s from les Esclatxes (Fig. 2J–K) fall within the range of occlusal variation of both *P. cuvieri* and *P. bavaricum* (Table S1). This tooth locus is quite variable, and unfortunately the only diagnostic feature (more reduced paraconid in *P. cuvieri*; Ginsburg and Chevrier 2001) cannot be ascertained in the studied specimens. Although *P. cuvieri* displays a significantly shorter p3 (Tables S2–S3), there is ample overlap and the p3 from les Esclatxes fits well with both

species (Figs. 3C and 4D; Table S4). Similarly, the p4 from les Escletxes resembles in morphology both *P. cuvieri* and *P. bavaricum* (Table S1). Although *P. cuvieri* displays significantly smaller p4 dimensions on average (Tables S2–S3), the MD length of the les Escletxes specimen fits well with both species (Fig. 4E; Table S4). Moreover, the morphology of the m1 from les Escletxes fits with both *P. cuvieri* and *P. bavaricum* (Table S1), even if it appears slightly more elongated than the m1 from el Canyet assigned to *P. cuvieri*; although the two species significantly differ in m1 BL breadth (Tables S2–S3), the size of the les Escletxes specimen agrees with both species (Fig. 4G; Table S4). Finally, in the els Casots m3, the talonid is less projecting and higher (almost cuspid-like) than in el Canyet m3 (see above), more closely resembling the m3 of *P. bavaricum* (Table S1).

Prodeinotherium sp.
Fig. 2A, F, P

Material Two molars from Can Mas, and a deciduous premolar probably from Can Canals (or Can Mas, see remarks below), both sites at el Papiol (see Table 1 for measurements and further details).

Description The partial dp4 from Can Canals? (Fig. 2A) preserves only two mesially-concave transverse lophids (the hypolophid and the somewhat narrower tritolophid). A loosely defined mesiodistal cristid originating from the hypoconulid approaches the hypolophid, partially blocking the distal transverse valley. The distal cingulid is moderately developed but buccolingually short.

A partial first molar from Can Mas (Fig. 2F) probably corresponds to an M1 buccal fragment, but it is too poorly preserved to assess any occlusal detail. The partial germ from Can Mas (Fig. 2P) is identified as an m3 because the hypolophid is somewhat narrower than the metalophid, but the development of the talonid cannot be ascertained.

Remarks The partial dp4 described above, recorded in the ICP collections as from Can Mas, is in all probability the same specimen reported by Bergounioux and Crouzel (1962b) from Can Canals, which is likely the correct provenance. Both the dp4 and m3 BL breadth fit well with both species (Fig. 4I; Table S1).

Discussion

Prodeinotherium Taxonomy and Evolution

Our comparisons of dental size and proportions (Figs. 3 and 4; Table S2) generally confirm Ginsburg and Chevier's (2001) assessment that *P. cuvieri* is somewhat smaller on average than *P. bavaricum*, but indicate that differences are

only significant for some dental positions (and generally only for MD length; Table S3). Given these slight differences, it is not surprising that the two species were synonymized by Huttunen (2002a). However, our morphological and metrical comparisons further suggest that the two species differ in some unexpected ways—including not only a longer and relatively more elongated M2 in *P. bavaricum* on average, but also a shorter and relatively broader m3 in the latter species compared with *P. cuvieri*. Despite a considerable overlap, the latter difference appears particularly relevant because it goes against the general trend of dental size increase from *P. cuvieri* to *P. bavaricum*. This might be attributable to a concomitant reduction of the m3 talonid—more developed (i.e., distally-projecting) in *Prodeinotherium* than in *Deinotherium* (von Meyer 1833; Huttunen 2002a), but also less contracted (i.e., wider) in *P. cuvieri* than in *P. bavaricum* according to Lartet (1859). These differences in the m3 would lend further support to the distinct species status of *P. cuvieri* and *P. bavaricum*, supported by most current authors (e.g., Pickford and Pourabrishami 2013; Konidaris et al. 2017), and previously justified based on overall dental size differences and p3 occlusal morphology (Ginsburg and Chevier 2001).

Providing an emended diagnosis for *P. cuvieri* and *P. bavaricum* is outside the scope of this paper because it would require a taxonomic revision of all *Prodeinotherium* species at an intercontinental level. The traditional recognition of three different species—*P. bavaricum* in Europe, *Prodeinotherium pentapotamiae* (Lydekker, 1876) in Asia, and *Prodeinotherium hobleyi* (Andrews, 1911) in Africa—was largely based on geography (Harris 1978) and has not proven particularly useful for deciphering the evolution of the genus. It is generally recognized that *P. hobleyi* may be distinguished from European *Prodeinotherium* in several occlusal details (greater separation between the p3 protoconid and metaconid, relatively less elongate p4, and a more distinct tubercle on the m3 talonid; Harris 1978; Sanders et al. 2010). However, *P. hobleyi* from the early Miocene appears smaller and somewhat more plesiomorphic (e.g., possession of more elaborated M2–M3 postmetaloph ornamentation, and presence of m1 ectostyle and p3 mesostyle) than younger material from the same continent (Harris 1978). In turn, both European and Asian *Prodeinotherium* species also appear somewhat more derived than their African counterparts in various occlusal details, whereas an evolutionary trend toward larger size apparently took place in parallel in Africa, Europe, and Asia from the early to the middle Miocene (Harris 1978). This pattern is overall consistent with *Prodeinotherium* originating in Africa and subsequently diversifying independently in several places of Eurasia. Unfortunately, it is not possible to determine to what extent morphological changes (other than size) occurred in parallel until the

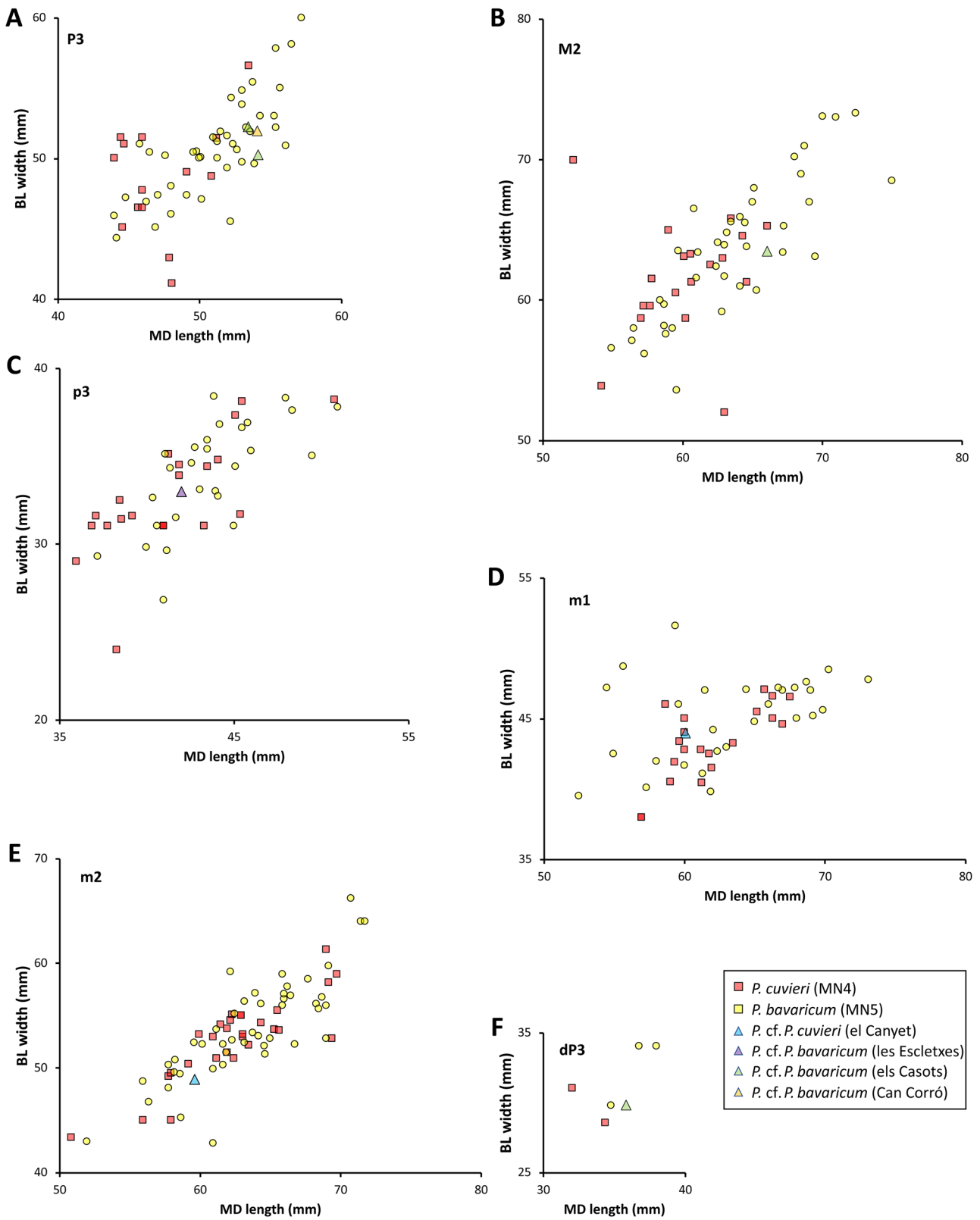


Fig. 3 Bivariate plots of BL breadth vs. MD length in *Prodeinotherium* remains from the Vallès-Penedès Basin compared with MN4 *P. cuvieri* and MN5 *P. bavaricum* from Europe (data taken from the literature, see Materials and methods). **A.** P3. **B.** M2. **C.** p3. **D.** m1. **E.** m2. **F.** DP3

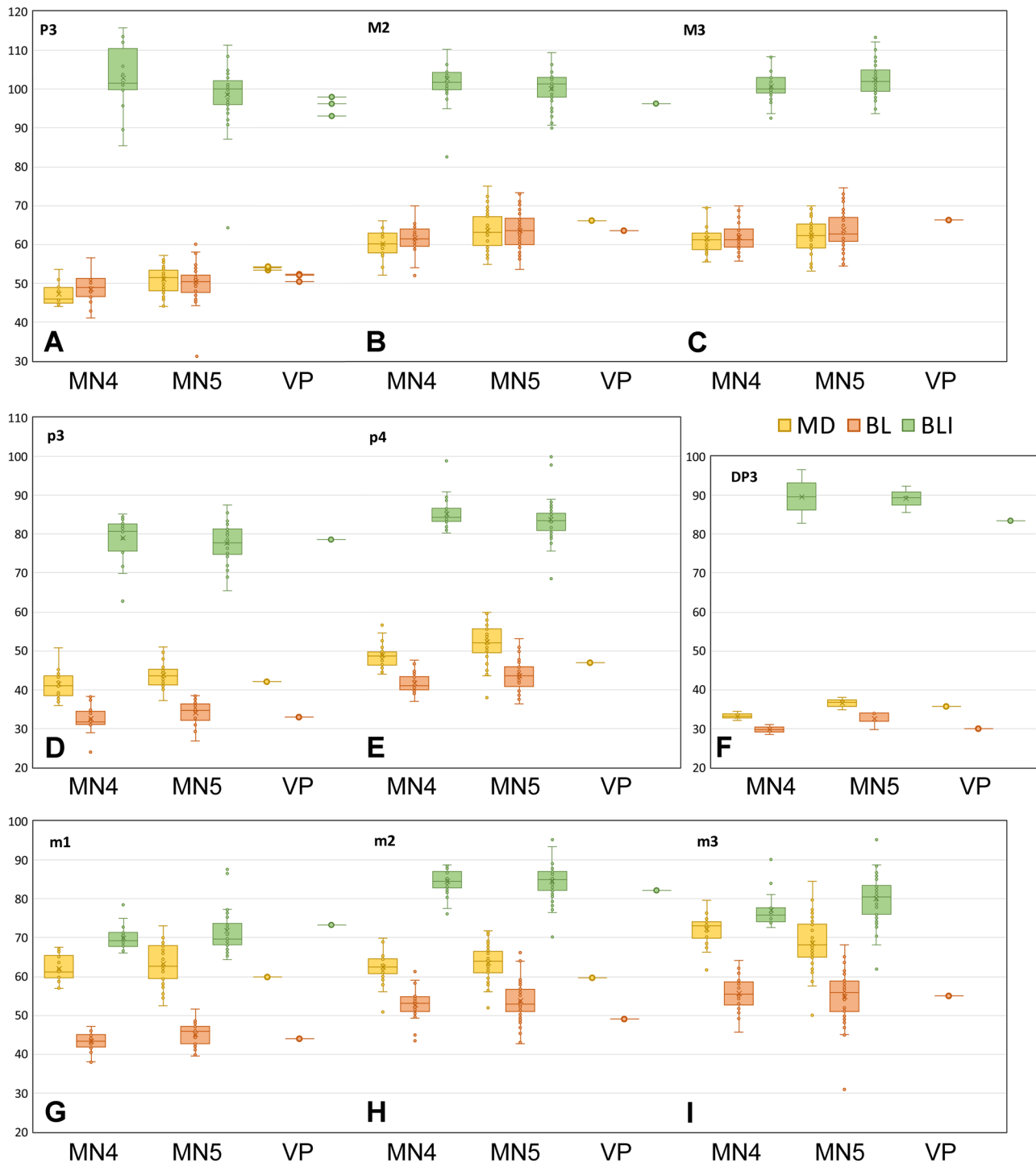


Fig. 4 Box-and-whisker plots of MD length, BL breadth, and BLI for *Prodeinotherium* remains from the Vallès-Penedès Basin compared with MN4 *P. cuvieri* and MN5 *P. bavaricum* from Europe (data taken from the literature, see Materials and methods). **A.** P3. **B.** M2. **C.** M3. **D.** p3. **E.** p4. **F.** DP3. **G.** m1. **H.** m2. **I.** DP3. Horizontal lines denote

the median, crosses the mean, boxes the interquartile range (25th to 75th), whiskers maximum-minimum values up to 1.5 times the interquartile range; individual specimens from the Vallès-Penedès Basin are denoted by large dots

alpha-taxonomy of *Prodeinotherium* is further clarified. As in Europe, the differences in dental size and shape noted by Harris (1978) for *P. hobleii* might justify the distinction

of additional African species, and the same holds for Asia, where some authors (Tiwari et al. 2006; Qiu et al. 2007) distinguish several species—*Prodeinotherium orlovii*

(Sahni and Tripathi, 1957) and *Prodeinotherium sinense* Qiu et al., 2007—in addition to *P. pentapotamiae*. The comparisons reported here for the European material of *Prodeinotherium* will hopefully contribute to clarify the taxonomy of this genus when an in-depth revision is undertaken in the future.

***Prodeinotherium* from the Vallès-Penedès Basin**

Unfortunately, the p3 occlusal morphology and the m3 proportions, which appear diagnostic between *P. cuvieri* and *P. bavaricum* (see above), cannot be adequately ascertained in the Vallès-Penedès sample, whose restricted and fragmentary nature recommends the use of open nomenclature in our species attributions. The great development of the m2 and m3 talonid in the el Canyet sample tentatively favors an assignment to *P. cf. P. cuvieri*. Conversely, the size of the els Casots M2, the more restricted talonid of the els Casots m3 and, especially, the MD length of the P3 from els Casots and Can Corró support an assignment to *P. cf. P. bavaricum*, while the samples from Can Mas and Can Canals? are best left unassigned to species. Given the range of these species elsewhere in Europe, our taxonomic identifications are consistent with a younger age for els Casots and les Escletxes, and an MN5 or MN6 age for Can Corró—thereby indicating that the early middle Miocene of the Vallès-Penedès Basin is better represented than previously assumed (e.g., Casanovas-Vilar et al. 2011b, 2016b). This indicates that the Vallès-Penedès Basin records the youngest *Prodeinotherium* remains from the Iberian Peninsula.

The Vallès-Penedès record of *Prodeinotherium* is further consistent with evidence from elsewhere in the Iberian Peninsula (Antunes and Ginsburg 2003) and Western Europe (e.g., Göhlich 1999; Ginsburg and Chevrier 2001) indicating that the arrival of *Prodeinotherium* occurred later (MN4) than the dispersal of *Gomphotherium* (MN3; Tassy 1990; Bulot and Ginsburg 1993; Göhlich 1999; Antunes and Ginsburg 2003; Mazo and Van der Made 2012). Some authors (Mazo 1996; Mazo and Van der Made 2012) concluded that gomphotheres were not recorded in the Iberian Peninsula until MN4, but indeed *Gomphotherium* has been reported from the Vallès-Penedès Basin in Torrent de Vilaroc (Crusafont and Truyols 1954; Crusafont et al. 1954, 1955; Bergounioux and Crouzel 1957, 1958; Mazo and Van der Made 2012) and Sant Andreu de la Barca (Agustí and Galobart 1998; Casanovas-Vilar et al. 2011b, 2016b). The latter site is conclusively correlated to MN3 (Agustí et al. 1985), and in particular to Ramblian zone A (Casanovas-Vilar et al. 2011b, 2016b), while Torrent de Vilaroc must be slightly younger but similarly correlated to the same zone, given its stratigraphic position just a few meters above Molí Calopa (Crusafont et al. 1955). Based on the upper limit of zone A (Van der Meulen et al. 2012), an

age older than 17 Ma can be inferred for both localities and, hence, for the dispersal of gomphotheres in the Vallès-Penedès Basin. In contrast, the oldest record of *Prodeinotherium* in the same basin could correspond either to the MN4 or earliest MN5. Els Casots and les Escletxes are unquestionably correlated to the early MN5 (as defined by Hilgen et al. 2012). Can Mas, Can Canals, and el Canyet are close to each other and located within the same alluvial unit, stratigraphically below les Escletxes and the marine Langhian deposits in this area. The scarce small mammal fauna recovered at el Canyet excludes an age older than MN4 for this site (Agustí 1981; Jovells-Vaqué and Casanovas-Vilar in press), and furthermore the three localities are several meters above the classical MN3 site of Molí Calopa. Therefore, they are certainly older than 16 Ma, but their correlation to MN4 or MN5 cannot be refined because of the lack of diagnostic small mammal data. However, the presence of *P. cf. P. cuvieri* at el Canyet is consistent with an older (MN4) age of this site as compared with les Escletxes, thus being chronologically similar to the other record of this species from Iberia, Artesilla (ca. 16.5 Ma; Azanza et al. 1993). Given the geographical location of the Iberian Peninsula, the proboscidean record from the early Miocene of the Vallès-Penedès Basin lends further support to the view that gomphotheres dispersed across Western Europe somewhat earlier than deinotheres.

Conclusions

The comparison of the *Prodeinotherium* remains from the Vallès-Penedès Basin with those from elsewhere in Europe indicates that two different species are recorded, which we tentatively assign to *P. cf. P. cuvieri* and *P. cf. P. bavaricum*. The presence of the latter taxon contrasts with the classical correlation of all the studied localities to the early Miocene (MN4) and supports recent studies that advocate for a somewhat younger age (early MN5) than previously assumed for most of them. In agreement with recent publications, our comparisons also support the distinct species status of *P. cuvieri*, and further indicate that, besides differences in overall tooth size, m3 size and proportions would be diagnostic between the two species. The record of *Prodeinotherium* in the Vallès-Penedès Basin further supports the view that deinotheres dispersed into western Europe somewhat later than gomphotheres.

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Data Availability The fossil material studied in this paper is housed and adequately curated in the Institut Català de Paleontologia Miquel Crusafont, as is accessible by other researchers. All the data generated in the course of this study is provided in the paper or the supplementary material.

Declarations

Conflicts of Interest We declare no conflict of interest.

References

- Agustí J (1981) Roedores miomorfos del Neógeno de Catalunya. PhD dissertation, Universitat de Barcelona, Barcelona, 284 pp
- Agustí J, Cabrera L, Moyà-Solà S (1985) Sinopsis estratigráfica del Neógeno de la fosa del Vallès-Penedès. *Paleontol Evol* 18:57–81
- Agustí J, Galobart À (1998) Noves localitats amb mamífers fòssils en el miocè de la Conca del Vallès-Penedès. *Trib Arqueol* 1996–1997:9–23
- Alba DM, Gasamans N, Pons-Monjo G, Luján ÀH, Robles JM, Obradó P, Casanovas-Vilar I (2020) Oldest *Deinotherium proavum* from Europe. *J Vertebr Paleontol* 40:e1775624
- Andrews CW (1911) On a new species of *Dinotherium* (*Dinotherium hobleyi*) from British East Africa. *Proc Zool Soc Lond* 1911:943–945
- Antoine P-O, Métais G, Orliac MJ, Crochet J-Y, Flynn, LJ, Marivaux L, Rajpar AR, Roohi G, Welcomme J-L (2013) Mammalian Neogene biostratigraphy of the Sulaiman Province, Pakistan. In: Wang X, Flynn LJ, Fortelius M (eds) *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*. Columbia University Press, New York, pp 400–422
- Antunes MT, Ginsburg L (2003) The *Deinotherium* (Proboscidea Mammalia): an abnormal tusk from Lisbon, the Miocene record in Portugal and the first appearance datum: evidence from Lisbon, Portugal. *Cièn Terra (UNL)* 15:173–190
- Antunes MT, Legoinha P, Nascimento A, Pais J (1996) The evolution of the lower Tagus basin (Lisbon and Setúbal Peninsula, Portugal) from lower to early middle Miocene. *Géol Fr* 4:59–77
- Aiglstorfer M, Göhlich UB, Böhme M, Gross M (2014) A partial skeleton of *Deinotherium* (Proboscidea, Mammalia) from the late middle Miocene Gratkorn locality (Austria). *Palaeobiodiv Palaeoenv* 94:49–70
- Azanza B, Cerdeño E, Ginsburg L, van der Made J, Morales J, Tassy P (1993) Les grands mammifères du Miocène inférieur d'Artesilla, bassin de Calatayud-Teruel (province de Saragosse, Espagne). *Bull Mus Natl Hist Nat* 15C:105–153
- Bergounioux FM, Crouzel F (1957) Les Mastodontes fossiles de l'Espagne. *Bol Inf Instit Paleontol Sabadell* 8–9:41–45
- Bergounioux FM, Crouzel F (1958) Les mastodontes d'Espagne. *Estud Geol* 14:224–345
- Bergounioux FM, Crouzel F (1962a) Les Déinothéridés d'Europe. *Ann Paléontol* 48:13–56
- Bergounioux FM, Crouzel F (1962b) Les Deinotheridés d'Espagne. *Bull Soc Geol Fr* 4:394–404
- Böhme M, Aiglstorfer M, Uhl D, Kullmer O (2012) The antiquity of the Rhine River: stratigraphic coverage of the Dinotheriensande (Eppelsheim Formation) of the Mainz Basin (Germany). *PLoS One* 7:e36817
- Bonaparte CL (1841) A new systematic arrangement of vertebrated animals. *Trans Linnean Soc Lond* 18:247–304.
- Bulot C, Ginsburg L (1993) Gisements a Mammifères miocènes du Haut-Armagnac et âge des plus anciens Proboscidiens d'Europe occidentale. *C R Acad Sci Paris* 316:1011–1016
- Casanovas-Vilar I, Alba DM, Moyà-Solà S. (2011a) Parada 1. Panoràmica general de la cuenca y yacimiento de Els Casots (Subirats): una fauna de vertebrados del Aragoniense inferior. *Paleontol Evol Memòria especial* 6:81–88
- Casanovas-Vilar I, DeMiguel D, Galindo J, Robles JM, Garcés M, Cabrera L (2011b) The continental Burdigalian (early Miocene) of the Vallès-Penedès Basin (Catalonia, Spain). In: Pérez-García A, Gascó F, Gasulla JM, Escaso F (eds) *Viajando a Mundos Preterritos*. Ayuntamiento de Morella, Morella, pp 93–100
- Casanovas-Vilar I, Garcés M, Jovells-Vaqué S, DeMiguel D, García-Paredes I, Alba DM, Cabrera L (2019) Biochronology of the early Miocene mammal record of the Vallès-Penedès Basin (Catalonia). In: *The Palaeontological Association 63rd Annual Meeting*. 15th–21st December 2019 University of Valencia, Spain. Programme Abstracts AGM papers, pp 64–65
- Casanovas-Vilar I, Garcés M, Van Dam J, García-Paredes I, Robles JM, Alba DM (2016a) An updated biostratigraphy for the late Aragonian and the Vallesian of the Vallès-Penedès Basin (Catalonia). *Geol Acta* 14:195–217
- Casanovas-Vilar I, Madern A, Alba DM, Cabrera L, García-Paredes I, Van den Hoek Ostende LW, DeMiguel D, Robles JM, Furió M, Van Dam J, Garcés M, Angelone C, Moyà-Solà S (2016b) The Miocene mammal record of the Vallès-Penedès Basin (Catalonia). *C R Palevol* 15:791–812
- Crusafont M, Truyols J (1954) Catálogo Paleomastológico del Mioceno del Vallès-Penedés y de Calatayud-Teruel. Segundo Cursillo Internacional de Paleontología. Museo de la Ciudad de Sabadell, Sabadell
- Crusafont M, Villalta JF de, Truyols J (1954) Sobre la caracterización del Burdigaliense continental de la cuenca del Vallès-Penedés. *Mem Com Inst Geol Prov* 11:63–73
- Crusafont M, Villalta JF de, Truyols J (1955) El Burdigaliense continental de la cuenca del Vallès-Penedés. *Mem Com Inst Geol* 12:1–272
- Cuvier G (1822) *Recherches sur les Ossements Fossiles, où l'On Rétablit les Caractères de Plusieurs animaux dont les Révolutions du Globe ont Détruit les Espèces*. Tome Second, 1^{re} Partie. G. Dufour et E. D'Ocagne, Paris
- Daams R (1976) Miocene rodents (Mammalia) from Cetina de Aragon (prov. Zaragoza) and Buñol (prov. Valencia), Spain. *Proc Kon Ned Akad Wetensch B* 79:152–182
- Depéret C (1887) Recherches sur la succession des faunes des vertébrés miocènes de la vallée du Rhône. *Arch Mus Hist Nat Lyon* 4:45–313
- Duranthon F, Antoine P-O, Laffont D, Bilotte M (2007) Contemporanéité de *Prodeinotherium* et *Deinotherium* (Mammalia, Proboscidea) à Castelnau-Magnoac (Hautes-Pyrénées, France). *Rev Paléobiol Genève* 26:403–411
- Éhik J (1930) *Prodinotherium hungaricum* nov. gen., nov. spec. *Geol Hung Ser Paleontol* 6:1–18
- Gasparik M (1993) *Deinotheres* (Proboscidea, Mammalia) of Hungary. *Ann Hist Nat Mus Natl Hung* 85:3–17
- Gasparik M (2001) Neogene proboscidean remains from Hungary; an overview. *Frag Paleontol Hung* 19:61–77

- Ginsburg L, Chevri er F (2001) Les Dinotheres du bassin de la Loire et l'evolution du genre *Deinotherium* en France. *Symbioses* 5:9–24
- Gohlich UB (1999) Order Proboscidea. In: R ossner GE, Heissig K (eds) *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, M unchen, pp 157–168
- Hammer  , Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. *Palaeontol Electron* 4:4
- Harris JM (1973) *Prodeinotherium* from Gebel Zelten, Libya. *Bull Brit Mus Nat Hist Geol* 23:285–348
- Harris JM (1978) Deinotherioidea and Barytherioidea. In: Maglio VJ, Cooke HBS (eds) *Evolution of African Mammals*. Harvard University Press, Cambridge, pp 315–332
- Harzhauser M, Kroh A, Mandic O, Piller WE, Gohlich U, Reuter M, Berning B (2007) Biogeographic responses to geodynamics: a key study all around the Oligo–Miocene Tethyan Seaway. *Zool Anz* 246:241–256
- Hilgen FJ, Lourens LJ, Van Dam JA (2012) The Neogene period. In: Gradstein FM, Ogg JG, Schmitz MD, Ogg GM (eds) *The Geologic Time Scale 2012, Volume 2*. Elsevier, Amsterdam, pp 923–978
- Huttunen K (2002a) Systematics and taxonomy of the European Deinotheriidae (Proboscidea, Mammalia). *Ann Naturhist Mus Wien* 103A:237–250
- Huttunen K (2002b) Deinotheriidae (Proboscidea, Mammalia) dental remains from the Miocene of lower Austria and Burgenland. *Ann Naturhist Mus Wien* 103A:251–285
- Huttunen K (2004) On a *Prodeinotherium bavaricum* (Proboscidea, Mammalia) skeleton from Franzensbad, Czech Republic. *Ann Naturhist Mus Wien* 105A:333–361
- Huttunen K, Gohlich UB (2002) A partial skeleton of *Prodeinotherium bavaricum* (Proboscidea, Mammalia) from the middle Miocene of Unterzolling (Upper Freshwater Molasse, Germany). *Geobios* 35:489–514
- Illiger C (1811) *Prodromus Systematis Mammalium et Avium Additis Terminis Zoographicis utriusque Classis*. C. Salfeld, Berlin.
- ICZN (International Commission on Zoological Nomenclature) (1999) *International Code of Zoological Nomenclature*. The International Trust for Zoological Nomenclature, London. <http://www.nhm.ac.uk/hosted-sites/iczn/code/>
- Jovells-Vaqu e S, Casanovas-Vilar I (in press) Dispersal and early evolution of the first modern cricetid rodents in Western Europe: new data from the Vall es-Pened es Basin (Catalonia). *C R Palevol*
- Jovells-Vaqu e S, Casanovas-Vilar I, Garc es M, DeMiguel D, Garc ia-Paredes I, Alba DM, Cabrera L (2019) Biomagnetostratigraphy of the early Miocene mammal record of the Vall es-Pened es Basin (Catalonia). In: *Program and Abstracts XVII Conference of the EAVP - Brussels, Belgium 2 - 6 July 2019*, p 53
- Jovells-Vaqu e S, Ginest ı M, Casanovas-Vilar I (2017) Cricetidae (Rodentia, Mammalia) from the early Miocene site of els Casots (Vall es-Pened es Basin, Catalonia). *Fossil Imprint* 73:141–154
- K alin D, Kempf O (2009) High-resolution stratigraphy from the continental record of the middle Miocene Northern Alpine Foreland Basin of Switzerland. *N Jb Geol Pal ontol Abh* 254:177–235
- Kaup J (1829) *Deinotherium giganteum*. *Isis von Oken* 22:401–404
- Kaup J-J (1832) Description d'Ossements Fossiles de Mammif eres Inconnus jusqu' a Pr esent, qui se Trouvent au Mus eum Grand-Ducal de Darmstadt. Premier Cahier, Contenant le genre *Dinotherium* (*Tapirus giganteus*, Cuv.). J.G. Heyer, Darmstadt
- Konidaris GE, Roussiakis SJ, Athanassiou A, Theodorou GE (2017) The huge-sized deinother *Deinotherium proavum* (Proboscidea, Mammalia) from the late Miocene localities Pikermi and Halmyropotamos (Greece). *Quat Int* 430:5–21
- Koufos GD, Zouros N, Mourouzidou O (2003) *Prodeinotherium bavaricum* (Proboscidea, Mammalia) from Lesvos island, Greece; the appearance of deinotheres in the Eastern Mediterranean. *Geobios* 36:205–315
- Lartet   (1859) Sur la dentition des proboscidiens fossiles (*Dinotherium*, *Mastodontes* et *Elephants*) et sur la distribution g eographique et stratigraphique de leurs d ebris en Europe. *Bull Soc Geol Fr* 16:469–515
- Lydekker R (1876) Molar teeth and other remains of Mammalia. In: *Indian Tertiary and Post-Tertiary Vertebrata*. Mem Geol Surv India Ser. 10 (Palaeontologia Indica) 1:19–87
- Markov GN (2008) Fossil proboscideans (Mammalia) from the vicinities of Varna: a rare indication of middle Miocene vertebrate fauna in Bulgaria. *Hist Nat Bulg* 19:137–152
- Mayet L (1908)  tude des Mammif eres Mioc enes des Sables de l'Orl eanais et des Faluns de la Touraine. *Ann Univ Lyon* 24:1–336
- Mayet L (1909)  tude sommaire des Mammif eres fossiles des Faluns de la Touraine. Proprement dite Boss e, Le Louroux, Manthelan, La Chapelle-Blanche, Sainte Maure, Paulmy, Ferri ere-Lar on, Savign e-sur-Lathan. *Ann Univ Lyon* 26:1–72
- Mazo AV (1996) Gomphotheres and mammutids from the Iberian Peninsula. In: Shoshani J, Tassy P (eds) *The Proboscidea. Evolution and Palaeoecology of Elephants and Their Relatives*. Oxford University Press, Oxford, pp 136–142
- Mazo AV, Van der Made J (2012) Iberian mastodonts: geographic and stratigraphic distribution. *Quat Int* 255:239–256
- Mein P (1999) European Miocene mammal biochronology. In: R ossner GE, Heissig K (eds) *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, M unchen, pp 25–38
- M etais G, Antoine P-O, Baqri SRH, Crochet J-Y, de Franceschi D, Marivaux L, Welcomme J-L (2009) Lithofacies, depositional environments, regional biostratigraphy and age of the Chitarwata Formation in the Bugti Hills, Balochistan, Pakistan. *J Asian Earth Sci* 34:154–167
- Moy a Sol a S, Rius Font L (1993) El jaciment paleontol gic dels Casots (Subirats, Alt Pened es). *Trib Arqueol* 1991:7–12
- Osborn HF (1936) Proboscidea. A Monograph of the Discovery, Evolution, Migration and Extinction of the Mastodonts and Elephants of the World. Volume I. Moeritherioidea. Deinotherioidea. Mastodontoidea. The American Museum Press, New York
- Permany er A (1990) Sedimentologia i Diag enesi dels Esculls Mioc enes de la Conca del Pened es. Institut d'Estudis Catalans, Barcelona
- Pickford M, Pourabrishami Z (2013) Deciphering Deinotheriidae diversity. *Palaeobiodiv Palaeoenv* 93:121–150
- Qiu Z-X, Wang B-Y, Li H, Deng T, Sun Y (2007) First discovery of deinother in China. *Vertebr Palasiat* 45:261–277
- Rasmussen DT, Gutierrez M (2009) A mammalian fauna from the late Oligocene of northwestern Kenya. *Palaeontographica Abt A* 288:1–52
- R ogl F (1999) Circum-Mediterranean Miocene paleogeography. In: R ossner GE, Heissig K (eds) *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, M unchen, pp 39–48
- Sach VJ, Heizmann EPJ (2001) Stratigraphie und S ugetierfaunen der Brackwassermolasse in der Umgebung von Ulm (S udwestdeutschland). *Stuttg Beitr Naturk B Geol Pal ontol* 310:1–95
- Sahni MR, Tripathi C (1957) A new classification of the Indian deinotheres and description of *D. orlovii* sp. nov. *Mem Geol Surv India (Palaeontologia Indica)* 33(4):1–33
- Sanders WJ, Gheerbrant E, Harris JM, Saegusa H, Delmer C (2010) Proboscidea. In: Werdelin L, Sanders WJ (eds) *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp 161–251
- Sanders WJ, Kappelman J, Rasmussen DT (2004) New large-bodied mammals from the late Oligocene site of Chilga, Ethiopia. *Acta Palaeontol Pol* 49:365–392
- Sen S (2013) Dispersal of African mammals in Eurasia during the Cenozoic: ways and whys. *Geobios* 46:159–172
- Sol e Sabar ıs L (1936) Pres encia del *Dinotherium giganteum* Kaup a Caldes de Montbu ı. *Butll Inst Cat Hist Nat* 36:83–84

- Stehlin HG, Schaub S (1951) Die Trigonodontie der simplicidentaten Nager. Schweiz Pal Abh 67:1–385
- Tassy P (1990) The “Proboscidean Datum Event”: how many proboscideans and how many events? In: Lindsay EH, Fahlbusch V, Mein P (eds) European Neogene Mammal Chronology. Plenum Press, New York, pp 237–252
- The NOW Community (2020) New and Old Worlds Database of Fossil Mammals (NOW). <http://www.helsinki.fi/science/now/>. (accessed May 12, 2020)
- Tiwari BN, Verma BC, Bhandari A (2006) Record of *Prodeinotherium* (Proboscidea: Mammalia) from the Mid-Tertiary Dharmasala group of the Kangra Valley, NW Himalaya, India: biochronologic and palaeobiogeographic implications. J Palaeontol Soc India 51:93–100
- Van der Meulen AJ, García-Paredes I, Álvarez-Sierra MÁ, van den Hoek Ostende LW, Hordijk K, Oliver A, Peláez-Campomanes P (2012) Updated Aragonian biostratigraphy: small mammal distribution and its implications for the Miocene European chronology. Geol Acta 10:159–179
- von Meyer H (1831) [no title]. Jb Mineral Geogn Geol Petrefaktenk 2:296–297
- von Meyer H (1833) Beiträge zur Petrefaktenkunde. III. Das *Dinotherium Bavaricum*, mit Rücksicht auf die riesenmässigste fossile Thiergattung der Dinotherien überhaupt, und auf die Struktur der Mahlzähne in den Tapiren. Nov Acta Phys-Med Acad Caes Leopold-Carol Nat Curios 16:487–516
- Vörös I (1989) *Prodeinotherium petenyii* sp. n. from the lower Miocene at Putnok (North Hungary). Frag Min Palaeontol 14:101–110