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First occurrence of Palaeotheriidae (Perissodactyla) from the late–middle Eocene of eastern Thrace (Greece)



Première occurrence de Palaeotheriidae (Perissodactyla) de l'Éocène moyen–tardif de Thrace orientale (Grèce)

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ABSTRACT

A detailed assessment of postcranial fossils collected at Balouk Keui (Thrace, Greece) in the mid-19th Century by the naturalist Auguste Viquesnel enabled us to identify the material as pertaining to *Palaeotherium* sp., cf. *P. magnum*, which constitutes the easternmost occurrence of the genus during the Eocene. We have constrained the geographic and stratigraphic provenance of the fossil by reassessing information about Viquesnel's itinerary and observations. Although the exact age of the fossil remains uncertain, the occurrence of a palaeothere in the Thrace Basin during the Eocene indicates a wider geographic distribution for the genus, which had previously been restricted to western and central Europe. The palaeothere of Balouk Keui confirms that the palaeogeographic range of this group included the Balkans during the middle–late Eocene. This discovery also shows that at least intermittent land connections between western Europe, Southeast Asia, and perhaps Central Iran facilitated mammalian dispersal during the middle–late Eocene, before the famous Grande Coupure.

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R É S U M É

Une description détaillée de restes fossiles récoltés à Balouk Keui en Thrace (Grèce) par le naturaliste Auguste Viquesnel au milieu du XIX^e siècle nous a permis d'identifier *Palaeotherium* sp., cf. *P. magnum*, ce qui représente la présence la plus orientale de l'espèce durant l'Eocène. L'origine géographique et stratigraphique des fossiles est également abordée à travers nos observations recoupées avec les écrits de Viquesnel. Bien que son âge soit encore incertain, ce paléothère de Thrace confirme la large répartition géographique de la famille auparavant considérée comme endémique d'Europe occidentale. Cette découverte suggère une paléogéographie complexe au cours de l'Éocène moyen, qui permettait la dispersion de mammifères entre différents petits blocs continentaux nord-téthysiens, avant la fameuse Grande Coupure.

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1. Introduction

In his famous *Voyage dans la Turquie d'Europe, description physique et géologique de la Thrace*, published between 1855 and 1868, Auguste Viquesnel mentioned fossil bones near Balouk Keui, a small village in western Thrace (now part of Greece) which was then part of the Ottoman Empire (Fig. 1C). Viquesnel collected these fossils during his ultimate travel across SE Europe and the Levant between May of 1847 and January of 1848. These fossils consist of seven pedal elements belonging to a single large-bodied perissodactyl (Fig. 1B). These fossils were brought to the Natural History Museum in Paris for identification. There, A. Gaudry concluded “*Il est difficile de décider si la pièce recueillie par Viquesnel provient d'un petit Rhinocéros ou d'un Palaeotherium, car il n'y a pas de différences constantes entre les pieds de ces deux genres*” (Viquesnel, 1868: 470). Since then, this specimen, stored in the collection of the MNHN, has never been re-examined despite its potential scientific interest as a unique and fairly complete specimen from an otherwise undocumented fossiliferous site in western Thrace. Recently, one of us rediscovered it in the context of historical research on palaeontological investigations in NW Turkey (Sen, 2016). Here, we re-examine this “historic” specimen, recently re-located in the collection of the MNHN, and attempt to clarify its systematic affinities and stratigraphic provenance.

Palaeotheriids are fairly common perissodactyls from the middle–late Eocene and early Oligocene of western Europe (Cuvier, 1804, 1805; Franzen, 1968; Remy, 1967). They are considered a side-branch of equids (e.g., Franzen, 2010), and they are either divided into two subfamilies, the Plagiolophiinae and the Palaeotheriinae (Brunet and Jehenne, 1989; Cuesta, 1994; Franzen, 2010), or else maintained within a single sub-family Palaeotheriinae including the two genera *Palaeotherium* and *Plagiolophus*, which are subdivided into two and three sub-genera respectively (Danilo et al., 2013; Remy, 2000, 2004, 2015). Palaeotheriid systematics are mostly based on dental and cranial features (Franzen, 1968; Remy, 1967, 1976, 2004), because their postcranial skeletons are generally less thoroughly documented and much less studied than their skulls and dentitions. Consequently, generic and specific identifications of astragali at specific localities are often based on the sole criterion of size (Remy, 2004: 166). *Palaeotherium* Cuvier, 1804 is known by abundant material from various middle–late Eocene localities of western Europe, including the famous “gypses de Montmartre” that have yielded anatomically articulated material studied by G. Cuvier.

The number of species and subspecies referable to *Palaeotherium* is still a matter of debate (e.g., Remy, 1992), as is the range of intraspecific morphological and metric variation. Consequently, size is sometimes an important parameter in determining species assignment (Franzen, 1968). Although most paleotheriids became extinct during the late Eocene, *Palaeotherium medium* survived the Great Eocene–Oligocene turnover (also known as the “Grande Coupure”, Stehlin, 1909), but became extinct in the earliest Oligocene (MP21, Brunet, 1977). Several species of *Plagiolophus* survived the “Grande Coupure” (Heissig, 1987), and some of them are restricted to the Oligocene (Brunet, 1979;

Remy, 2000). *Pl. javali* from Le Garouillas (MP25) is the last known occurrence of paleotheriids (De Bonis, 1995).

2. Geographic and geological context

The Thrace Basin is the largest Tertiary basin of the North Aegean region. It is bounded by metamorphic rocks of the Rhodope massif of northern Greece, the Strandja Massif of southern Bulgaria and Turkey, and the Sakarya Massif of northwestern Turkey (Fig. 1A). Recent studies indicate that extensional deformation began either in the Eocene (Burchfiel et al., 2003) or earlier in the Late Cretaceous–Paleocene (Bonev et al., 2006). The Thrace Basin is interpreted as a forearc basin developed in the context of northward subduction along the Intra-Pontide suture zone (Görür and Okay, 1996), but various alternative hypotheses have been proposed to explain the origin and evolution of the basin (e.g., Kiliyas et al., 2013).

The sedimentary infill of the northern, western and central portions of the Thrace Basin started during the middle Eocene, and these strata uncomfortably overlie the basement complexes of the Rhodope–Strandja massifs. The western margin of the basin is characterized by an Eocene sequence of coarse-grained fan-deltas prograding eastward (Caracciolo et al., 2015). Rapid subsidence occurred during the late Eocene to Oligocene, after deposition of Lutetian alluvial–fluvial coarse sandstone and conglomerate (Caracciolo et al., 2011). A summary of the stratigraphy and sedimentology of the southern Thrace Basin fill can be found in Okay et al. (2010). The older Eocene sedimentary rocks of the basin are extensively exposed along the basin margins, and they form a complicated molassic sequence composed of intercalations of bedded conglomerates, breccia conglomerates, sandstones, nummulitic limestones, turbiditic layers and shales. In the Evros drainage basin (Feres area), sedimentation started with the deposition of Lutetian–Bartonian continental sediments (mainly breccia conglomerates and sandstones), followed during late Eocene–Oligocene time by marine turbiditic-type deposits and limestones interbedded with volcanogenic rocks (Caracciolo et al., 2012, 2015). The Palaeogene molassic sediments are intercalated with a large volume of calc-alkaline volcanics including lava flows, debris flows, hydroclastites, domes, dykes and numerous pyroclastics (Papadopoulos, 1980). According to geochronological and stratigraphic data the volcanism in the area started during the middle Eocene, but the high-K calc-alkaline volcanic activity culminated during the late Oligocene (Innocenti et al., 1984) with K/Ar ages ranging from 33.4 to 20 Ma (early Oligocene to early Miocene; Christofides et al., 2004).

3. Materials and methods

The material is stored in the collections of the “Muséum national d'histoire naturelle” in Paris.

Anatomical features and suprageneric systematics of rhinocerotids follow Becker et al. (2013). Dimensions are given in centimeters. The gracility index (Gr-I) calculated from the metapodials follows the definition of Guérin (1980): (Transverse diameter × 100)/length. This



Fig. 1. A. Geo-tectonic map showing the main structural units of the region, the Thrace Basin (the black square is the close of the Fig. 2C), and the two Eocene localities that have yielded remain of paleotheriids. B. Elements of the foot (MNHN.F.AC2374), as it is conserved at MNHN-Paris, of *Palaeotherium* sp., cf. *P. magnum*, and the original label “Balouk Keui, on the road to the village at Féré, Rhodope Massif” apposed on the back side of the specimen by mid-19th century. C. Original map of the region from the Atlas of A. Viquessel, with the location of Balouk Keui inland the Aegean Coast (star), and the different localities (Feredjik or Vira in the map) with their Ottoman names.

Fig. 1. A. Carte géo-tectonique montrant les principales unités structurales de la région, le bassin de Thrace (le cadre noir est une vue de près de la Fig. 2C) et les deux localités éocènes qui ont livré des restes de paléotheriïdes. B. Éléments du pied (MNHN.F.AC2374), tel qu’il est conservé au MNHN à Paris, de *Palaeotherium* sp., cf. *P. magnum*, et étiquette originale « Balouk Keui, sur la route vers le village de Féré, massif du Rhodope » apposée sur la face arrière du spécimen au XIX^e siècle. C. Carte originale de la région provenant de l’atlas de A. Viquessel, avec la localisation à l’intérieur de la côte égéenne de Balouk Keui (étoile) et des différents villages (Feredjik ou Vira sur la carte) avec leur noms ottomans.

index is generally calculated from the third metacarpal. We have calculated this index for the third metatarsal. It is worth noting that metatarsals are generally shorter than metacarpals in palaeotheriids (e.g., Stehlin, 1938), while the transverse diameter of metapodials does not differ substantially between the fore- and hindlimb. Consequently, the index calculated from the Mt3 is slightly higher than

that calculated from the Mc3. We have considered an error margin of 5 mm in the estimation of the length of Mt3 (see below), which corresponds to the variation of length for the distal diaphysis of the Mt3 in large Paleotheres and early Oligocene rhinos. The Gr-I decreases when the gracility of Mt3 increases. We estimate the Gr-I of MNHN.F.AC2374 as falling between 20.3 and 21.1. The LBI is another index of



Fig. 2. Foot bones (MNHN.F.AC2374) of *Palaeotherium* sp., cf. *P. magnum* from the middle–late Eocene of Balouk Keui, Thrace, Turkey. Metatarsal 2 in posterior (A), medial (B), lateral (C) views. Metatarsal 3 in medial (D), proximal (E), anterior (F), posterior (G) views. Metatarsal 4 in medial (H), anterior (I), posterior (J) views. Phalanx 1 of the digit 3 in anterior (K) and proximal (L) views. Ectocuneiform in proximal (M) and distal (N) views. Navicular in proximal (O) and distal (P) views. Astragalus in distal (Q), posterior (R), and anterior (S) views. The main articular facets discussed in the text are indicated

gracility proposed by Franzen (1968), which is widely used in the literature dealing with palaeotheriids (e.g., Remy, 2004). The LBI is calculated as follows: (length/minimal width of the Metapodial) \times 10. The LBI increases when the gracility of Mt3 increases. The LBI of MNHN.F.AC2374 is estimated to have been between 47 and 49 (reflecting the uncertainty in estimating the length of Mt3 in this specimen). We have compared the Gr-I and the LBI of the specimen from Balouk Keui with values obtained from the literature (Franzen, 1968) and from personal observations for palaeotheriids, and from Becker (2003: 254) for rhinocerotoids.

Anatomical abbreviations: APD: anteroposterior diameter; L: mesio-distal length; H: height; m.: muscle; Mc: metacarpal; Mt: metatarsal; OD: oblique diameter; TD: transverse diameter.

In order to strictly maintain the binomial system in the use of “cf.”, we have used throughout the text “*Palaeotherium* sp., cf. *P. magnum*” as suggested by Lucas (1986).

4. Systematic paleontology

Order Perissodactyla Owen, 1848

Superfamily Equoidea Gray, 1821

Family Palaeotheriidae Bonaparte, 1850

Genus *Palaeotherium* Cuvier, 1804

Type species *Palaeotherium magnum* Cuvier, 1804 from the gypsum of Montmartre (France)

Palaeotherium sp., cf. *P. magnum* Cuvier, 1804

Referred material: the specimen MNHN.F.AC2374 is a plaster support allowing the skeletal elements of a left pes to remain in anatomical position (Fig. 1B). The specimen comprises the astragalus, navicular, ecto- and mesocuneiforms, the metatarsals 2, 3, and 4 (the distal epiphysis of Mt3 is lacking), and a proximal phalanx, which based on its robustness and transverse diameter, belongs to digit 3, and not digit 4 as figured by Viquesnel (1868, atlas, Plate 21). Among the tarsal bones, only the cuboid, the calcaneus and the entocuneiform are lacking.

Measurements: astragalus (H = 5.3*, OD = 6.4, TD = 6.6*); navicular (ADP = 2.9, TD = 4.0); Mt2 (L = 10.0, TD = 1.6); Mt3 (12.3 < L < 12.8*, TD = 2.6); Mt4 (L = 10.2, TD = 2.2); Phalanx I of the Mt3 (L = 2.7, TD = 3.2). * indicates estimated values.

4.1. Description

The distal and plantar parts of the astragalus are damaged, thus limiting our observation of certain structures such as the exact outline of articular facets.

In anterior view, the column tali of the astragalus is low and close in proportion to what is observed in *Palaeotherium magnum* from Montmartre (e.g., specimen MNHN-GY416a). The medial process is broken and the lateral part of the facet with the cuboid is lacking (Fig. 2Q). The tibial trochlea is asymmetric and the medial lip is narrower than the lateral one. Although broken, the medial process gives the impression that the trochlea is “offset” from the rest of the astragalus (Fig. 2S). In anterior view, a distinct groove extends medio-laterally along the distal tibial trochlea, separating the trochlea from the neck (Fig. 2Q). The orientation of the fibular facet of the astragalus is oblique and slightly concave in anterior view.

On the posterior (plantar) side, the proximal calcaneal facet is large and strongly concave. The lateral process is damaged so that part of the proximal calcaneal facet is obliterated (Fig. 2R). The bony disto-lateral border of that facet is broken so that the presence or absence of a lateral expansion is not observable. The sustentacular facet is large and oval in outline with a distal “foot-like” extension vaguely forming an L-shaped structure (Fig. 2R). This distal expansion of the sustentacular facet reaches the distal border of the neck. The sustentacular facet does not seem to contact the distal calcaneal facet, although this part of the astragalus is fairly damaged on MNHN.F.AC2374 (Fig. 2R). The distal calcaneal facet forms a small rectangle, the medial extension of which seems to be obliterated by breakage.

The distal articular surface of the astragalus is entirely occupied by the large saddle-shaped navicular facet (partly broken), and the smaller and more lateral facet for the cuboid. The latter facet is posteriorly damaged, and forms a right angle with the preserved part of the distal calcaneal facet. The ridge between the cuboid and navicular facets is strongly oblique in distal view (Fig. 2Q) and there is no posterior stop on the cuboid facet.

The navicular is mesio-distally compressed, as it is in many other perissodactyls, and its proximal surface is entirely made up of the saddle-shaped and somewhat convex facet for the astragalus head (Fig. 2O). In proximal view, the navicular displays a lozenge-like outline, and its lateral border is not inflected (although this latero-posterior border of the navicular is partly broken). The distal face bears facets for the ectocuneiform and mesocuneiform (Fig. 2M–N rather P but those facets are not obvious). Although not directly observed, the presence of a postero-medially placed entocuneiform is confirmed by a facet for this element on Mt2 (Fig. 2A, C). The proximal face of the ectocuneiform is slightly concave, and its postero-lateral part is broken so that we cannot observe the facets for the cuboid. The medial facets for the mesocuneiform are barely visible.

in light red. Astragalus: cf: cuboid facet; dcf: distal calcaneal facet; nf: navicular facet; pcf: proximal calcaneal facet; scf: sustentacular facet. Metatarsals: c.f: cuboid facet; etc.f: ectocuneiform facet; ent.f: entocuneiform facet; MtIII.f: articular facet for the MtIII; MtIV.f: articular facet for the MtIV.

Fig. 2. Os du pied (MNHN.F.AC2374) de *Palaeotherium* sp., cf. *P. magnum* de l'Éocène moyen-supérieur de Balouk Keui, Thrace, Turquie. Métatarsien 2 en vues postérieure (A), médiale (B) et latérale (C). Métatarsien 3 en vue médiale (D), proximale (E), antérieure (F) et postérieure (G). Métatarsien 4 en vues médiale (H), antérieure (I), postérieure (J). Phalange I du doigt 3 en vues antérieure (K) et proximale (L). Ectocunéiforme en vues proximale (M) et distale (N). Naviculaire en vues proximale (O) et distale (P). Astragale en vues distale (Q), postérieure (R), et antérieure (S). Les principales facettes articulaires discutées dans le texte sont indiquées en rouge. Astragale : cf : facette pour le cuboïde ; dcf : facette distale pour le calcanéum ; nf : facette pour le naviculaire ; pcf : facette proximale pour le calcanéum ; scf : facette sustentaculaire. Métatarsiens : c.f : facette pour le cubide ; etc.f : facette pour l'ectocunéiforme ; ent.f : facette pour l'entocunéiforme ; MtIII.f : facette articulaire pour le MtIII ; MtIV.f : facette articulaire pour le MtIV.

The pes is tridactyl with three functional digits, suggesting a digitigrade foot posture and mediportal locomotion probably close to that of extant tapirs. In medial view, the three metatarsals display a diaphysis with a concave posterior border. As much as one can observe, the three metatarsals have long medial and lateral insertions for the *m. interossei*. The second metatarsal (Fig. 2A–C) has a concave and anteroposteriorly elongated proximal face that articulates with the mesocuneiform. There is also a distinct posteromedial facet for the entocuneiform (Fig. 2A, C). It is well marked and sub-rectangular in shape (Fig. 2A). Laterally, there are two anteroposteriorly elongated facets that may have primarily articulated with the ectocuneiform since no (even tiny) facet is distinguishable on the proximo-medial side of the third metatarsal. The proximal face of the third metatarsal is flat and notched on its lateral border (Fig. 2E). The Mt3 primarily articulates with the ectocuneiform but there is a small sub-rectangular antero-lateral facet which suggests a contact with the cuboid (Fig. 2E). There are two rounded articular facets for the Mt4 (Fig. 2D): the anterior facet is almost triangular, and the posterior is oval in shape. In anterior view, the distal part of the diaphysis is slightly concave suggesting that it was a young adult. The distal epiphysis of Mt3 is lacking but there is a distal widening of the diaphysis. The fourth metatarsal (Fig. 2H–J) primarily articulates with the cuboid facet, but the breakage of the ectocuneiform does not allow one to conclude whether this bone had a small contact with the Mt4. There are two medial facets for the Mt3 (Fig. 2H): the anterior facet is large and sub-square, and the posterior is oval. The proximal epiphysis of Mt4 has a strong posterolateral tuberosity (Fig. 2J), and the lateral border of the diaphysis is strongly concave. There are well-developed lateral protuberances just above the proximal border of the distal articulation of the Mt4 for attachment of the collateral ligament (Fig. 2J). There is no trace of a digit 1. There is only one preserved proximal phalanx (Fig. 2K–L). It is robust and symmetrical along the mesiodistal axis. In dorsal view, there are two protuberances for the common digital extensor tendon. Its transverse diameter is 30% larger than the distal transverse diameter of Mt4, suggesting that this phalanx pertains to Mt3, and not Mt4 as suggested in the reconstruction of the pes made in the 19th century (Fig. 1B).

4.2. Discussion

When these fossil remains were given to Gaudry for his assessment, he stressed the difficulty of differentiating remains of *Palaeotherium* from those of rhinocerotids. Our comparisons confirm that the tarsal and metatarsal features that differentiate palaeotheriids from Palaeogene ceratomorphs are fairly tenuous.

We first compared MNHN.F.AC2374 with rhinocerotids that are commonly found in late Eocene–Oligocene localities of Eurasia, and more specifically in early Oligocene sites in Europe. The astragalus of the amynodontid *Cadurcotherium cayluxi* from Le Garouillas (MP25) is almost 30% larger than that of MNHN.F.AC2374, and it differs from the latter in its reduced collum tali, the strong latero-distal extension of the lateral keel of the tibial trochlea, and the marked posterior bulge of the navicular (De Bonis, 1995).

Moreover, the Mt4 in *Cadurcotherium cayluxi* is reduced and its Mt3 is more gracile (Gr-I: 28.7 based on the mt3 figured in De Bonis, 1995) than that of the specimen from Balouk Keui (20.3 < Gr-I < 21.1).

Extensive comparisons were made with the Oligocene rhinocerotids *Epiaceratherium*, *Mesaceratherium*, *Protaceratherium*, and *Ronzotherium* (Becker, 2009; Brunet, 1979; Dal Piaz, 1930; Ménouret and Guérin, 2009; Uhlig, 1999). Very little is known about the postcranial anatomy of *Molassitherium*, and comparisons with this genus are thus limited (Becker et al., 2013). The autopodium's proportions in MNHN.F.AC2374 do show trends toward brachypody like that found in *Diaceratherium massiliae* from the Oligocene clays (MP26) of Saint-André in southern France (Ménouret and Guérin, 2009). The ratio TD/H of the astragalus for MNHN.F.AC2374 is estimated as 1.2, which is close to the value of *Ronzotherium*, *Mesaceratherium*, and *Protaceratherium*, but higher than *Epiaceratherium*, stressing the significantly higher collum tali of the astragalus of the latter. Likewise, the fibular facet is oblique and slightly concave in our specimen, unlike all of the examined rhinocerotids in which this structure is generally vertical (this part of the astragalus is damaged in *Epiaceratherium bolcense*). The angle between the tibial trochlea and the distal articulation is high in MNHN.F.AC2374 but not as high as in Oligocene rhinocerotids such as *Ronzotherium filholi* (Brunet, 1979) and *Epiaceratherium bolcense* (Dal Piaz, 1930). The proximal calcaneal facet is damaged laterally and distally on our specimen, thus preventing comparisons of its outline and distal expansion, but its concavity and overall proportions resemble those of *Ronzotherium filholi* (Brunet, 1979), *Epiaceratherium bolcense* (Dal Piaz, 1930) and *Epiaceratherium magnum* (Uhlig, 1999). This facet is also similar to that of *Palaeotherium magnum* (Cuvier, 1804; Franzen, 1968). The sustentacular facet is oval or roughly circular, and generally independent from the distal calcaneal facet in Oligocene rhinocerotids, but none of them display the L-shaped distal expansion found in MNHN.F.AC2374 (Fig. 2R). Although broken on the astragalus from Balouk Keui, the medial border of the medial process is rounded, and not straight like that of *E. bolcense*, in which it forms an acute angle with the navicular facet (Dal Piaz, 1930: pl. XIX.5). The posterior stop on the cuboid facet is absent in MNHN.F.AC2374, unlike the condition seen in the amynodontid *Cadurcotherium* (De Bonis, 1995) and the rhinocerotids *Epiaceratherium*, *Ronzotherium*, *Mesaceratherium*, and *Protaceratherium* (Becker et al., 2013). While this character alone is not an ultimate argument to exclude MNHN.F.AC2374 from rhinocerotids, the absence of a posterior stop on the cuboid facet remains very rare among the latter (Antoine, 2002).

Like in *Epiaceratherium bolcense* and *Mesaceratherium welcommi*, the diaphysis of Mt3 widens distally, although the epiphysis is not preserved in our specimen. The anterior border of Mt3 is straight like in *Ronzotherium filholi* (Brunet, 1979) and *Epiaceratherium magnum* (Uhlig, 1999), and unlike *Epiaceratherium bolcense* (Dal Piaz, 1930), *Protaceratherium minutum*, and *Mesaceratherium welcommi* (Becker et al., 2013). Like in *Ronzotherium filholi* and *Epiaceratherium bolcense*, the cuboid facet is present on the Mt3, but it is smaller than in the latter species. Perhaps

because of preservation issues, we have not observed any articular facets for Mt2 on the third metatarsal. One or two such facets are always present in rhinocerotids.

The gracility index (Gr-I) calculated on the Mt3 of our specimen varies from 20.3 to 21.1 depending on the estimated value of the mesiodistal length of Mt3, 12.3 cm and 12.8 cm respectively. These values are close to the Gr-I of *Ronzotherium filholi* (20.2 calculated from the Mc3; Becker, 2003). However, these values are lower than the Gr-I of *Epiceratherium magnum* (22.7 calculated from the Mc3), *Protaceratherium minutum* (22.5 from the Mc3; Becker, 2003), and *Ronzotherium romani* (23.7 calculated from the Mt3; Becker, 2003), all of which were more squat than our specimen. The Gr-I of MNHN.F.AC2374 is also comparable to some extent to that of gracile lophodontids such as *Lophiodon leptorhynchum* (22.3) from the early middle Eocene of southern France (Depéret, 1907). However, the morphology of the astragalus of the latter strongly contrasts with that of MNHN.F.AC2374. There is no contact between the cuboid and the Mt3, and the morphology of the astragalus is stout and block-like with a shallower tibial trochlea and higher collum tali that set the tarsus of *L. leptorhynchum* apart from our specimen.

Plagiolophus is the other genus among palaeotheriids that is known by several sub-genera (Remy, 2004 for a synthesis), including slender and more “squat” species. None of the species attributed to the genus *Plagiolophus* match the size of the specimen of Balouk Keui, which is about 30% larger than *Pl. fraasi*, the largest species of *Plagiolophus*. Within the genus *Plagiolophus*, the gracility index (LBI) varies from ~60 for the squat species such as *Pl. fraasi* or *Pl. javali* (Remy, 1995) to over 80 for the slender species like *Pl. minor* (Stehlin, 1938). These values are higher than the LBI of MNHN.F.AC2374, which varies between 47 and 49 depending on the estimated length of the Mt3. Generally, the metatarsals of *Plagiolophus* are much more elongated mesiodistally, probably indicating lesser contact with the ground for the lateral digits during locomotion (Remy, 2004). The cuboid facet of the astragalus is generally absent in *Plagiolophus* (even in large and relatively squat species such as *Pl. fraasi*), while it is always present in *Palaeotherium*. This character, probably related to cursorial capabilities, may be a useful postcranial feature to differentiate the two genera. In that regard, the retention of a cuboid facet in *Palaeotherium* is a primitive feature associated with a more generalist terrestrial locomotion, comparable to that of rhinos. Moreover, the astragalus of *Plagiolophus* noticeably differs from that of large species of *Palaeotherium* in being slender (its collum tali is higher), the tibial trochlea is generally more oblique, and its groove deeper than in *Palaeotherium*, the distal articular surface of the astragalus is anteroposteriorly reduced, and the sustentacular facet tends to form a J which generally joins the distal calcaneal facet (Holbrook, 2009).

In fact, MNHN.F.AC2374 shows the strongest resemblance with the pes of *Palaeotherium magnum*. We have mostly compared our specimen with the material of *Palaeotherium* from La Débruge (MP18) and from the “Gypse de Paris” (MP19) described and figured by Cuvier (1804) and currently housed at MNHN, Paris. In terms of size, MNHN.F.AC2374 fits best with the large palaeotheriid

Palaeotherium magnum, although it is smaller than the type material of the species reported by Cuvier (1804) from the “Gypse de Paris” (Fig. 3). Consequently, we prefer to refer to the fossil from Balouk Keui as *Palaeotherium* sp., cf. *P. magnum*. The Balouk Keui specimens recall in size some middle and late Eocene forms from France and Germany that Franzen (1968) identified as “*P. cf. magnum*”. The height of the collum tali varies among the material referred to *P. magnum* (see Franzen, 1968, pl. 2–4; Franzen, 1983), but the larger individuals (*P. magnum magnum*) tend to show a higher collum tali than on MNHN.F.AC2374. The TD/H ratio varies in *P. magnum* from 0.92 (specimen GY416a, Montmartre) to 1.25 (specimen LAD33, La Débruge); it is about 1.2 for the material from Balouk Keui. The groove on the tibial trochlea is comparable to that of large sized *Palaeotherium magnum* from Montmartre (e.g., specimen GY416a). In dorsal (anterior) view, the orientation of the fibular facet on the astragalus is oblique and slightly concave as in *Palaeotherium* (Casanovas-Cladellas, 1978; Casanovas-Cladellas et al., 1992; Franzen, 1968), but in contrast to Oligocene rhinocerotids. On the posterior (plantar) side, the proximal calcaneal facet is large and strongly concave and resembles that of *Palaeotherium magnum*, but this is not a conclusive character. However, the configuration of the oval sustentacular facet is most reminiscent of large *P. magnum* from Montmartre, although the specimen from Balouk Keui displays a distal extension of this facet (forming vaguely an “L”) that reaches the distal border of the neck. The latter configuration was never observed in *P. magnum* specimens we inspected, in which the sustentacular facet is generally oval in shape. Damage on the distal border of the neck in posterior view does not allow one to observe the lateral extent of this facet, which is almost continuous transversely in *P. magnum* (see GY416a from Montmartre), and similar to the configuration of MNHN.F.AC2374 on the astragalus (LAD33) from La Débruge. In distal view, the ridge between the cuboid and navicular facets is strongly oblique (Fig. 2Q) and comparable in morphology (although slightly smaller) to the astragalus (LAD33) of *P. magnum* from La Débruge. Although not preserved, the entocuneiform was posteromedially placed (according to the facet on Mt2) like what is observed in large species of *Palaeotherium*, including the *Palaeotherium curtum* figured in Stehlin (1938: 273). The proximal phalanx is proximo-distally short and squat, and the distal diameter is smaller than the proximal diameter like in *Palaeotherium*. Finally, the Gr-I calculated from the Mt3 varies roughly between 20 and 21 in *Palaeotherium magnum* (Franzen, 1968: Fig. 3), which is compatible with the estimated Gr-I for MNHN.F.AC2374 (20.3 < Gr < 21.1).

5. Stratigraphic provenance

A. Gaudry hesitantly identified MNHN.F.AC2374 as a palaeothere, and this occurrence was consistent with the provenance of the specimen provided by the collector (i.e. well below the “nummulitic beds”) (Viquésnel, 1868: 471). However, the exact provenance of the fossil remains problematic, particularly considering the complexity of the local tectonic context and the abundance of terrestrial Neogene deposits in the Feres area.

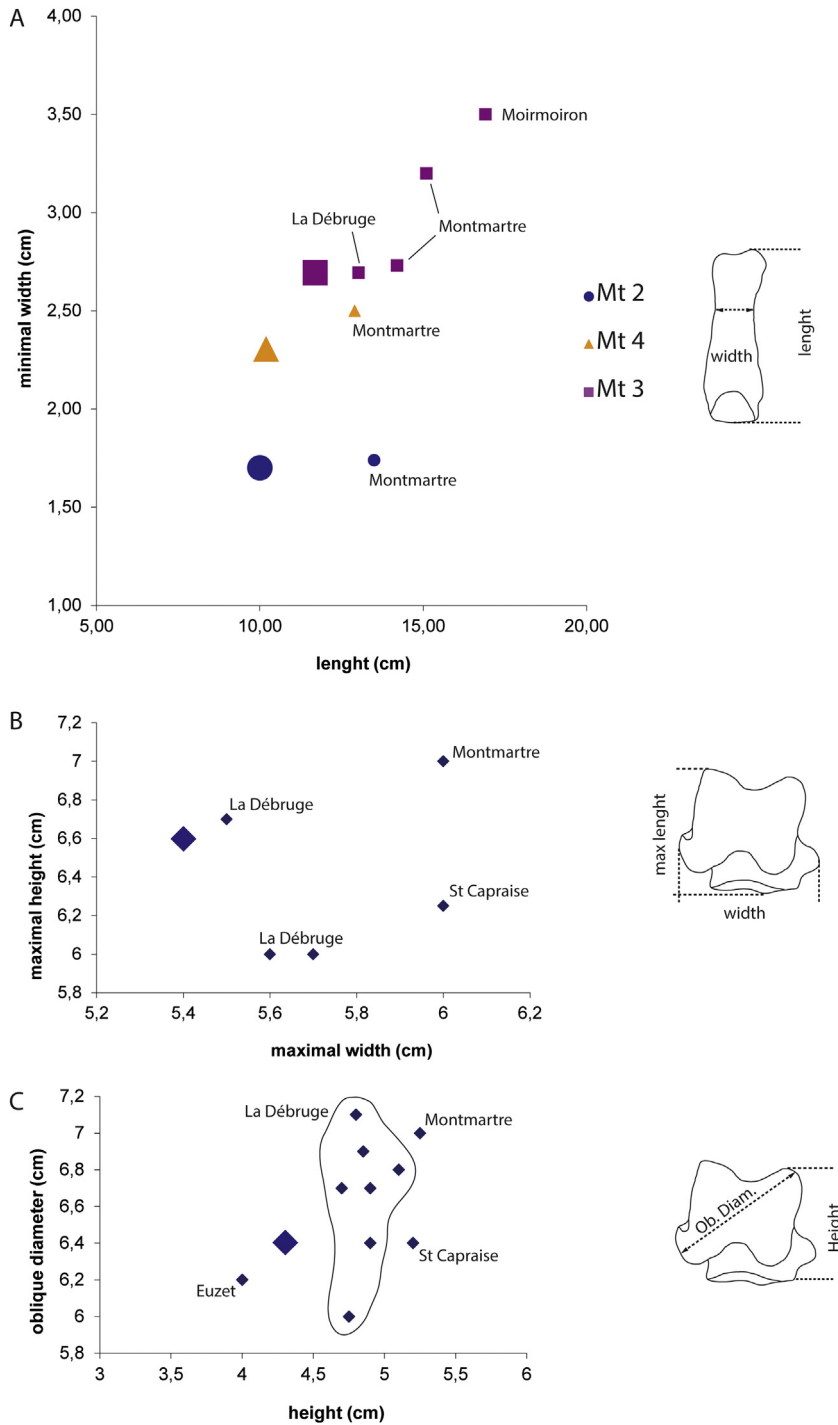


Fig. 3. Bivariate plots showing the measurements of different pedal elements of MNHN.F.AC2374 compared to those of *Palaeotherium magnum* from different localities of western Europe: Euzet (MP17), La Débruge (MP18), Montmartre (MP19), Mormoiron (MP19), St-Capraise d'Eymet (MP20) (from Franzen, 1968). The measured parameters are indicated directly in the drawings of bones on the right of the corresponding graph.

Fig. 3. Graphique bivarié avec les mesures des différents os du pied du spécimen MNHN.F.AC2374, comparées à celles de *Palaeotherium magnum* de différentes localités d'Europe occidentale : Euzet (MP17), La Débruge (MP18), Montmartre (MP19), Mormoiron (MP19), St-Capraise d'Eymet (MP20) (d'après Franzen, 1968). Les paramètres mesurés sont indiqués sur les dessins d'os à droite du graphique correspondant.

The geographic and stratigraphic origins of the fossil are mentioned twice in Viquesnel's monograph. According to Viquesnel (1868: 331), the fossil material was collected while Viquesnel was taking a stratigraphic log of the "mountain East of Balouk Keui" (today Pylaia). The log was taken from base to top, and the fossil bones were found in the first logged beds consisting of green to red sandy clays (Fig. 4C). Later, after a brief morphological description of the fossil and a short discussion about its taxonomic affinities, Viquesnel (1868: 471) remarks that this fossil was collected in micaceous grey marls of the Balouk Keui Hill, on the road from this village to Feredjik (today Feres). In fact, Viquesnel probably reached Feredjik via Kutchuk Okouf (today Kavisos), a locality east of Balouk Keui, and 3 km to the north of Feredjik, because he walked down the tributary ravine near Balouk Keui and joined the main ravine to a small village Buyuk Okouf (Viquesnel, 1868: 332). This latter locality has been localized on the present map of Greece, but according to the map provided in Viquesnel's atlas, Buyuk Okouf was about 1 km NNW in right line from Kutchuk Okouf (today Kavisos).

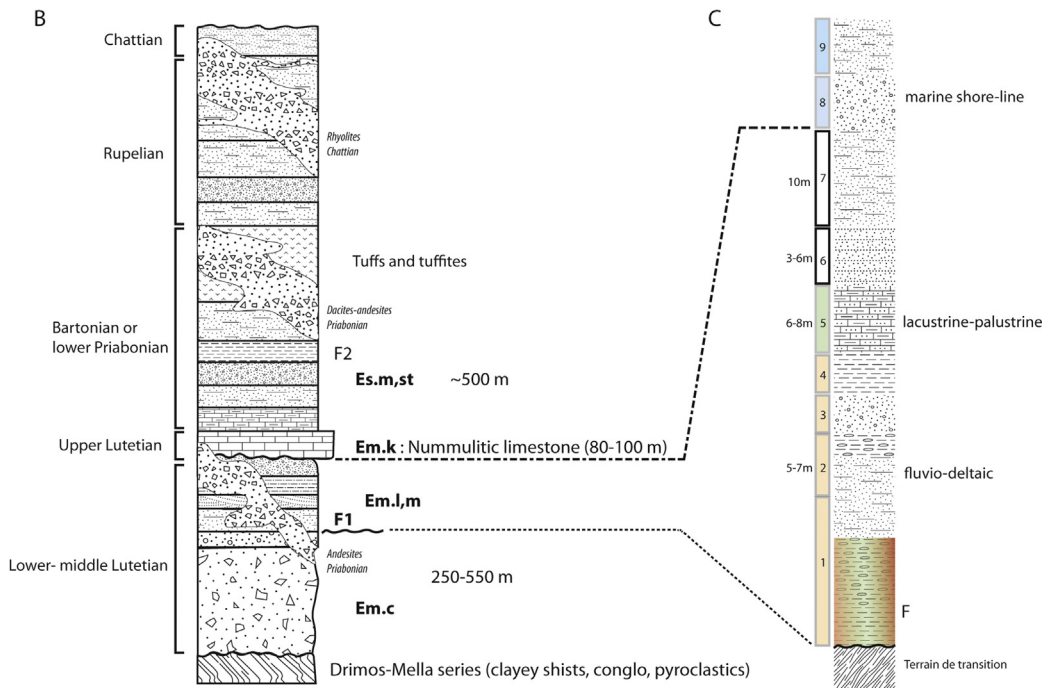
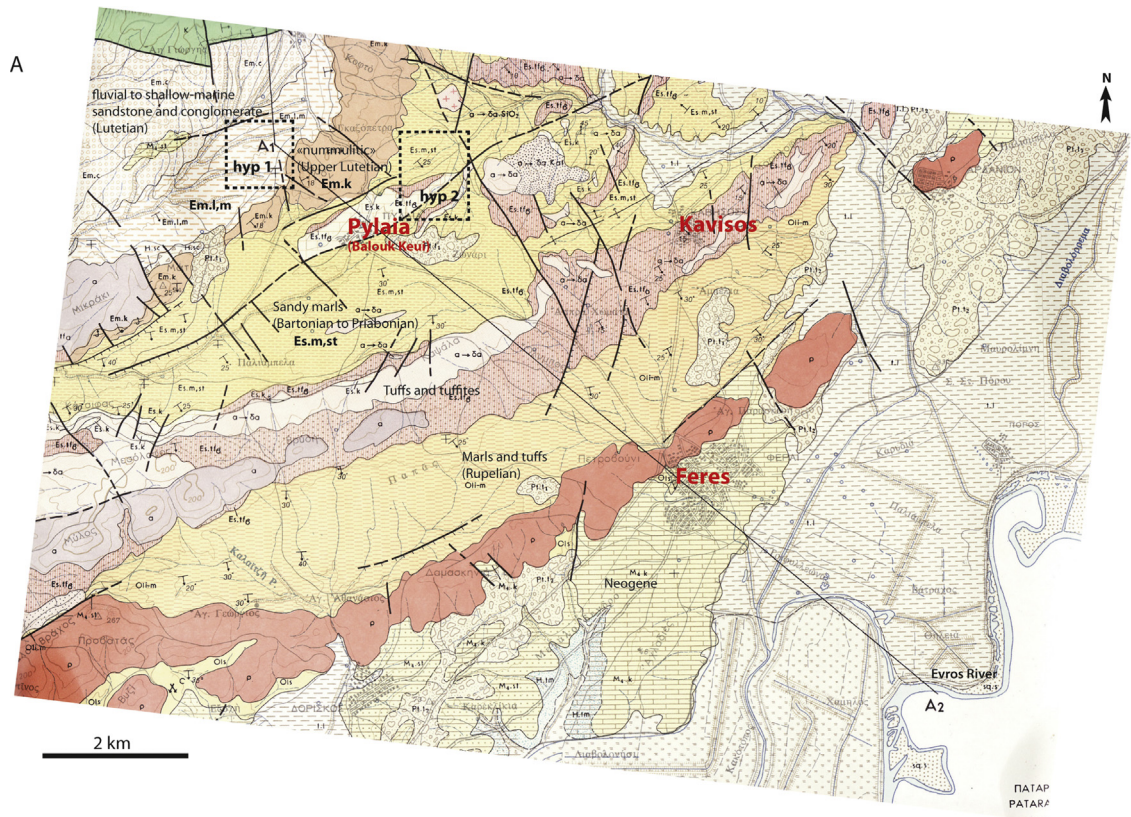
A topographic map of the region shows a wooded hill reaching about 183 m to the East of Pylaia. It seems that Viquesnel ended his section at the top of that hill, because he noted somewhat thick beds of limestone plunging to the southeast (the average dip of the stratigraphic series varies between 30 and 50° to the SE in the area; Papadopoulos, 1980). At issue is determining where Viquesnel started his section. The thickness of beds is not systematically mentioned in his report, and we noted about 30 m without counting the four beds for which the thickness is not mentioned. We can reasonably assume that his section probably did not exceed 50 m, which would cover only a small part of the units of molasse-type deposits underlying the nummulitic limestone (Papadopoulos, 1980). Moreover, Viquesnel obviously did not follow the road to Feredjik (southeastward from Balouk Keui) in making his section. Indeed, he went to the northwest of Balouk Keui to see the unconformable contact between the base of his section (red clays yielding fossils) and the "terrain de transition", which probably corresponds to the breccia, conglomerates, and coarse-grained sandstones that form the base of the molassic sequence locally (Fig. 4B).

The fossil comes from green-red clays with calcareous nodules (likely a paleosol) occurring at the base of the section, he took to the east of Balouk Keui (Fig. 4C). The geological map of this area indicates that different formations of the Palaeogene molassic series are widely exposed around Pylaia (formerly Balouk Keui) (Papadopoulos, 1980). This molassic sequence rests unconformably on the Cretaceous basement, which consists of metasedimentary rocks of the circum-Rhodian belt (Drimos-Mella series, Papadopoulos, 1980), and underlies the late middle Eocene nummulitic sandstone. Chronostratigraphic control for this thick (up to 550 m; Papadopoulos, 1980; d'Atri et al., 2012) clastic succession remains fairly poor, but the base of the sequence is considered as Lutetian on the basis of forams (Papadopoulos, 1980). According to Viquesnel (1868: 471), the fossil bones were collected below the argillaceous limestones yielding freshwater gastropods (unit 5 of his section, Fig. 4C), and so well below the nummulitic limestone dated

as late Lutetian (Papadopoulos, 1980). In the Feres area (Evros drainage basin), the molassic sequence consists of different formations of middle to late middle Eocene age, and they are intruded by several episodes of volcanic lava and tuffs dated as Priabonian, thus giving a minimum age for the remains of *Palaeotherium* sp., cf. *P. magnum*. In his short section, Viquesnel did not mention any volcanic rocks, but he extensively described the red clastics exposed in the bottoms of ravines. These red clastics show various sedimentary facies ranging from conglomerates, coarse grained sandstones to sands and clays, and Viquesnel (1868: 332) stressed the important lateral variation, probably accentuated by the substantial faulting in the area.

The base of the Palaeogene sequence (Fig. 4B) consists of an erosional sequence of the basement with red breccia, green-brown unsorted and un-bedded conglomerates (Em.c on the Ferai-Peplos sheet and of variable thickness, 250 to 550 m; Papadopoulos, 1980) passing upward to cross-bedded sandstones. There is an erosional unconformity between these coarse sediments and the clayey, marly and fine-grained sandstone forming the upper part of the middle Eocene continental sequence (Caracciolo et al., 2011). This succession suggests an alluvial fan evolving upward into braided river and deltaic deposits that might have yielded the remains of the palaeothere. Although no clayey beds or paleosols are reported in the upper clastic unit on the Ferai-Peplos geological map, we can expect that such facies can occur on exposed river banks or inland terrain not immediately juxtaposed to the braided river system. The upper clastic unit (Em.l,m on the Ferai-Peplos sheet) is a succession of pelitic, clayey, marly and fine-grained sandstone that fits better with facies described by Viquesnel as yielding fossil bones. The molassic sequence described above is widely exposed to the NW of Pylaia and it is therefore inconsistent with the Balouk Keui Mountain to the East of Balouk Keui, where the fossil was purportedly found. If we consider the rocks exposed to the east of Pylaia on the geological map, the fossil necessarily has to come from the sandy marls and pyroclastics (Es,m on the Ferai-Peplos sheet and about 500 m thick) that overlie the Lutetian nummulitic limestone (Fig. 4B). In that case, it contradicts the statement of Viquesnel about the origin of fossils from beds well below the Lutetian nummulitic limestone. Those limestones show biomicritic, oolitic and biohermic facies that are unlikely to have yielded palaeothere remains. According to Papadopoulos (1980), the nummulitic limestone is upper Lutetian or lower Bartonian, and andesites intruding the molassic sequence are Priabonian in age. The sandy marls and pyroclastics overlying the nummulitic limestone are intruded by Priabonian dacites-andesites suggesting an upper Bartonian to lower Priabonian age for these deposits exposed to the east of Pylaia. Rupelian strata are also exposed between Pylaia and Feres. They form a band of terrain exposed SE of Pylaia, and their sedimentary facies are typical of terrestrial environments (Papadopoulos, 1980). However, these Oligocene rocks are exposed more than 5 km away from Pylaia, which does not match the notes of Viquesnel.

In conclusion, there are two hypotheses about the stratigraphic origin of the fossil remains, depending whether one



prioritizes the geographic or stratigraphic information provided by Viquesnel, and assuming that he was not confused by duplicated sequences due to tectonics (mostly faulting). The presence of a large *Palaeotherium* in the late Lutetian of Thrace would be the earliest occurrence of the genus, since *P. magnum* is unknown in Europe prior to the MP17 reference level (Bartonian). Hence, the second hypothesis of a Bartonian or early Priabonian age is consistent with the known stratigraphic range of *P. magnum* in western Europe. It is worth noting that the nummulitic limestone rests with a slight erosional and angular unconformity on the underlying units including the lower molassic series, and the age of this marine unit remains poorly constrained (Caracciolo et al., 2011; Maratos et al., 1977).

6. Palaeogeography, and distribution of palaeotheriids during the middle–late Eocene

The discovery of sub-articulated fossils suggests minimal transportation. The Eocene succession exposed in the Feres area indicates an influx of terrigenous material and important volcanic activity. d'Atri et al. (2012) documented the Eocene filling history of this basin, with middle Eocene proximal, coarse-grained sedimentary facies (fan-deltas and alluvial fans) draining directly the basement terrains of the Rhodopian Massif. It is worth noting that middle Eocene deposits consist of a fluvial to shallow-marine sandstone and conglomerate across the Rhodopes, suggesting a broad area of emergent land during that interval (Zagorchev, 1998). The palaeogeography of the Thrace Basin and its continuation to the north in Bulgaria during the middle Eocene remains poorly known. The palaeogeographic maps of Aegean region for the late Eocene (Popov et al., 2004, Fig. 5A) indicate that the Rhodope Highland was part of an archipelago that developed in the geodynamic context of the southwest-ward accretion of a number of structural units of mainly continental origin, sandwiched between the Eurasian blocks in the north and the Adriatic–Apulia continental block of Gondwanan origin in the south (Bonev et al., 2006). The western part of the Thrace Basin was filled by continental clastics during the middle Eocene before the extensional deformation of the basin that started in the late Eocene (Burchfiel et al., 2003; Kiliyas et al., 2013), and transformed the depositional environment to deep shelfal depression with subaerial volcanos (Caracciolo et al., 2011, 2012). This palaeogeographic history of the Thrace Basin is in accordance with

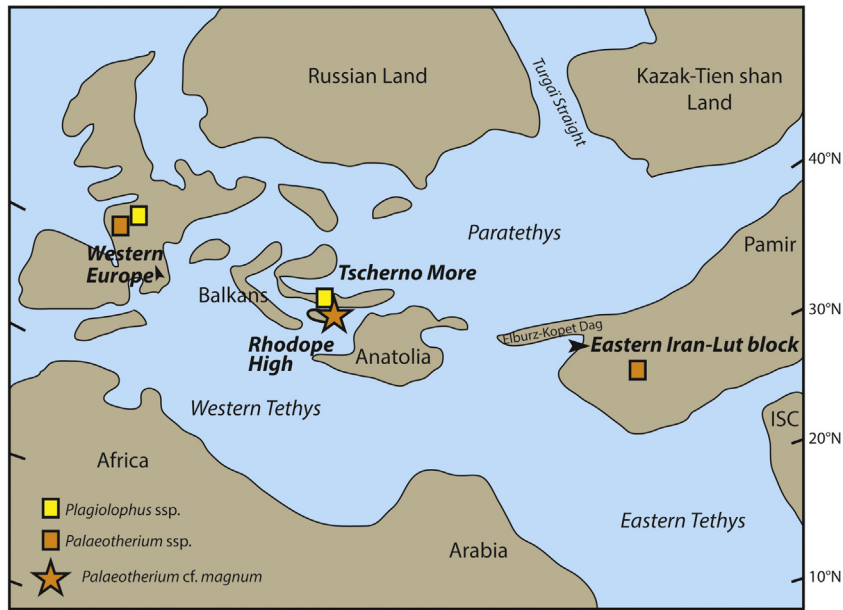
a middle Eocene (late Lutetian or Bartonian) age for the molassic succession exposed in the area of Feres.

Palaeotheriids are known in western Europe between the early middle Eocene to the early Oligocene (Franzen, 2003; Hooker, 2005; Remy, 2004). They are usually considered as a typical group of mammals endemic to western Europe. However, the easternmost occurrence of palaeotheriid remains is from the late Eocene of Tscherno More, Bulgaria, where Nikolov and Heissig (1985) reported dental remains of *Plagiolophus* cf. *minor*. Interestingly, footprints of palaeothere-like mammals have been reported from Eocene deposits of the Birjand (Sistan; Ataabadi and Sarjeant, 2000; Ataabadi and Khazaei, 2004) and Zanjan (Alborz; Abbassi and Lockley, 2004) areas in Iran. These possible occurrences would be the easternmost occurrences of palaeotheres in Eurasia, although the absence of diagnostic dental or skeletal elements cannot substantiate the presence of the palaeotheriids in this palaeogeographically isolated zone during the middle Eocene (Barrier and Vrielynck, 2008). The age of the volcanoclastic sediments yielding the footprints near Birjand is not well constrained, but they are certainly pre-Oligocene (Pang et al., 2013). The presence of palaeothere-like mammals in eastern Iran would substantially extend the geographical range of palaeotheres and raises questions about the origin and distribution of this group of mammals during the middle Eocene. It would also indicate that faunal exchanges were possible along the northern margin of the Neotethys during the late Eocene (Böhme et al., 2013), and Oligocene (Métails et al., 2015; Sen et al., 2011). However, the biogeographic connection between the different terranes in a context of Tethys closure was probably intermittent through time as attested by the Eocene fauna of central Anatolia, which clearly shows endemism probably related to continental isolation (Kappelman et al., 1996; Maas et al., 2001). It is worth noting that this middle Eocene (~44 Ma, Licht et al., in press) fauna shows no evidence of such common Eocene Laurasian mammal taxa as artiodactyls, perissodactyls, and rodents, but the persistence of pleuraspidotheriid “condylarths”, about 15 Ma after their extinction in western Europe (Métails et al., in press). The late Lutetian or Bartonian age of the palaeothere from Balouk Keui (i.e. younger than the middle Eocene fauna of central Anatolia) may indicate that faunal exchanges between the different islands along the northern margin of the Neotethys became possible by the late middle Eocene. The Rhodope Highland was probably land connected to

Fig. 4. A. Geological map of Ferai-Peplos (Papadopoulos, 1980) with the mains localities discussed in the text, and brief lithological and stratigraphic information of the main stratigraphical units discussed in the text; the dash-lined squares show the two possible areas where A. Viquesnel might have collected the foot of *Palaeotherium* sp., cf. *P. magnum*. B. Synthetic log of the succession of Paleogene clastic in the region (adapted from Papadopoulos, 1980); F indicates the two hypotheses concerning the likely stratigraphic provenance of the foot of *Palaeotherium* sp., cf. *P. magnum*. C. Log of the section East of Balouk Keui, as reported and described in Viquesnel (1868: 331); the red-green clays at the base of the section have yielded the foot of *Palaeotherium* sp., cf. *P. magnum*. The tentative (and preferred) correlation clearly gives support to the first hypothesis, which would imply a Lutetian or early Bartonian age of the fossil from Balouk Keui (F1).

Fig. 4. A. Carte géologique de Ferai-Peplos (Papadopoulos, 1980), avec les principales localités discutées dans le texte et des informations lithologiques et stratigraphiques sur les principales formations discutées dans le texte ; les cadres en pointillés indiquent les deux régions possibles où A. Viquesnel pourrait avoir collecté les restes de *Palaeotherium* sp., cf. *P. magnum*. B. Log synthétique de la succession clastique paléogène dans la région (modifié d'après Papadopoulos, 1980) ; F indique les deux hypothèses concernant la provenance stratigraphique probable du pied de *Palaeotherium* sp., cf. *P. magnum*. C. Log de la coupe à l'est de Balouk Keui, tel que décrit dans Viquesnel (1868: 331) ; les argiles rouges-vertes à la base de la coupe ont livré le pied de *Palaeotherium* sp., cf. *P. magnum*. La corrélation probable (et préférée) corrobore la première hypothèse qui implique un âge Lutétien ou début Bartonien pour le fossile de Balouk Keui (F1).

A



B

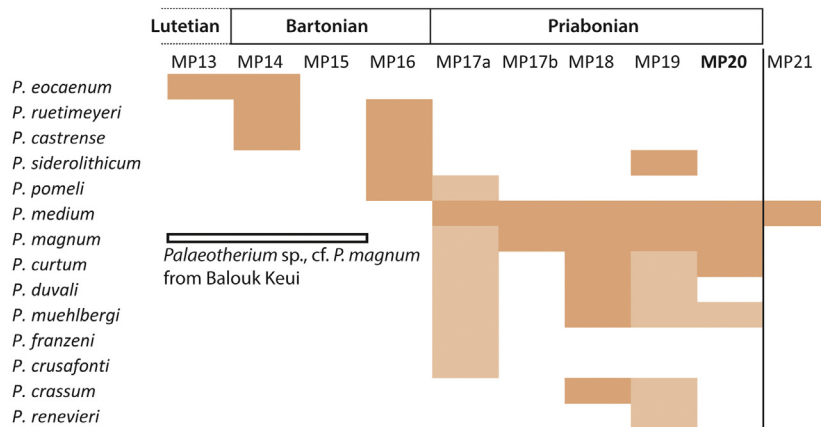


Fig. 5. A. Geographic distribution and possible dispersal routes used by palaeotheriids during the late middle Eocene. Paleogeographic map modified from Popov et al., 2004 (Late Eocene, 37–34 Ma). B. Stratigraphic range of the different species of *Palaeotherium* in western Europe, with the estimated occurrence of the *Palaeotherium* sp., cf. *P. magnum* from Balouk Keui. The calibration of the MP reference levels with the GTS follows Legendre and Lévêque (1997). The light red rectangles designate uncertain occurrences. The Grande Coupure occurred between MP20 and MP21.

Fig. 5. A. Distribution géographique et voies de dispersions possibles des paléotheriïdes durant la fin de l'Éocène moyen. Carte paléogéographique modifiée d'après Popov et al., 2004 (Éocène supérieur, 37–34 Ma). B. Répartition stratigraphique des différentes espèces de *Palaeotherium* en Europe occidentale, avec l'âge estimé du *Palaeotherium* sp., cf. *P. magnum* de Balouk Keui. La calibration des niveaux repères MP avec le GTS est issue de Legendre et Lévêque (1997). Les rectangles rouge clair indiquent les occurrences incertaines. La Grande Coupure se situe entre MP20 et MP21.

Dinarian lands during the low sea level periods, allowing mammal dispersals to occur. The strong resemblance of the Eocene mammal faunas from Viet Nam and eastern Europe corroborates the biogeographic connection between mainland Asia and the Tethyan islands during the middle to late Eocene, and supports trans-continental mammal dispersal along the northern Tethys margin (Böhme et al., 2013). However, the palaeogeography of the northern margin of Tethys is extremely difficult to reconstruct because of its extensive orogenic overprint (Popov et al., 2004), although the presence of intermittent continental bridges are hypothesized in the Balkans, Anatolia, and central Iranian

domains (Barrier and Vrielynck, 2008). The occurrence of *Palaeotherium* sp., cf. *P. magnum* in the middle–late Eocene of the Thrace Basin augments our knowledge of the biogeography of mammals long considered as geographically restricted to western Europe, and stresses the need to better document the fossil record of Tethyan micro-continents such as Balcano-Rhodia, Anatolia or central Iran.

In western Europe, there are two main intra-Eocene turnovers of mammal faunas, both characterized by the first occurrence of taxa that have no close ancestors on what was then the European Archipelago (Franzen, 2003). The first one occurs around the MP12–13 European

biohorizons (~45 Ma), and the second one takes place around MP16-17 (~37 Ma) that marks the boundary between the Robiacian and Headonian European Land Mammal Ages (Hooker and Weidmann, 2000; Sen, 1997). The second turnover (here named EBE-2 for Eocene Biotic Exchange 2) is particularly well marked among artiodactyls and perissodactyls, and is obviously related (at least in part) to the sudden appearance of immigrants, probably from Asia, but via unknown dispersal routes (Erfurt and Métais, 2007). The EBE-2 is characterized by the appearance of selenodont artiodactyls such as amphimerycids, anoplotherines, and xiphodontids (Hooker and Weidmann, 2000; Sudre, 1978), which became taxonomically and ecologically dominant during the late Eocene in western Europe. Moreover, the EBE-2 led to a considerable replacement of taxa among the palaeotheriids, with the appearance of species showing mesodont and molarized premolars such as *Palaeotherium magnum*, *P. medium*, *P. curtum* and *P. muehlbergi* (Franzen, 2003). This species replacement among palaeotheres is characterized by immigrants showing dental adaptations (higher crowned cheek teeth, development of cement) that are indicative of more abrasive foods, suggesting the exploitation of new ecological niches. The origin of these newcomers in western Europe remains enigmatic, and Franzen (2003) proposed that they dispersed via land bridges appearing between the West and the central European Island by the end of the Lutetian. In that hypothesis, the Rhodope and other continental blocks of central Tethys may have been a new corridor for the dispersal of Asian mammals, thus explaining the mammalian faunal turnover that occurred by the middle–late Eocene boundary about 37 Ma ago. The Aegean area may have played the role of a filter for large mammals as anthracotheres and brontotheres which are present in the late middle Eocene Tscherno More fauna (Nikolov and Heissig, 1985), but only anthracotheres immigrated to western Europe during the late Eocene (De Bonis, 1964). This corridor was also used later during the Grande Coupure as the palaeotheriid *Pseudopalaeotherium longirostratum* Franzen (1972), immigrated at the beginning of the Oligocene together with other large mammalian taxa (rhinocerotids, hyracodontids, amynodontids, entelodontids) of obviously Asian origin (e.g., Becker, 2009).

7. Conclusions

The postcranial remains from Balouk Keui collected by A. Viquesnel, and identified by A. Gaudry 150 years ago as a putative palaeotheres belong to a large Palaeotheriinae close to *Palaeotherium magnum*. The slightly smaller size with respect to the type material of the species *P. magnum* and the lack of more diagnostic dental and skeletal remains lead us to consider this fossil as *Palaeotherium* sp., cf. *P. magnum*. The stratigraphic provenance of the fossil remains uncertain, but the age of the continental deposits in the Feres area (Caracciolo et al., 2012) suggests a late Lutetian or lower Bartonian age, which represents an early occurrence of large *Palaeotherium* compared to that of western Europe (Fig. 5B). Long considered as restricted to western Europe, palaeotheriids actually enjoyed a broader distribution that extends to SE Europe with occurrences in Thrace

(Bulgaria and Greece), and potentially in eastern Iran where trace fossils have been referred to *P. medium* (Ataabadi and Khazae, 2004). *Palaeotherium* sp., cf. *P. magnum* from Balouk Keui thus represents the easternmost occurrence of the genus, which was long considered as restricted to western Europe. The poor fossil record along the northern continental margin of the Neo-Tethys probably hampers estimating the distribution and biogeography of mammals that are still thought as being restricted to western Europe. This key biogeographic area at the crossroads between Africa, Asia, Europe, and to a lesser extent India, requires further field investigation because it is key to understanding the relationship of western European and Asian faunas, and to estimating the impact of tectonic activity and related palaeogeographic remodeling on the dispersal of mammals during the middle and late Eocene, prior to the Grande Coupure. In light of his tentative identification, A. Gaudry was appropriately cautious in interpreting the significance of this discovery. The presence of palaeotheriids in SE Europe and western Asia reopens the debate about the origin of the family (Franzen, 1989), although current data are still insufficient in Asia to test the phylogenetic and biogeographic history of the palaeotheriids.

Acknowledgments

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