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Prominatherium dalmatinum from the late Eocene of Grancona (Vicenza, NE Italy). The oldest terrestrial mammal of the Italian peninsula

Prominatherium dalmatinum *de l'Éocène supérieur de Grancona (province de Vicence, Nord-Est de l'Italie). Le plus ancien mammifère terrestre de la péninsule Italienne*

Federica Grandi[a], Fabio Bona[b,*]

[a] *Department of Evolution and Biology "Turchi di Bagno", University of Ferrara, Corso Ercole I d'Este 32, 44100 Ferrara, Italy*
[b] *Department of Earth Sciences "A. Desio", University of Milan, via Mangiagalli 34, 20133 Milano, Italy*

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ABSTRACT

So far, the oldest terrestrial mammal associations in Italy dates to the beginning of the Oligocene, with Anthracotheriidae being the most represented taxon. Sites from northern Italy yielded remains of the genus *Anthracotherium* that spread from Asia to western Europe after the Grande Coupure. A finding at Grancona, which is Priabonian in age, implies that Anthracotheriidae family reached the Italian Peninsula before the Eocene–Oligocene boundary. Thus, the dispersal of this family in northern Italy is anterior than previously believed. The fossil consists of a poorly preserved right hemi-maxilla with well-preserved P4 and M3. The shape and the size of the teeth are not compatible with the genus *Anthracotherium*. On the contrary, the closer affinities with the Croatian species *Prominatherium dalmatinum* suggest a connection between the Balkan area and the Italian peninsula and a possible new way of dispersal for this family.

RÉSUMÉ

Jusqu'à présent, les associations de mammifères terrestres les plus anciennes d'Italie dataient du début de l'Oligocène, les Anthracotheriidae étant le taxon le mieux représenté. Les sites du Nord de l'Italie fournissent des restes du genre *Anthracotherium*, qui s'est répandu depuis l'Asie jusqu'à l'Europe de l'Ouest, après la Grande Coupure. Une découverte à Grancona, d'âge Priabonien, implique que la famille des Anthracotheriidae a atteint la péninsule Italienne à la limite Éocène–Oligocène. Donc la dispersion de cette famille dans le Nord de l'Italie est antérieure à ce que l'on pensait jusqu'alors. Le fossile consiste en un hémi-maxillaire droit mal conservé, avec une P4 et une M3 bien conservées. La forme et

* Corresponding author.
E-mail addresses: rean90@gmail.com (F. Grandi), fabgeo@libero.it (F. Bona).

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la taille de ces dents ne sont pas compatibles avec le genre *Anthracotherium*. Au contraire, de proches affinités avec l'espèce croate *Prominatherium dalmatinum* suggèrent une connexion entre la zone des Balkans et la péninsule Italienne, ainsi qu'un nouvel itinéraire de dispersion pour cette famille.

1. Introduction

The aim of this paper is to describe a new finding related to Anthracotheriidae and to discuss its palaeogeographic value in the context of the European late Eocene. Although the material is poor and very badly preserved, we are sure that its discovery provides interesting new data to understand the mammalian dispersal in Europe during the Paleogene.

The subject of this paper is a fossil donated to the Archaeological and Natural Science Museum "G. Zannato" in Montecchio Maggiore (VI) thirty years after its the discovery. At the time of the recovery, there were maintenance works on a road between Corrubbio di Grancona and San Gaudenzio di Grancona (Fig. 1B). An amateur palaeontologist was looking for fossils when he found what was later identified as the remains of a member of the family Anthracotheriidae Leidy, 1869.

Anthracotheres have often been early members of large-scale mammalian dispersal events, suggesting phases of connection between landmasses. This taxon probably originated in Asia during the late middle Eocene and spreading later into Europe and North America (Lihoreau and Ducrocq, 2007; Tsubamoto et al., 2002).

The genus *Anthracotherium* was first identified in Italy at Cadibona (Savona) by Cuvier (1822). This early Oligocene lignitic site (MP 21–24) is one of the most important deposit in which anthracotheres were studied (Fig. 1A). Cadibona yielded mainly fossils of *Anthracotherium magnum* (Cuvier, 1822; Kotsakis, 1984, 1986; Palazzi, 1922; Squinabol, 1890).

Another important site is located at Monteviale (Vicenza), where Beggiato (1865) described an intermediate species between *A. magnum* and *A. minus* (Fig. 1A). Later Dal Piaz (1926, 1932) attributed the remains of Monteviale to *Anthracotherium monsvialense*, previously described by De Zigno (1888). This site is early Oligocene in age (MP 21) and all the remains were found in a lignitic layer (Ghezzo and Giusberti, 2016; Kocsis et al., 2014; Mietto, 1997; Pandolfi et al., 2016).

The province of Vicenza yielded also two other lignite deposits in which *A. magnum* and *A. monsvialense* were discovered during the twentieth century: Zovencedo and Chiuppano (Accordi, 1951), both Oligocene in age (Kotsakis, 1984, 1986; Mietto, 1997) (Fig. 1A). Others isolated anthracotherid findings are reported in Kotsakis et al. (2005).

The taxa discovered in Italy until now belong to the genus *Anthracotherium* that appeared in the European continent after the Eocene–Oligocene boundary (MP 20–21), when the Grande Coupure, a big faunal turnover, happened (Costa et al., 2011; Stehlin, 1910).

The specimen from Grancona dates from the end of the Eocene, at the Priabonian age (MP 17–20), before any other anthracothere discovery in Italian sites until now. Thus, the recovery of these remains led to a series of questions: Is it possible that Anthracotheriidae reached the Italian peninsula before the Grande Coupure? Which way did they used? Were there several phases for the anthracothere dispersal?

The anthracotheriid dental terminology and the taxonomy follows Lihoreau and Ducrocq (2007) and Boisserie et al. (2010).

2. Geological context

Grancona is a small town located in the Berici Hills, South-West of the Veneto region (Fig. 1A). These hills are situated in the Pianura Padana and pre-Alps context, which is mainly characterized by deposition of shallow-marine carbonates with lower-middle Eocene and Oligocene volcanic activity (Rasser et al., 2008).

Thin and discontinuous upper Paleocene to lower Eocene red marly limestones — called Scaglia Rossa — are widely distributed in the whole area, which encompasses Lessini Shelf, Berici Hills and Euganei Hills. At the beginning of the Eocene, this area was submerged by the sea and the presence of Scaglia Rossa as basal facies is an evidence of a marine environment. Scaglia Rossa is overlaid by turbiditic tuffs, marls and tuffaceous marls, moving upward into marly calcarenites named Pietra di Nanto (Fabiani, 1915), Lutetian in age (Rasser et al., 2008).

In the subsequent several million years, volcanic activity led to the rise of marine platforms in some areas of Berici Hills. This caused the sedimentation of calcarenites associated with nummulites named Calcari Nummulitici (Fabiani, 1915) that testifies a change in water depth. In the western Colli Berici, shallow-marine carbonate sedimentation was interrupted by extrusion of basalt flows. Hence, during the late Eocene, some areas of Berici Hills emerged creating a new configuration characterized by low-level waters, lagoons and islands (Rasser et al., 2008).

It is only during the Oligocene epoch that some areas of Berici hills were partially emerged, as shown by the presence of lignitic deposits in which abundant fossils of anthracotheres were found (e.g., Kotsakis, 1984, 1986; Rasser et al., 2008).

2.1. Age of the fossil

Specimen MCZ 3422 was found along a road right outside Grancona (Fig. 1B), where the section was exposed during maintenance works thirty years ago and then

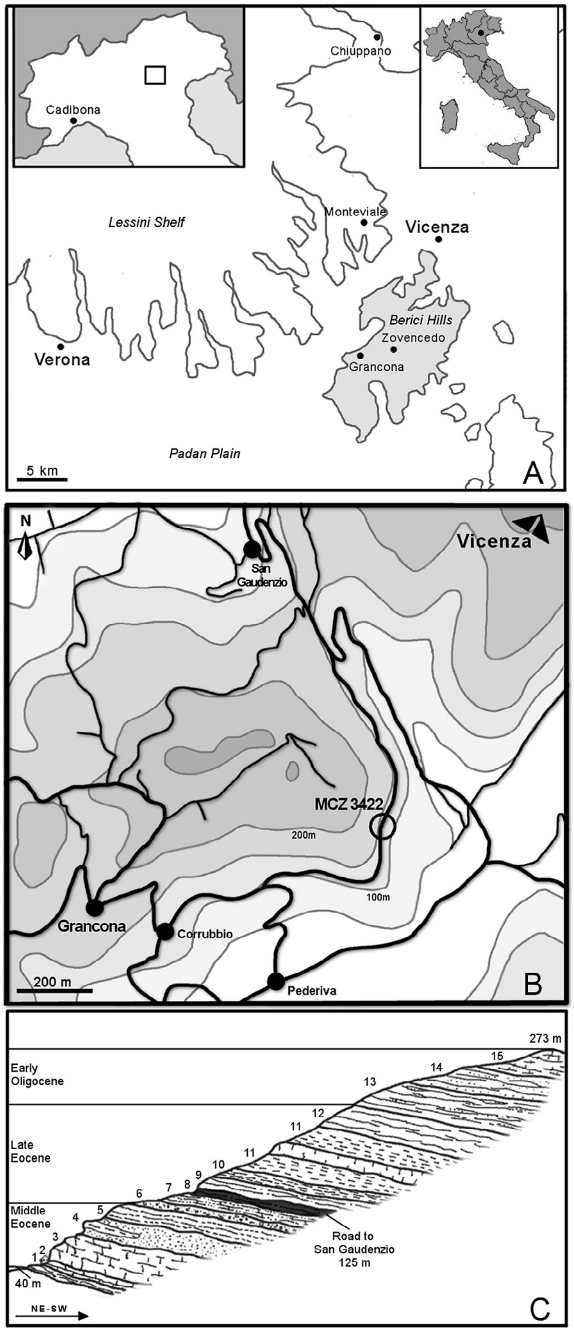

Fig. 1. Location map of Grancona, NE Italy. **A.** View of all known Italian sites with *Anthracotherium* sp. **B.** view of the area where MCZ 3422 was found. **C**. Stratigraphical section reconstructed from Fabiani (1915). The layer No. 8 corresponds to the road where the fossil was found.

Fig. 1. Carte de localisation de Grancona, Nord-Est de l'Italie. **A.** Vue de tous les sites italiens connus contenant *Anthracotherium* sp. **B.** Vue de la zone où l'échantillon MCZ 3422 a été trouvé. **C.** Coupe stratigraphique reconstituée d'après Fabiani (1915). Le niveau n° 8 correspond à la route où le fossile a été trouvé.

covered by landslides in subsequent years. Being the fossil found during the last century and having been studied only recently, it is not possible to locate the exact position where it was discovered, which makes the information regarding the context of recovery incomplete. However, the characteristics of the sediment still associated with the fossil and the literature about the local stratigraphy partly compensated this lack of information.

The studies of Fabiani (1908, 1915) describe in detail the stratigraphy from the Zengele quarry (Fig. 1C) on the same road where the fossil was found. He identified a series of marly layers in which he has found abundant fossils of *Nummulites* Lamarck, 1804 and from which he formalized a stratigraphic sequence spanning from the middle Eocene to the early Oligocene (Fig. 1C).

The remains have been found associated with Naticidae Guilding, 1834 and included in an orange-yellowish marly limestone. From the descriptions of Fabiani's works, there is only one layer with these characteristics (Fig. 1C), matching one of the facies with *Nummulites*, Priabonian in age (Fabiani, 1908, 1915; Papazzoni and Sirotti, 1995).

A comparison with the geographic chart (sheet No. 50, Carta d'Italia-scale 1:100.000) confirms that the area in which the remains were discovered lies within the Priabonian formation. Its stratotype is located in Priabona, in the Lessini shelf, and is well represented in the Berici Hills (Mietto, 1997, 2006; Rasser et al., 2008).

3. Systematic palaeontology

Order Cetartiodactyla Montgelard, Douzery and Catzeflis, 1997

Family Anthracotheriidae Leidy, 1869

Subfamily Anthracotherinae Leidy, 1869

Genus ***Prominatherium*** Teller, 1884

Prominatherium dalmatinum (von Meyer, 1854)
(Fig. 2A–C)

Type species—*Prominatherium dalmatinum* (von Meyer, 1854); late Eocene of Croatia

Locality and Type Horizon—Mt. Promina, North of Drniš, Croatia

Stratigraphical Range—late Eocene of Croatia and Romania (Patrulius, 1954)

Short History—The remains collected on Mt. Promina (Croatia) date to the late Eocene (Hellmund and Heissig, 1994, Popov et al., 2001; Russell et al., 1982). Because of its resemblance to *A. magnum*, the best-known relative at the time, this new species has been attributed to *Anthracotherium dalmantinum* by the discoverer (von Meyer, 1854). Later on, Teller (1884) proposed to create a new genus and named it *Prominatherium dalmatinum* (von Meyer, 1854). Upper molars of *Prominatherium* (Teller, 1884) differ from those of *Anthracotherium* in their smaller size and present a more mesiodistally-compressed crown. Also the cusps are more defined with no crests in the transverse valleys (Boisserie et al., 2010; Lihoreau and Ducrocq, 2007).

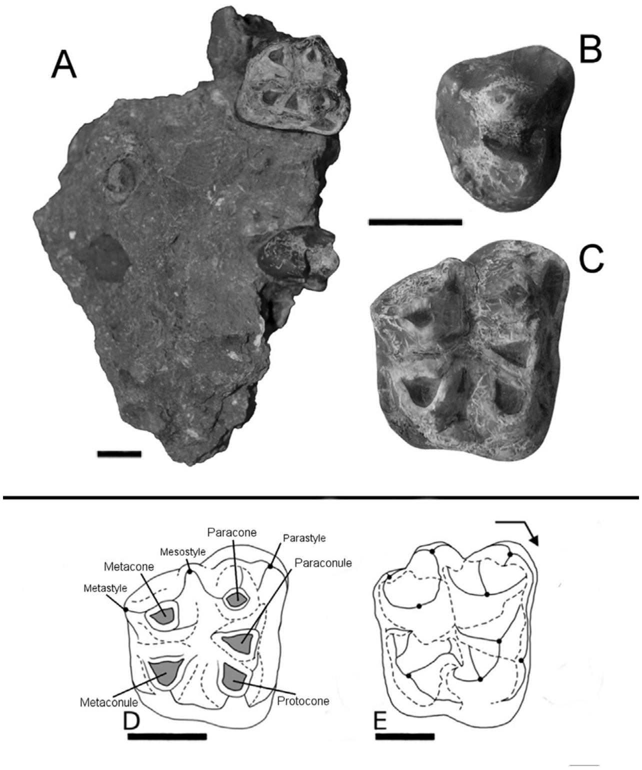

Fig. 2. Above*: Prominatherium dalmatinum*. MCZ 3422. **A.** Ventral view with an endocast of a mollusc on the left portion. **B.** Occlusal view of the premolar. **C.** Occlusal view of the molar. Scale: 20 mm. **Below**: morphological comparison between right M3 of Anthracotheriidae. **D.** MCZ 3422. **E.** General structure of *Anthracotherium* sp. from Lihoreau and Ducrocq (2007). Scale: 20 mm.

Fig. 2. En haut : *Prominatherium dalmatinum*. MCZ 3422. **A.** Vue ventrale avec le moule interne d'un mollusque sur la portion gauche. **B.** Vue occlusale de la prémolaire. **C.** Vue occlusale de la molaire. Barre d'échelle = 20 mm. En bas : comparaison morphologique entre des molaires M3 d'Anthracotheriidae. **D.** MCZ 3422**. E.** Structure générale d'*Anthracotherium* sp. d'après Lihoreau et Ducrocq (2007). Barre d'échelle = 20 mm.

3.1. Morphological and biometrical data

Specimen MCZ 3422 consists of a fragment about 10 cm long and represents the right portion of the maxilla (Fig. 2A). The specimen is poorly preserved but two teeth are still present: a fourth premolar (Fig. 2B) and a third molar (Fig. 2C), brachyodont and bunoselenodont in structure. Along with the hemi-maxilla there are also endocasts of *Naticidae* Guilding, 1834 and bivalves (Fig. 2A).

The relic is deformed and the molar is misaligned. When found, the molar was separated from the rest of the maxilla and it has been reattached by the discoverer. Unfortunately this happened thirty years before this study and it is not possible to find the original position. The space between the molar and the premolar is clearly not enough to host the first and the second molar. On the other hand, the space seems excessive for one tooth only (Fig. 2A).

The M3 has a trapezoidal shape with a more developed mesial side (Fig. 2C–D). It has five well-defined cusps: a paracone and a metacone on labial side; a protocone and a metaconule on lingual side and a paraconule. The molar also presents three styles: the parastyle, metastyle and the mesostyle (Fig. 2D). The molar does not have crests in the transverse valleys. However, the occlusal surface is worn and the morphology is not completely clear.

The P4 has two well-developed cusps separated by a deep mesio-distal valley. It has three styles: the parastyle, the mesiostyle and the distostyle (Fig. 2B). The general shape is quite triangular.

3.2. Comparisons and attribution

According to Lihoreau and Ducrocq (2007) the oldest representatives of the Anthracotheriidae are known from the middle Eocene of Asia from where the family spread towards Europe and North America. Remains of anthracotheres in Europe are well known from the Oligocene of several sites in France, Germany, England, Switzerland, Czech Republic and Northern Italy (e.g., Antoine et al., 2011, Bastien et al., 2012; Fejfar et al., 2005; Kotsakis et al., 2005; Russell et al., 1982). The first European occurrences of the family were discovered at La Débruge in southern France with the bothriodontine *Elomeryx crispus* (Gervais, 1849), dated to the late Eocene (MP 18) (Ducrocq and Lihoreau, 2006), and in the upper Eocene of Tscherno More, eastern Bulgaria, with the genus *Bakalovia* (Nikolov and Heissig, 1985). Also the remains of *P. dalmatinum* (von Meyer, 1854) from the same stage of Croatia and Romania testify to an early presence of this family in Europe (Hellmund and Heissig, 1994; Patrulius, 1954; Teller, 1884).

Table 1
Selected dental measurements of species of *Anthracotherium* and *Prominatherium*. Measurements are given in millimetres.
Tableau 1
Mesures dentaires sélectionnées chez les espèces *Anthracotherium* et *Prominatherium*. Ces mesures sont données en millimètres.

	Tooth	*L*	*W*
MCZ 3422	P4	17.1	14.1
A. monsvialense (Monteviale, Dal Piaz, 1932)		29	19
A. magnum (Cadibona, Squinabol, 1890)		26	21
A. magnum (Cadibona, Squinabol, 1890)		29	20
A. crassum (Pondaung, Soe, 2008)		16.1	8.5
A. crassum (Pondaung, Soe, 2008)		18.5	11.5
A. pangan (Pondaung, Soe, 2008)		20.6	12.3
A. pangan (Pondaung, Soe, 2008)		15.5	21.25
A. pangan (Pondaung, Soe, 2008)		19.6	13.3
P. dalmatinum (Mt. Promina, Teller, 1884)		16.7	12
MCZ 3422	M3	24.5	20.3
A. monsvialense (Monteviale, Dal Piaz, 1932)		40	33
A. monsvialense (Monteviale, Dal Piaz, 1932)		46	39
A. magnum (Cadibona, Squinabol, 1890)		55	45
A. magnum (Cadibona, Squinabol, 1890)		42	42
A. crassum (Pondaung, Soe, 2008)		36.4	19.6
A. crassum (Pondaung, Soe, 2008)		38.1	20.5
A. pangan (Pondaung, Soe, 2008)		42	22.5
A. pangan (Pondaung, Soe, 2008)		40	20.5
P. dalmatinum (Mt. Promina, Teller, 1884)		26	24
P. dalmatinum (Mt. Promina, Teller, 1884)		25	20
P. dalmatinum (Mt. Promina, Teller, 1884)		28	23

Generally, anthracotheres have brachyodont and bunoselenodont molars, with an increasing size toward the last one. Upper molars possess four or five cusps with a paraconule and metaconule; the mesostyle is prominent in primitive forms and pinched-in in the recent ones (Boisserie et al., 2010; Lihoreau and Ducrocq, 2007).

The worn state of the third molar of the specimen of Grancona does not allow to estimate the original extension of the crests in the transverse valley, but it seems rather bunodont as the cuspids are well defined. It shows a general structure compatible with the subfamily Anthracotheriinae (Fig. 2D–E). The mesostyle is prominent and connected with the cingulum as in *Anthracotherium* sp. from northern Italy (Dal Piaz, 1932; Ghezzo and Giusberti, 2016; Pandolfi et al., 2016; Squinabol, 1890). Once more, the comparative measurements show that these finds are way larger than the specimen from Grancona (Table 1).

The fossil resembles some species from Asia such as *Anthracotherium pangan* and *A. crassum* (Soe, 2008; Tsubamoto et al., 2002, 2011), but the third molar of Grancona has a more trapezoidal shape.

Comparisons with the other genera found in Europe were also taken into account, particularly the genus *Elomeryx* Marsh, 1894, found in southern France, England, Switzerland, Germany and other localities (Bastien et al., 2012; Ducrocq and Lihoreau, 2006; Lihoreau et al., 2009; Russell et al., 1982). However, the morphological characters of *Elomeryx* do not match with the general shape of the remains of Grancona as the cusps are more selenodont and the mesostyle is pinched-in like most of the Bothriodontinae (Lihoreau and Ducrocq, 2007).

According to literature, the mesostyle of *Prominatherium* is less prominent (Hellmund and Heissig, 1994; Patrulius, 1954) than in the Grancona specimen, but otherwise the general structure agrees well with the taxon. The metastyle of the specimen of Grancona is distally positioned compared to that of *Anthracotherium* sp. (Fig. 2D–E) similarly as in *Prominatherium* and the measurements are convincing for its attribution to this genus (Table 1). In short, the morphometrical characters of MCZ 3422 are consistent with an attribution to the species *P. dalmatinum* (Fig. 2A).

4. Discussion

Anthracotheres have been often early members of large-scale mammalian dispersal (Lihoreau and Ducrocq, 2007). According to Popov et al. (2001), this could be explained by the palaeogeographic settings during the Eocene, when the Parathetys had a key role in the selection of species that could spread from Asia to Europe. As theorized by Böhme et al. (2013), the dispersal of taxa during this period was influenced by the presence of islands, thus only some taxa could reach the European landmass during the middle–late Eocene (e.g., Baciu and Hartenberger, 2001).

The dispersal of anthracotheres in Europe could be explained considering that most of the Anthracotheriidae lived in strict contact with water sources (Clementz et al., 2008; Lihoreau and Ducrocq, 2007) as demonstrated by the numerous fossils discovered in lignitic deposits (e.g., Dal Piaz, 1932; Kotsakis, 1984, 1986; Russell et al., 1982; Squinabol, 1890). Anthracotheres were probably able to cross low marine water passages between islands and continental areas (Lihoreau et al., 2015). However, only recent lineages of this group can be considered as equivalent to modern hippos (Lihoreau et al., 2014) and other taxa supposedly had different lifestyles (Lihoreau and Ducrocq, 2007).

The first occurrence of anthracotheres in Europe is during the late Eocene at La Débruge in France (MP 18) (Fig. 3) with the species *Elomeryx crispus* (Gervais, 1854) (Ducrocq and Lihoreau, 2006; Lihoreau and Ducrocq, 2007). Another late Eocene representative of Bothriodontinae was found in Bulgaria and was originally attributed to *Elomeryx* sp. The remains were later considered to represent a new genus, *Bakalovia* (Ducrocq and Lihoreau, 2006; Lihoreau and Ducrocq, 2007; Nikolov, 1967; Nikolov and Heissig, 1985) (Fig. 3). Next to bothriodontines, *P. dalmatinum* is the

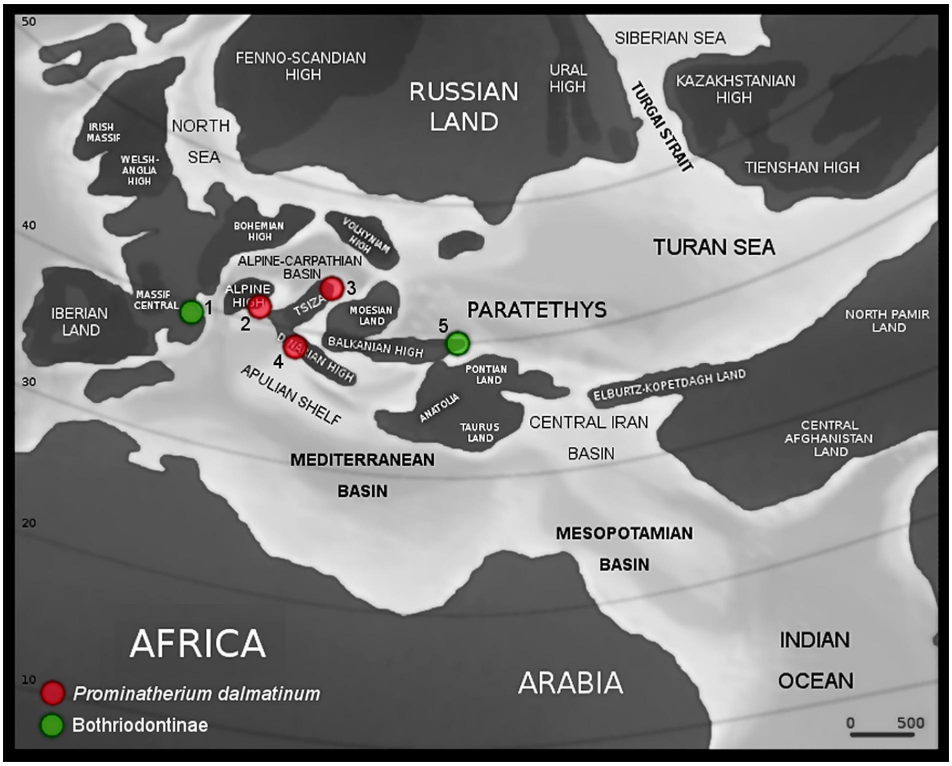

Fig. 3. Distribution map of anthracotheres in Europe during the Late Eocene. The landmasses are based on Popov et al., 2004. **1.** *Elomeryx crispus* from La Débruge, (France) (Ducrocq and Lihoreau, 2006; Lihoreau and Ducrocq, 2007). **2.** *Prominatherium dalmatinum* from Grancona (Italy). **3.** *Prominatherium dalmatinum* from Săcel (Romania) (Patrulius, 1984). **4.** *Prominatherium dalmatinum* from Mt. Promina (Croatia) (von Meyer, 1854). **5.** *Bakalovia* sp. from Bulgaria (Nikolov, 1967; Nikolov and Heissig, 1985).

Fig. 3. Carte de distribution des anthracothères en Europe au cours de l'Éocène supérieur. Les masses continentales sont issues de Popov et al., 2004. **1.** *Elomeryx crispus* de La Débruge, France (Ducrocq et Lihoreau, 2006 ; Lihoreau et Ducrocq (2007)). **2.** *Prominatherium, dalmatinum* de Grancona, Italie. **3.** *Prominatherium dalmatinum* de Săcel, Roumanie (Patrulius, 1984). **4.** *Prominatherium dalmatinum* de Mt Promina, Croatie (von Meyer, 1854). **5.** *Bakalovia* sp. de Bulgarie (Nikolov, 1967 ; Nikolov et Heissig, 1985).

only anthracotherine found in Europe before the Grande Coupure event (MP 20–21) (Costa et al., 2011) as it was found in Eocene calcareous and lignitic layers from Romania and Croatia respectively (Hellmund and Heissig, 1994; Patrulius, 1954).

The specimen of Grancona provides more information about the distribution of this family in Europe. The Italian peninsula was almost entirely submerged during the Eocene, with sporadic volcanic islands emerging in the pre-Alps context (Rasser et al., 2008) (Fig. 3). So far, there are no records of this family in Italy before the early Oligocene (MP 21) (Ghezzo and Giusberti, 2016; Kotsakis, 1986; Pandolfi et al., 2016).

P. dalmatinum from Grancona, dated to the Priabonian, significantly contributes to the understanding of the dispersal of Anthracotheriidae in Europe. Its discovery could demonstrate a connection between Italy and the Balkan area and a possible way of dispersal for the anthracotheres. Concerning *Elomeryx* from La Débruge, although with different species, it could be theorized that this bothriodontine reached France through the Alpine High (Fig. 3).

The distribution of the late Eocene anthracotheres (Fig. 3) shows how this family surely spread before the Eocene–Oligocene Boundary (MP 20–21) with various lineages. We know from the fossil record that only *Elomeryx* survived this transition, as demonstrated by the numerous remains discovered in southern France, England, Switzerland, Germany and Greece (e.g., Bastien et al., 2012; Kostopoulos et al., 2012; Lihoreau et al., 2009; Russell et al., 1982). The genus *Prominatherium*, however, does not appear in Oligocene sequences suggesting that it did not survive the Grande Coupure.

Hence it is possible that anthracotheres spread in Europe in two different phases: 1) during the late Eocene with *P. dalmatinum* and representative of Bothriodontinae, 2) during the early Oligocene with the genus *Anthracotherium*.

On the other hand, the similarities between *Prominatherium* sp. and *Anthracotherium* sp. could mean that the first one evolved into the latter during the Eocene–Oligocene boundary. However, the available evidence is not sufficient for a proper phylogenetic analysis.

4.1. *Palaeogeographical implications*

The discovery of a representative of the genus *Prominatherium* in northern Italy — found only in the Balkan region until now — might testify for a connection between the Balkan and the Berici area. This connection could have facilitated the spread of anthracotheres from eastern to western Europe (Böhme et al., 2013; Kotsakis et al., 2005; Popov et al., 2001). The deposits in which the Italian material was found are similar to those where the *Prominatherium* specimen was discovered in Romania (Patrulius, 1954), as both were included in a shallow marine calcareous sediment. Therefore it is likely that this species reached the Italian peninsula via water, as it was previously theorized by Lihoreau et al. (2015). It is plausible that the Grancona remains could have been transported from the mainland to the marl layer by a water stream as well. A large portion of northeastern Italy would have had fully emerged areas, perhaps an archipelago of islands not far from the mainland, to allow the survival and the migration of these artiodactyls.

Considering that only recent lineages of Anthracotheriidae had lifestyles supposedly similar to Hippopotamidae (Lihoreau and Ducrocq, 2007), the idea that *P. dalmatinum* was able to cross the sea to reach other islands seems unlikely. However, the palaeogeographical settings of the Paratethys during the Priabonian show how the islands were connected by shallow-marine waters (Popov et al., 2001; Popov et al., 2004, Rasser et al., 2008) (Fig. 3).

Fig. 3 shows that, notably, the bothriodontines are present during the same period in two localities distant from each other — Czech Republic and France — but not in the area where *Prominatherium* was found (Fefjar, 2005; Lihoreau and Ducrocq, 2007). However, specimens of *Elomeryx* sp. were found in Switzerland, France and Greece (Bastien et al., 2012; Ducrocq and Lihoreau, 2006; Kostopoulos et al., 2012; Lihoreau and Ducrocq, 2007; Lihoreau et al., 2009; Russell et al., 1982) starting from the Oligocene.

5. Conclusions

Comparison between specimen MCZ 3422 and the most compatible characteristics of *P. dalmatinum* is somewhat tentative, due to the presence of only two well-preserved teeth. Still, the structure of the third molar resembles more the *Prominatherium* genus than the other coeval species found in Europe. Also the measurements are convincing and as a result, specimen MCZ 3422 is referred to *P. dalmatinum.*

It is not possible to locate the exact position of finding, but the context of recovery is clear. There are no doubts regarding the age of the fossil of Grancona, considering the literature (Fabiani, 1915; Rasser et al., 2008) and the adhered matrix. The specimen was deposited into a calcareous layer dated to the Priabonian (MP 17–20).

The attribution of the material to the late Eocene implies that anthracotheres reached western Europe before *Anthracotherium*, which is the former oldest terrestrial mammal taxon spread in Italy (Ghezzo and Giusberti, 2016; Kotsakis, 1984, 1986; Kotsakis et al., 2005; Pandolfi et al., 2016; Russell et al., 1982). This makes the fossil of Grancona the oldest representative of terrestrial mammals in the Italian peninsula.

Furthermore, the matrix in which the fossil is embedded–a marly limestone with endocasts of molluscs–is certainly a marine sediment. Hence, the specimen is likely to have died somewhere in the proximity of water. *Prominatherium* may in fact have reached the Italian Peninsula via sea, as it was previously theorized by Lihoreau et al. (2015).

Concerning its distribution in the European continent, the dispersal of the anthracotheres appears to have had multiple phases. *P. dalmatinum* was one of the oldest species that reached Europe with the bothriodontines *Elomeryx* sp. and *Bakalovia* sp. (Lihoreau and Ducrocq, 2007; Nikolov and Heissig, 1985).

After the Eocene–Oligocene boundary *Prominatherium* presumably did not survived the Grande Coupure and *Anthracotherium* spread into Europe from Asia as evident from several remains found in northern Italy, Switzerland, France, Greece and other localities (e.g., Bastien et al., 2012; Lihoreau and Ducrocq, 2007; Lihoreau et al., 2009; Ghezzo and Giusberti, 2016; Kostopoulos et al., 2012; Pandolfi et al., 2016; Russell et al., 1982).

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