

Late Miocene large mammals from Yulaflı, Thrace region, Turkey, and their biogeographic implications

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Collecting over the last twenty years in sand and gravel quarries near Yulaflı in European Turkey has yielded a substantial fauna of large mammals. The most significant of these for biochronology are well-preserved remains of the ursid *Indarctos arctoides*, the suid *Hippopotamodon antiquus*, and several rhino genera. They point to a late Vallesian (MN 10-equivalent) age. Several other taxa, of longer chronological range, are in good agreement with this dating. The Proboscidea include, besides the Eastern Mediterranean *Choerolophodon*, the *Deinotherium* + *Tetralophodon* association, commonly found in Europe, and the rare “*Mastodon*” *grandincisivus*, here reported for the first time in the Vallesian. The age of Yulaflı shows that the large size of some taxa, such as *Deinotherium* (size close to that of *D. gigantissimum*) and *Dorcatherium*, does not always track chronology. The Yulaflı fauna is close in composition and ecology to other localities in Turkish Thrace, and also shares several taxa unknown in Anatolia, especially *Dorcatherium*, with the North-Western European Province. It reflects a forested/humid landscape that extended in Vallesian times along the Aegean coast of Turkey, perhaps as far South as Crete, quite distinct from the open environments recorded at the same period in Greek Macedonia and Anatolia, and probably more like the central European one. Together with the establishment of a Tethys–Paratethys marine connection, this “Eastern Aegean Province” likely acted as an ecological barrier that hindered East–West migrations of open-country large mammals, such as bovids or long-limbed giraffes, and might have contributed to the differentiation of *Ouranopithecus* and *Ankarapithecus*.

Key words: Miocene, Vallesian, Proboscidea, Artiodactyla, Perissodactyla, Yulaflı, Turkey.

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Introduction

The site of Yulaflı is situated 10 km NW of Çorlu in Thrace (Fig. 1A). Faunal remains were first described by Saraç (1987), who listed *Hipparion* sp., *Chilotherium* sp., and *Palaeotragus* sp. Later, Kaya and Heissig (2001) added *Aceratherium incisivum* Kaup, 1832, *Acerorhinus zernowi* (Borissiak, 1914), and *Dihoplus schleiermacheri* (Kaup, 1832). New fossils collected from the same locality (CY, co-ordinates N 41°12'13'', E 27°49'46'') and from another sand quarry in the same formation (CYA, co-ordinates N 41°11'21'', E 27°48'46'') by Ishak Benbanaste (Çorlu) and Sevkert Ersen (Çorlu) were kindly made available to us for study. A short field campaign by the authors in 2003 led to further increase of the collection. In the present study the entire collection from Yulaflı is described and a revision of the faunal age is given.

The generalised stratigraphic section (Fig. 1B) is modified after Saraç (1987). The Danisment formation consists of yellowish, gray-brown sandstone and claystone. The Ergene formation, which rests unconformably on the Danisment formation, consists of yellowish gray, sandy to muddy fluvial facies. The mammalian fossils occur in a channel-filling sand horizon

of the Ergene formation. Measurements are given in mm. Uppercase refers to upper teeth, lowercase to lower teeth.

Institutional abbreviations.—MNHNP, Muséum National d'Histoire Naturelle, Paris, France; MTA, Madden Tetkik ve Arama, Ankara, Turkey; NHMW, Naturhistorisches Museum Wien, Austria; NMNHA, National Museum of Natural History, Assenovgrad, Bulgaria; TTMEU, Tabiat Tarihi Muzesi (Natural History Museum), Ege University, Izmir, Turkey. The new material is deposited in the TTMEU.

Systematic palaeontology

Order Carnivora Bowdich, 1821

Family Ursidae Gray, 1825

Genus *Indarctos* Pilgrim, 1913

Type species: *Indarctos salmontanus* Pilgrim, 1913: 290; Hasnot, Pakistan, late Miocene.

Indarctos arctoides (Depéret, 1895)

Type locality: Montredon, France.

Material from Yulaflı.—TTMEU-CY-46, an almost complete left dentary, lacking only the incisors, the tip of the canine, p1, m3, and part of the coronoid process (Fig. 2).

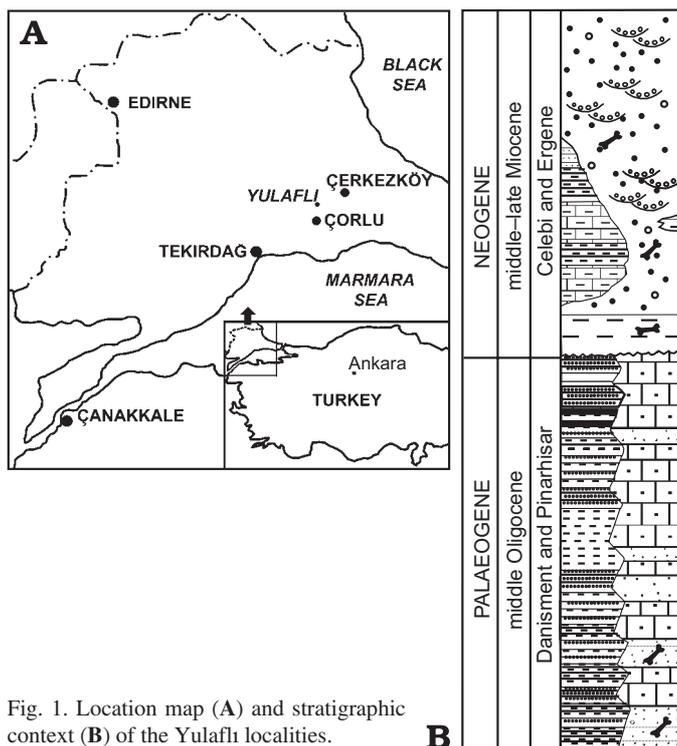


Fig. 1. Location map (A) and stratigraphic context (B) of the Yulaflı localities.

Description.—The corpus is robust, but not extremely so, with a uniform depth from p4 to m2. The ventral border forms a rather regular curve, being only slightly more convex posteriorly. The anterior border of the coronoid process is slightly inclined backwards.

The canine is short and stout, and strongly curved. It has a weak posterior keel, and a stronger mesio-lingual one, with an enamel notch just in front of it.

The missing first premolar had a single, rather large root, strongly inclined forwards. It is separated by a short diastema from p2, which has two roots, almost fused but well distinct labially. Its crown is long, and consists of a single low cuspid, whose apex is more anterior than mid-length, so that the longitudinal cristid has a steeper mesial slope. There is a lingual cingulid, especially marked in the distal half, where it increases tooth width. A longer diastema separates p2 from p3, which has two well-distinct roots and is morphologically intermediate between p2 and p4. The main cuspid is higher and more posterior than on p3, the disto-lingual cingulid is weaker, but there is an incipient distal cingulid. In labial view, both edges of the main cuspid are convex. A short diastema separates this tooth from p4, which is much larger, but not disproportionately so. Its main cuspid is relatively still higher than on p3; there is a hint of a mesial accessory cuspid where the base of the main cristid turns inwards, and the distal cingulid is somewhat enlarged, forming a narrow shelf. The tooth is only slightly broader above the distal root.

The m1 has the usual morphology for *Indarctos*, with a very open trigonid, much narrower than the talonid, a reduced metaconid, and an entoconid larger and higher than the entoconulid (see Beaumont 1982). Although the teeth are

slightly worn, it is clear that there was no cuspid between protoconid and hypoconid. The m2 is a large tooth, broader than m1, without paraconid, but with a transverse cristid between protoconid and metaconid.

Comparisons.—Several species of *Indarctos* have been named, but only a few are now currently recognised in Eurasia. *Indarctos atticus* (Weithofer, 1888, ex Dames) is mostly known in the classic Turolian localities of Pikermi, Samos, and Maragha. *Indarctos atticus* probably includes *I. salmonitanus* Pilgrim, 1913, the type species, probably from the Dhok Pathan zone of the Siwaliks, *I. lagrelii* Zdansky, 1924 and *I. sinensis* Zdansky, 1924, from Loc. 31 and Loc. 30, respectively, in China, and *I. bakalovi* Kovachev, 1988, from Kalimantsi in Bulgaria. The recently described *I. zdanskyi* Qiu and Tedford, 2003, from Baode, China, is similar, but is more derived in several features. All these localities are also of MN12/13-equivalent age. *Indarctos arctoides* (Depéret, 1895) is best known from Montredon (MN10; Depéret and Gomez-Llueca 1928; Beaumont 1988), Westhofen (MN 9?; Tobien 1955), Pfaffstetten (MN11?; Thenius 1959), and Küçükçekmece (Petter and Thomas 1986), while *I. vireti* Villalta and Crusafont, 1943, is mostly known from the Vallesian of Spain, chiefly from Can Llobateres (MN9; Crusafont and Kurtén 1976), but has also been reported from Sinap (Viranta and Werdelin 2003). The status of *I. anthracitis* Weithofer, 1888, from Monte Bamboli, is disputed.

The dentary from Yulaflı compares best with a dentary of *I. atticus* from Samos in the NHMW (Thenius 1959: fig. 7), except that the depth of the latter, as in all *I. atticus*, increases caudally. Robustness is variable in other specimens of *I. atticus* but some of them, such as those from Crevillente-2 (Montoya et al. 2001: pl. 2: 1) and Kalimantsi (NMNHA) have an extremely convex lower border of the corpus, and an anterior border of the ramus which is slightly inclined forwards. This is of course a consequence of the shortening of the cranial basis in this species. The dentaries from the Vallesian of Spain seem to have a much less upright ramus that is, however, largely reconstructed. The dentary from Küçükçekmece (Petter and Thomas 1986: fig. 5) is extremely slender, and perhaps even pathological.

The lower canine is poorly known. The description of those of *I. vireti* by Crusafont and Kurtén (1976) perfectly matches that of our specimen, except that they are smaller.

The relatively large p2 and p3, which are both double-rooted, contrast with the sharp reduction of these teeth in typical *I. atticus* (and still more with the loss of these teeth in *I. zdanskyi*). On the contrary, p4 is enlarged in *I. atticus*, so that there is a sharp difference between p3 and p4, whereas size harmoniously increases from p2 to p4 in our specimen. Molar morphology does not provide many discriminating features. The m1 of *I. atticus* often has a labial tubercle behind the protoconid; it is absent in TTMEU-CY-46.

Discussion.—The specific distinction between the middle and late Turolian *I. atticus* and the early Vallesian form (whether it is called *I. vireti* or *I. arctoides vireti*) is widely

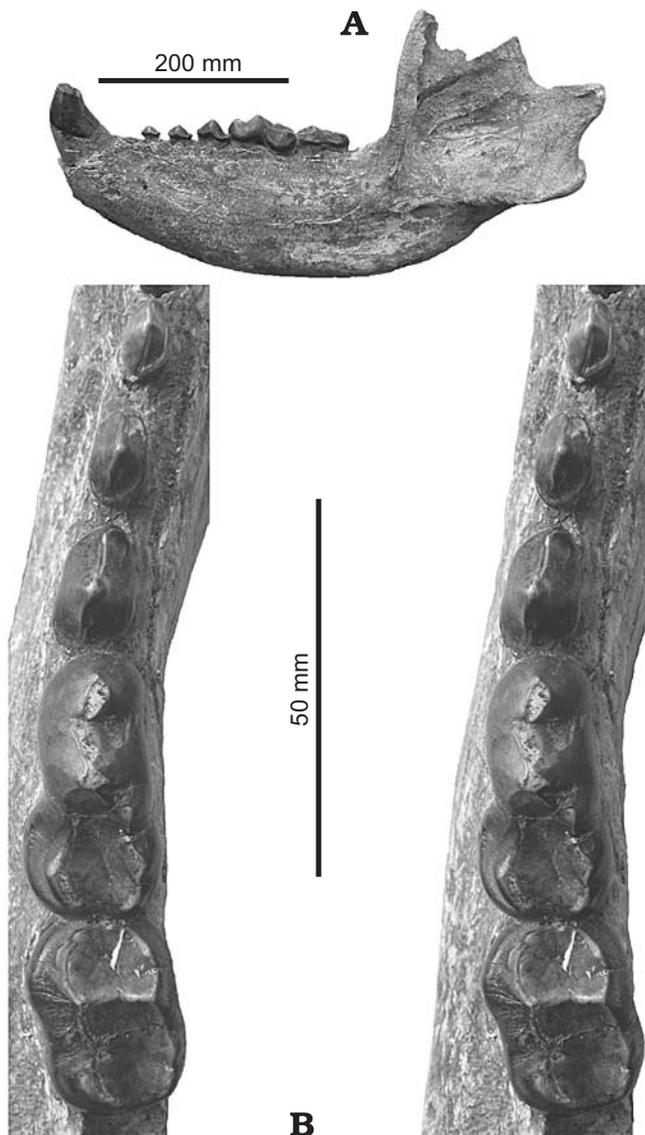


Fig. 2. *Indarctos arctoides*, TTMEU-CY-46, Yulaflı, Turkey, Vallesian, late Miocene. Left mandibular ramus, lateral (A) and occlusal (B) views of p2–m2 (stereo).

acknowledged. The former differs from the latter by (1) its larger size; (2) its shortened dentary, and cranial base; (3) its much smaller p2 and p3, with only one root; (4) its enlarged and broadened p4. Other features of the molars do not prove very discriminant. The trigonid/talonid ratio of m2, used by Petter and Thomas (1986), although potentially meaningful, is too hard to estimate precisely.

It is nonetheless clear that species demarcation is blurred when chronologically intermediate forms, many of them called *I. arctoides*, are taken into consideration. The size of m1, taken as an indicator of overall size, forms an almost perfect continuum (Fig. 3; the apparent gap in Montoya et al. 2001: fig. 4 results from the non-inclusion of two intermediate specimens, the type of *I. lagrelii* and the Samos specimen in NHMW). The Lm2/Lm1 ratio, stated by Montoya et al. (2001) to be smaller in *I. arctoides* than in both other species, is in fact

variable. It is always large in *I. atticus*, but may be small (Küçükçekmece) or large (Pfaffstetten) in *I. arctoides*, as well as in *I. vireti* (respectively, Can Purull and Can Llobateres). Morphological characters are also intermediate. For instance, at Montredon, the lower border of the dentary is strongly curved, as in several *I. atticus*, and the p3 has its roots “étroitement soudées” (Depéret and Gomez-Llueca 1928).

At two localities, both usually included in biozone MN11, Dorn-Dürkheim (Roth and Morlo 1997) and Crevillente 2 (Montoya et al. 2001), *I. atticus* has been reported to coexist with a more primitive form, *I. arctoides* in the former site, and with *I. cf. vireti* in the second. In both cases, this second species is documented by rather poor or fragmentary material. At Crevillente-2, the identification of two species rests mostly upon size, but the differences certainly do not exceed what can be expected in a single population. Even the “*I. atticus*” there has primitive features: it is rather small, its p2 and p3 are bi-radicated, the parastyle of its P4 is stronger than in *I. vireti*, but clearly smaller than in typical *I. atticus* (Montoya et al. 2001: fig. 5). At Dorn-Dürkheim, an M2 referred to *I. atticus* is almost identical in size to a tooth from Montredon, type-locality of *I. arctoides*. Two M3s, each referred to a different species, are little different in size (18.8×15.2 and 21.4×17.85).

It is far more likely that, in both localities, we are dealing with a single species, intermediate between the Vallesian and middle Turolian forms. This is not unexpected in early Turolian sites. Features of these taxa appear to have evolved mosaically, with intermediate forms displaying a mixture of primitive and derived traits. On the whole, not a single trait forbids hypothesising an anagenetic evolution from *I. vireti* to *I. atticus*, through *I. arctoides*.

The *Indarctos* from Yulaflı clearly belongs to this intermediate stage. Its m1 is smaller than those of all *I. atticus*, and close in size to *I. arctoides* from Montredon, but its m2 is large, near the lower range of *I. atticus* (however, an m2 from Can Llobateres is almost as large). It has no cuspid between protoconid and hypoconid on m1, in contrast to *I. atticus*. The clearest primitive features of the Yulaflı specimen are found in the premolars. The harmonious increase in size from p2 to p4 is quite unlike *I. atticus*, where p4 is much enlarged in respect to the reduced p3. Correlatively, p2 and p3 are still two-rooted, while the former is already one-rooted at Pfaffstetten and Küçükçekmece, and the latter may also be one-rooted in *I. atticus*.

Typical *I. atticus* (large size, much reduced and one-rooted p2 and p3, enlarged p4) are known only in MN12–13 or equivalent age. Records of earlier age are either doubtful in age, or display more primitive features. Besides those mentioned above, *I. atticus* is present in Mecquenem’s collection from Maragha (Mecquenem 1925), but the dating of this collection, which may well not be homogeneous, is unknown. According to Bernor (1986: 83), *Indarctos* “was collected by Mecquenem presumably from somewhere within the middle Maragheh sequence”. At Terrassa, at site referred to MN10, the record of *I. atticus* (Pons-Moyà 1990) is based

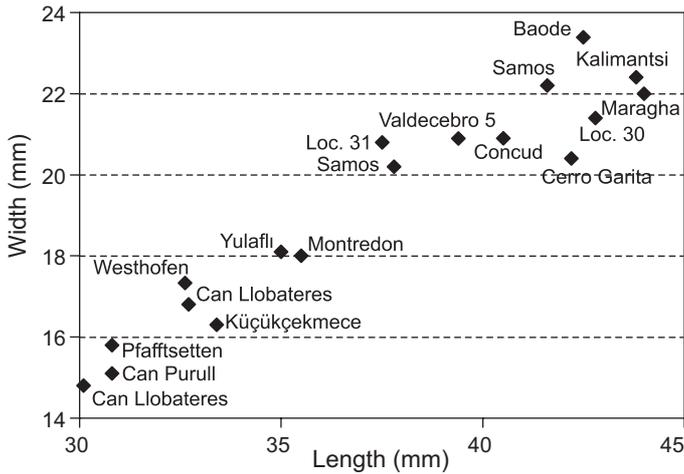


Fig. 3. Length versus width plot of m1 in the genus *Indarctos*, showing continuous variation.

upon a fragment of m1, not a sound basis for specific identification. The identification of *I. atticus* at Aubignas I (Petter and Thomas 1986) looks reasonable but, pending detailed analysis of the fauna, the age of the site, given as MN 11 (Azanza et al. 1993), is debatable, all the more as the site underlies a basalt dated to 6.4 Ma. Reciprocally, primitive forms are absent from MN12–13 sites, except three isolated teeth at Hatvan in Hungary (Bernor et al. 2003) that are so small that their identification is not fully certain. *Indarctos arctoides* occurs only in the late Vallesian–early Turolian, while *I. atticus* occurs only in the middle–late Turolian.

Order Proboscidea Illiger, 1811

For the classification, we follow Shoshani et al. (2001).

Family Deinotheriidae Bonaparte, 1845

Genus *Deinotherium* Kaup, 1829

Type species: Deinotherium giganteum Kaup, 1829; Eppelsheim, Germany, Vallesian, Miocene.

Deinotherium giganteum Kaup, 1829

Material from Yulaflı.—TTMEU-CY-30, right P4 (Fig. 4G); TTMEU-CY-31, left M3; TTMEU-CY-109, incomplete toothless dentary.

Description.—Both teeth are large (P4: 71 × 90; M3: 94 × w1 = 105 × w2 = 91). The P4 is rectangular in outline, being wider than long (Fig. 4G). The protoloph is complete and united with the paracone, but the metaloph is only a half-loph. The ectoloph is well developed, with a labial ectoflexus. The mesostyle (Harris 1973: fig. 7) is low and located on the mesio-lingual surface of the hypocone. The median valley is wide and opens lingually only. The anterior cingulum forms a ridge along the mesial side, but the distal cin-

gulum is weaker, and there is no labial cingulum. There are three roots; two of them are located under the lophes, the third one is lingual.

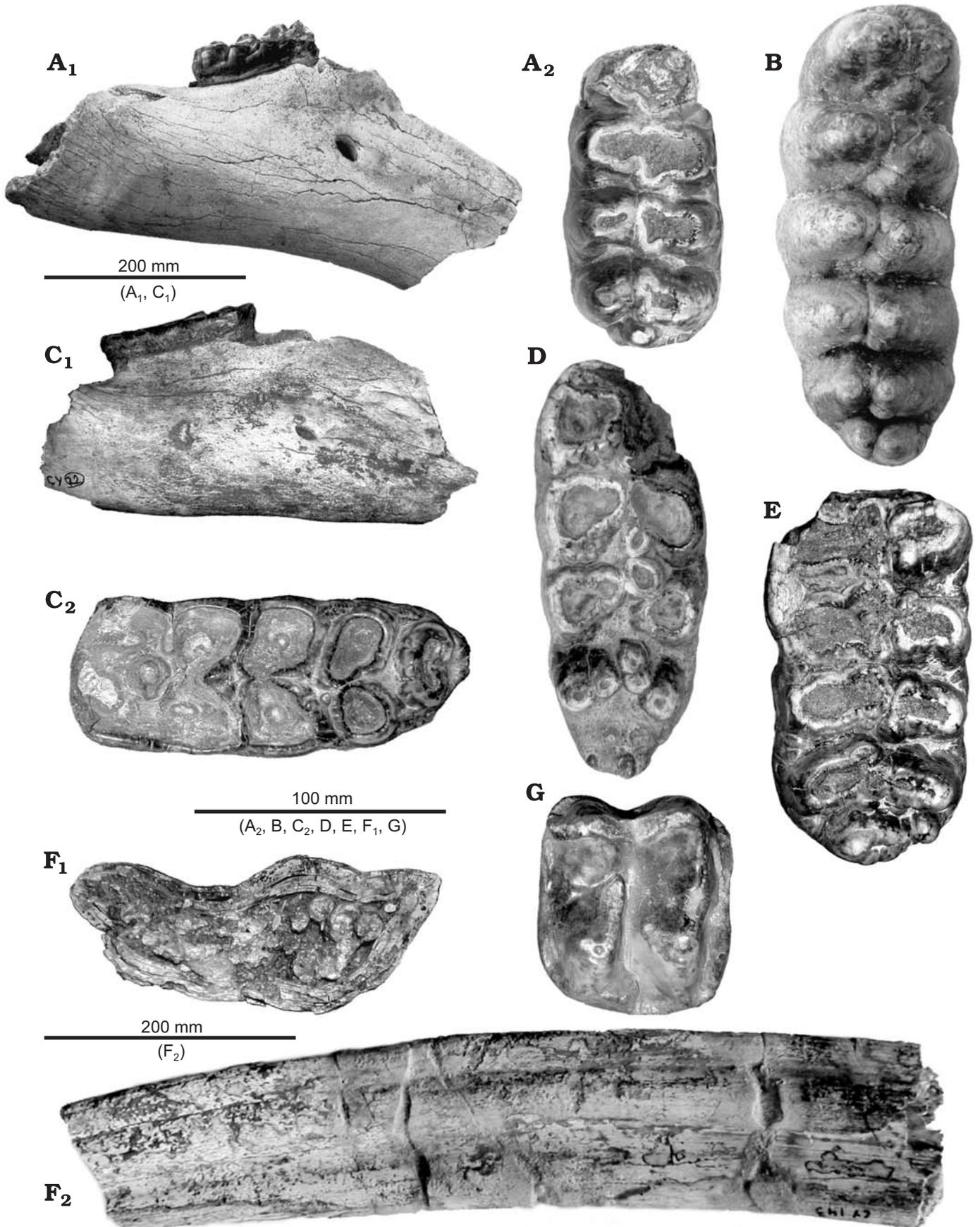
The M3 is rectangular in outline, with the protoloph wider than the metaloph. The median valley opens lingually and labially. The anterior cingulum forms a ridge along the anterior side, but the posterior cingulum is weak. There are no lingual or labial cingula, except a small labial cingulum at the opening of the median valley. There are three roots. The anterior root corresponds to the mesio-lingual part of the protoloph, the second root is along the metaloph, and the third root extends along the labial side. The lingual ornamentation of the protoloph is stronger than the labial one. The postmetaloph ornamentation is weak, and forms a small tubercle. The enamel of the tooth is finely wrinkled along the lophes and the lingual and labial surfaces.

The dentary TTMEU-CY-109 has lost its teeth, and the rostral part of the tusk sheaths is also broken away, revealing two parallel alveoli, only slightly decreasing in diameter ventrally, and separated by a narrow septum. The maximum width across the sheaths is 240 mm.

Comparisons.—In Eurasia, deinotheres are known in early Miocene to middle Pliocene localities (Bergounioux and Crouzel 1962; Tobien 1988; Huttunen 2002a), but their taxonomy has long been debated. In this study, following Harris (1973), the name *Deinotherium* is used for a large-sized deinotheres, which have been recorded from many localities in Europe (review in Huttunen 2002a). In Turkey, it is known from Tire (Ozansoy 1961), Paşalar (Tobien 1990), Kayadibi (Gaziry 1976), Çandır (Gaziry 1976; Geraads and Güleç 2003), Sinap (Sanders 2003), Küçükçekmece (Malik and Nafiz 1933), and Düzyayla (Kaya and Forstén 1999).

The large-size, the presence of the mesostyle, and the reduced postmetaloph ornamentation are diagnostic characters for *Deinotherium* that distinguish it from *Prodeinotherium* (Harris 1973). By the presence of a strong anterior cingulum, of a mesostyle, and of incomplete lophes, the P4 from Yulaflı resembles those of *D. giganteum* from various localities in Austria described by Huttunen (2002b). There is a clear general trend for size increase in *Deinotherium* in the Miocene; e.g., the teeth from Yulaflı are much larger than those of *Prodeinotherium*, and also than those of *D. aff. levius* from the middle Miocene of Paşalar (Tobien 1990) and than the unpublished teeth of *P. bavaricum* from the middle Miocene of Tire (Figs. 5, 6). However, late Miocene forms exhibit a great size-range not obviously linked with age or geography. The teeth from Yulaflı are larger than those of *D. giganteum* from many European sites, and close to the maximum recorded size for specimens from Vallesian sites such as Montredon, Mannersdorf, Kohfidisch, Eppelsheim or from some

Fig. 4. A, B. *Tetralophodon longirostris*. A. TTMEU-CY-202a; A₁, right mandibular corpus with m2 and alveoli of m1, labial view; A₂, same specimen, right m2. B. TTMEU-CY-202b; right m3. C, D. *Choerolophodon anatolicus*. C. TTMEU-CY-22; C₁, right mandibular corpus with m3 and alveolus of m2, labial view; C₂, same specimen, right m3. D. TTMEU-CY-32, isolated right m3. E, F. *Amebelodon grandincisivus*. E. TTMEU-CY-203, left M2. F. TTMEU-CY-143; F₁, left i2, cross section in distal view; F₂, same specimen, dorsal view. G. *Deinotherium giganteum*, TTMEU-CY-30, right P4. All from Yulaflı, Turkey, Vallesian, late Miocene.



Hungarian finds (Gräf 1957; Tobien 1988; Huttunen 2002b; Mazo and Montoya 2003), but they are only slightly smaller than specimens referred to *D. gigantissimum*, so that it is hard to draw biochronological conclusions from them.

Superfamily Elephantoida Gray, 1821

Family Gomphotheriidae Hay, 1922

Genus *Choerolophodon* Schlesinger, 1917

Type species: Mastodon pentelicus Gaudry and Lartet, 1856; Pikermi, Greece, middle Turolian, Miocene.

Choerolophodon anatolicus Ozansoy, 1965

Type locality and age: Yassiören, Turkey, Vallesian, Miocene.

Material from Yulaflı.—TTMEU-CY-22, right dentary with m3 and alveolus of m2 (Fig. 4C); TTMEU-CY-201, left dentary with m3; TTMEU-CY-32, isolated m3 (Fig. 4D).

Description.—Both dentaries are morphologically similar and certainly belong to the same individual. The corpus is slender relative to that of *Tetralophodon* of the same locality (Table 1); its depth slightly decreases posteriorly. The ventral border of the corpus is almost straight. The interalveolar crest is curved outward and slopes ventro-mesially, with an angle of about 25° relative to the alveolar border. The symphysis is broken, but extends distally as far as the mesial part of m2. The mandibular foramen, 25 mm in diameter, is located below the middle of m2. The mandibular canal lies along the corpus, small and square in section anteriorly, becoming broader and triangular posteriorly.

Heavy wear on TTMEU-CY-22 and TTMEU-CY-201 does not allow description of the structure of the conelets and accessory conules. Both m3s have five lophids and a small posterior cingulum with small conelets. The half-lophids of the third and fourth lophids are nearly fused to each other. The mesoconelets are located anterior to the main cones, contributing to an anteriorly-pointing “V” shape of the lophids in occlusal view, or “chevroning”. The fifth lophid is reduced in width and is composed of a main cusp and a small pretrite mesoconelet.

The m3 TTMEU-CY-32 has four lophids and a long talonid, which is composed of an irregular arrangement of four small conelets. Wear gradient is strong. It is certainly from a male individual (measurements: Table 1 and Fig. 7). On the pretrite side, the first two half-lophids are accompanied by posterior accessory conules, as on the specimen AS 92.605 from Sinap (Sanders 2003). The fourth lophid has a double mesoconelet. The cement is weak at the base of the interlophids and well developed on the lingual and labial walls of the crown. The chevrons are well developed in the last three lophids. The teeth of Yulaflı have well developed ptychodonty, but by contrast weak choerodonty.

Comparisons.—During the late Miocene, *Choerolophodon* was abundant in Turkey, contrasting with its less common occurrences in other Eurasian faunas. It has been recorded, among other sites, at Pikermi, Samos, Ravin de la Pluie in Greece, Veles in FYROM, Maragha in Iran, Ezerovo and

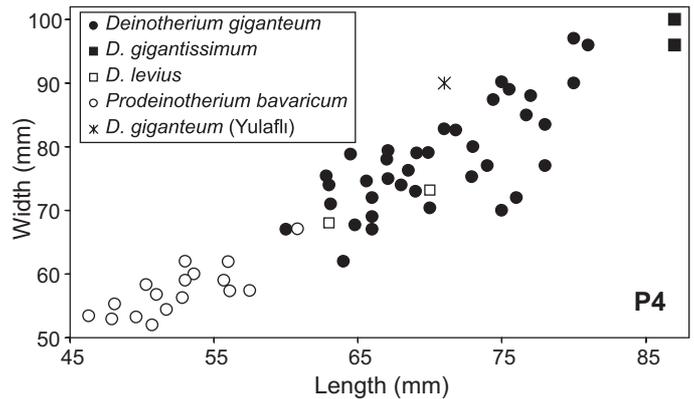


Fig. 5. Length versus width plot of *Deinotherium* P4s.

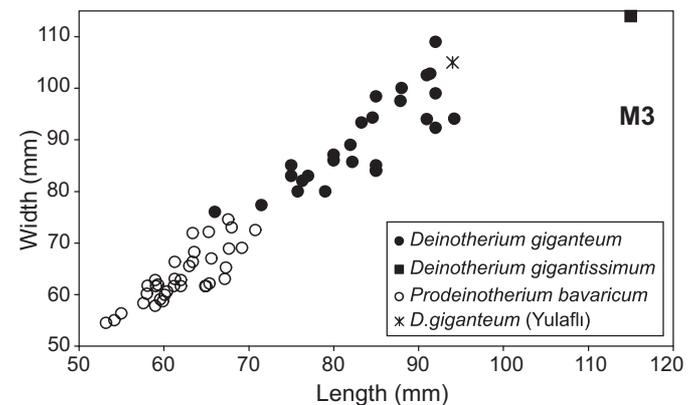


Fig. 6. Length versus width plot of *Deinotherium* M3s.

Ahmatovo in Bulgaria (Tassy 1983, 1989; Bakalov and Nikolov 1962, as *Trilophodon angustidens*). The contemporaneous *C. corrugatus* is documented from Dhok Pathan and Nagri formations of the Siwalik (Tassy 1983), while choerolophodonts span the middle to late Miocene in Kenya (Tassy 1986; Pickford 2001). In Turkey, late Miocene *Choerolophodon* are known from Çorakyerler, Garkin, Kinik, Gülpınar, Gökdere, Kayadibi, upper and lower levels of Kemiklitepe, Eşme-Akçaköy, Ramiz in Istanbul, and Sinap (Şenyürek 1952; Viret 1953; Ozansoy 1965; Gaziry 1976; Tassy 1994; Tassy et al. 1989; Sanders 2003). Moreover, a few middle Miocene *Choerolophodon* have been recorded in Turkey (e.g., Sofça) and Chios (Gaziry 1976; Tobien 1980).

Turkish *Choerolophodon* are commonly assigned to *Choerolophodon pentelici*, except that from Sinap, which was assigned to *C. anatolicus* (Ozansoy 1965). Sanders (2003) also suggested that some other early samples of *Choerolophodon* (Eşme-Akçaköy, Kayadibi, Kemiklitepe-D and Gökdere) also belong to *C. anatolicus*, which would subsume *C. pentelici lydiensis* Tassy, Sen, Jaeger, Mazin, and Dalfes, 1989. Ozansoy's species would then range from the Vallesian to the early Turolian, subsequently replaced by *C. pentelici* at the end of the early Turolian (late MN11).

The fossils from Yulaflı compare with those of *C. anatolicus* from Sinap described by Sanders (2003). They share a

Table 1. Measurements of the proboscidean molars and dentaries from Yulaflı, in mm.

	length	width 1st loph(id)	width 2nd loph(id)	width 3rd loph(id)	width 4th loph(id)	width 5th loph(id)
<i>Choerolophodon. anatolicus</i>	m3					
TTMEU-CY-32	172	(55)	71,5	71	65,5	–
TTMEU-CY-201	163	63.2	63.3	67.7	64.5	55.5
TTMEU-CY-22	160	61	64.2	66.2	62.5	51
<i>Tetralophodon longirostris</i>	m3					
TTMEU-CY-23	192	70	80	84.5	79	71
TTMEU-CY-202b	195.5	66.2	77.2	77.2	75.5	65
<i>Tetralophodo longirostris</i>	intermediate molars					
TTMEU-CY-111 (m1)	120	–	–	61	–	–
TTMEU-CY-202 (m2)	121	–	59.7	65.1	60.2	–
TTMEU-CY-48 (M2)	122	–	–	71.5	–	–
<i>Anebelodon grandincisivus</i>	M2					
TTMEU-CY-203	156	84.3	82.6	86.5	89.4	
	<i>C. anatolicus</i>			<i>T. longirostris</i>		
Maximum height of horizontal ramus	TTMEU-CY-201	TTMEU-CY-22	TTMEU-CY-112	TTMEU-CY-23	TTMEU-CY-202	TTMEU-CY-111
	161	178	208	162	194	154

slight downward inclination of the symphyseal segment, simple crowns, a similar lophid formula, and weak expression of choerodonty. TTMEU-CY-32 closely resembles the m3 of *C. anatolicus* (AS 92.605) from Sinap, except that, in our material, the ptychodonty is stronger and the cement is weaker. The molars of *C. anatolicus* from Eşme-Akçaköy (Gaziry 1976: pl. 5), referred to his new subspecies *C. pentelici lydiensis* by Tassy (1989), differ from those of Yulaflı by having well developed choerodonty, a moderately developed cement at the base of the interlophids, and a slightly smaller size (Fig. 7), but the inclination of the mandibular rostrum is similar, and like TTMEU-CY-32 the mesoconelet of the third pretrite half-lophid remains isolated. The teeth from Yulaflı are similar to those of *Choerolophodon* from Küçükçekmece (“*Mastodon*

sp.” of Malik and Nafiz 1933: pls. 5, 6), and to a much worn m3 from Ramiz in Istanbul (Viret 1953). The record of *C. pentelici* from the upper level of Kemiklitepe (Tassy 1994: fig. 2) and Gökdere (Senyürek 1952: fig. 6) is based upon deciduous teeth only. They have well developed choerodonty and ptychodonty and a complex occlusal pattern.

The m3s from Yulaflı fall within the size ranges of *C. pentelici*, *C. anatolicus*, and also *C. corrugatus* (Fig. 7), but the size of the cheek teeth appears to be less important than occlusal morphology, since there is much size overlap between species, partly because of sexual dimorphism (Sanders 2003). The morphological characters of the Yulaflı sample suggest an intermediate form showing more resemblance to *C. anatolicus* than to *C. pentelici* sensu stricto.

Genus *Tetralophodon* Falconer, 1857

Type species: Mastodon longirostris Kaup, 1832; Eppelsheim, Germany, Vallesian, Miocene.

Tetralophodon longirostris (Kaup, 1832)

Material from Yulaflı.—TTMEU-CY-23, left dentary, with m2–m3 and alveoli of m1; TTMEU-CY-202a, right dentary with m2 and alveoli of m1 (Fig. 4A); TTMEU-CY-202b, isolated right m3 (Fig. 4B); TTMEU-CY-111, right dentary with heavily worn m1; TTMEU-CY-112, right dentary with heavily worn m2, and anterior part of m3; TTMEU-CY-48 isolated left M2.

Description.—TTMEU-CY-23 and TTMEU-CY-202 belong to adult individuals. The corpus of each specimen is robust and broadens posteriorly. The interalveolar crest and the mandibular foramina are missing in TTMEU-CY-23, but the

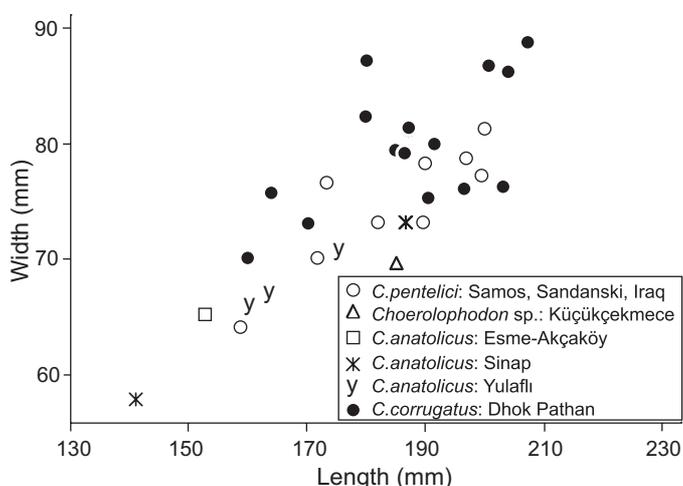


Fig. 7. Length versus width plot of *Choerolophodon* m3s.

interalveolar crest of TTMEU-CY-202 is straight, long and mesio-ventrally sloping. It is deflected downward at $\sim 45^\circ$ relative to the alveolar border, while the ventral margin of the symphysis exhibits a downward deflection of 15° . These measurements for TTMEU-CY-112 are 40° and 17° , respectively. There are four mandibular foramina on TTMEU-CY-202. The largest one is positioned below the alveoli of m1, the others are positioned anteriorly on the symphysis. TTMEU-CY-111 belongs to a juvenile individual with a slender corpus exhibiting three mandibular foramina.

The m2 of TTMEU-CY-202 has four lophids, plus a small and low distal cingulum. The anterior margin of the tooth is broken. The pretrite half-lophids 2 and 3 preserve large posterior accessory conules while the fourth one has a smaller one. All other intermediate molars have four loph(id)s, but due to the wear stage in all specimens, it is impossible to determine their precise composition.

All m3s are morphologically similar. They each have five lophids and a bituberculate talonid, which could also be considered as a lophid. Each half-lophid is composed of a large main cone, a smaller mesoconelet and anterior and posterior accessory conules on the pretrite half-lophids and a posterior accessory conule on the first posttrite half-lophid. The pretrite half-lophids 4 and 5 of TTMEU-CY-23 do not exhibit any accessory conules. The anterior cingulum is well developed in all teeth. There are no traces of labial and lingual cingula except a thick basal one on the labial side of the last lophid of TTMEU-CY-23. There is a trace of cement at the base of the interlophids.

Comparisons.—Tetralophodont records are scarcer in Turkey than those of choerolophodonts, but they are more numerous

in other Eurasian localities. *Tetralophodon longirostris* ranges from the late middle Miocene to the late Miocene. It is well known from Eppelsheim, Dorn-Dürkheim 1, Belvedere in Austria, and Nombrevilla in Spain (Tobien 1978; Gaziry 1997; Göhlich 1999). The genus *Tetralophodon* has also been recorded in Istanbul (Viret 1953).

The materials from Yulaflı are very similar in size and morphology to those of *Tetralophodon longirostris* from Eppelsheim (Tobien 1978: pl. 10: 1) and Dorn-Dürkheim 1 (Gaziry 1997: pl. 1: 2). The m3s have five lophids and a talonid, a simple crown pattern without anancoidy, a slight cement cover in the posterior interlophids, and the symphysis is down-turned. The fossils from Yulaflı are distinguished from other tetralophodonts ("*Mastodon*" *longirostris* forma *gigantorostris* and "*Mastodon*" *grandincisivus*) (Tobien 1978; Mazo and Montoya 2003) by having a simple crown pattern, a weak cement cover, and smaller cheek teeth. The material from Yulaflı falls within the size range of *T. longirostris* from late Miocene localities (Eppelsheim, Esselborn, Mannersdorf), which is clearly distinct from that of "*T. longirostris*-*grandincisivo*id form"—"*Mastodon*" *grandincisivus* (Fig. 8).

Genus *Amebelodon* Barbour, 1927

Type species: Amebelodon fricki Barbour, 1927; Cambridge quarry, Nebraska, middle Pliocene.

Amebelodon grandincisivus (Schlesinger, 1917)

Mastodon (Bunolophodon) grandincisivum Schlesinger, 1917

Type locality and age: Maragheh, Iran, Turolian, Miocene.

Material from Yulaflı.—TTMEU-CY-143, left i2 (Fig. 4F); TTMEU-CY-203, isolated left M2 (Fig. 4E).

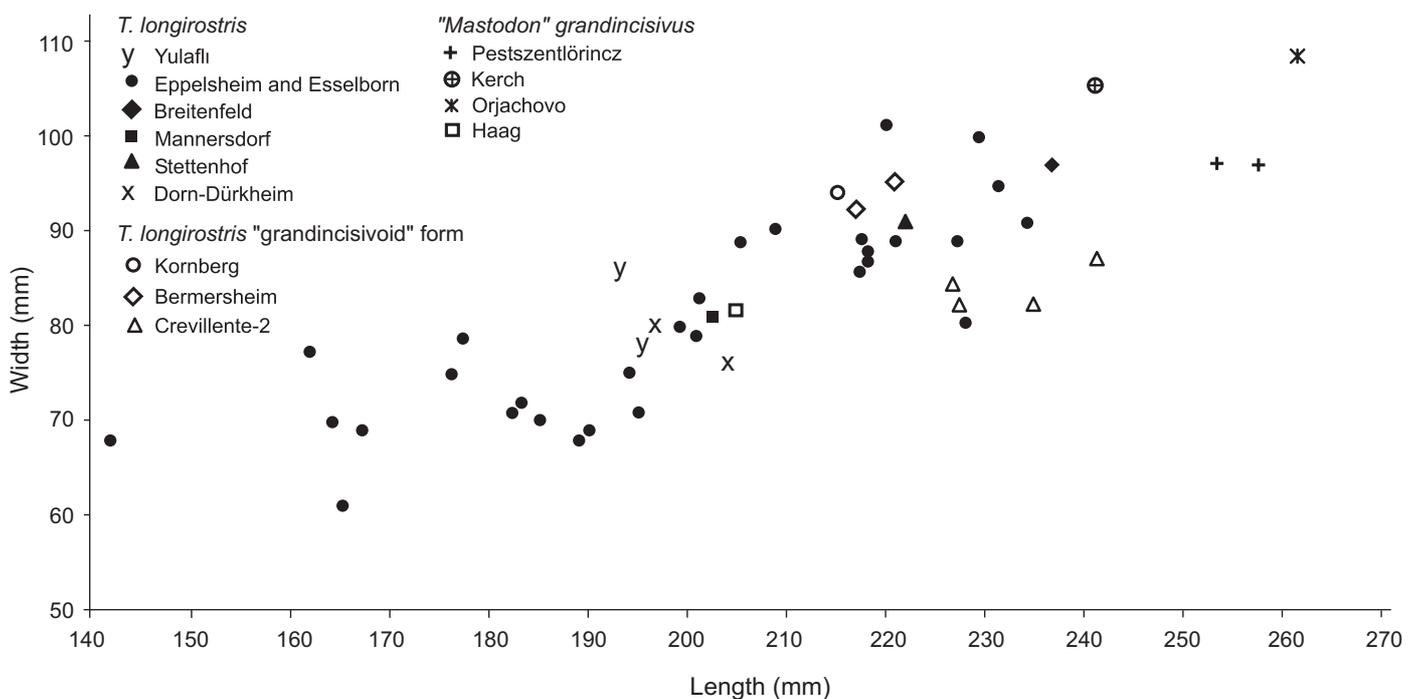


Fig. 8. Length versus width plot of *Tetralophodon* and "*Mastodon*" *grandincisivus* m3s.

Table 2. Dimensions of the lower incisors of *Amebelodon grandincisivus* from various localities, in mm.

i2	Yulafli	Maragha	Kerch	Pestszentlőrincz	Orjachovo
Length	718	—	1400	1610	
Largest diameter	148	175	180	195	164–185

Description.—The incisor is slightly curved outwards (Fig. 4F₂). It has a rather flattened transverse section (145 × 65 mm). There is no trace of enamel. On the dorsal side there are two grooves; the labial one being deeper than the lingual one. On the ventral side, there are five shallow grooves. The tip of the incisor has a thin cement layer, underneath follows a concentric laminated dentine layer (10 mm), then a uniform core dentine (max. 41 mm). The basal part has a regular dentine layer (10 mm), but the core of the tooth (max 44 mm) consists of rod-cone structures, or tubular dentine (Tassy 1999).

TTMEU-CY-203 is a nearly complete, heavily worn left M2 with four lophs, a weak anterior cingulum and a well-developed double talon. The tooth is rectangular. The pretrite half-lophs are composed of a main cone, a smaller mesoconelet and anterior and posterior accessory conules that exhibit trefoil wear pattern in the first two half-lophs. On the posttrite side, the posterior accessory conules are present on the first and third half-lophs; and an incipient anterior accessory conule on the second half-loph. The last two half-lophs show an incipient anancoidy with the pretrite side positioned anterior to the posttrite side. There is a trace of cement at the base of the interlophs.

Comparisons.—The systematic position of “*Mastodon*” *grandincisivus* among late Neogene elephantoids has long been debated. It was included in *Stegotetrabelodon* by Tobien (1978), and more recently in the amebelodonts (Tassy 1999). We follow this latter opinion, since the dorso-ventral compression and tubular dentine structure of the holotype (Schlesinger 1922) clearly demonstrate affinities with this group.

Similar incisors are known from some (but not many) localities in Eurasia, Africa, and North America, of middle to late Miocene age, but the differences in outline of the cross-

section point to the occurrence of two or more different species (and/or sexual dimorphism) in the Old World. The structure of the rod cones from Yulafli is similar to that of an incisor from Arapli, near Tekirdağ, referred to *Amebelodon* (*Platybelodon*) by Gaziry (1976: pl. 3: 2), but the latter was certainly more dorso-ventrally compressed, and more regularly compressed dorsally. At Kerch in Crimea (Pavlov 1904) and Sahabi in Libya (Gaziry 1987), the section is almost rectangular, whereas it is more irregular, and thus more similar to that of Yulafli, at Maragha and Pestszentlőrincz in Hungary (Schlesinger 1917; 1922; comparisons in Tassy 1999: fig. 18.8), and perhaps also in Gansu, China (Tobien et al. 1986: fig. 24). However, the incisor from Yulafli is smaller and more convex ventrally than the teeth from Maragha and Pestszentlőrincz (Table 2 and Fig. 9). Perhaps the specimen most similar to the tooth from Yulafli is from Orjachovo in Bulgaria (Bakalov and Nikolov 1962: pl. 66).

The M2 TTMEU-CY-203 differs from that of *T. longirostris* from Yulafli, which has a simpler lophid structure and a clearly smaller size. It resembles the Mannersdorf sample of “*Mastodon*” *grandincisivus* (Schlesinger 1917: pl. 15: 1). They share the pretrite trefoil pattern in the first two half-lophs, posterior accessory conules on the posttrite side, and secondary conules blocking the interlophs, but the teeth from Mannersdorf are larger. The mastodont from Arapli is trilophodont, and this is a further difference, if in both sites the molars are correctly referred to the same taxon as the incisors.

Thus, there is little doubt that these two teeth should be referred to what is often called “*Mastodon*” *grandincisivus*, but what should more correctly, even if provisionally, be called *Amebelodon*. Its smaller size than the similar form from Kerch and Maragha suggests that it might be earlier, but given the great size variability in proboscideans, this conclusion is, admittedly, quite weak.

Order Perissodactyla Owen, 1848

Family Rhinocerotidae Gray, 1821

Kaya and Heissig (2001) referred the Yulafli rhinos to *Aceratherium incisivum* Kaup, 1832, *Acerorhinus zernowi* (Borissiak, 1914) and *Dihoplus schleiermacheri* (Kaup, 1832). No important material has come to light since then, and this list can be kept unchanged.

Family Equidae Gray, 1821

Genus *Hippotherium* Kaup, 1832

Type species: Equus primigenius von Meyer, 1829; Eppelsheim, Germany, Vallesian, Miocene.

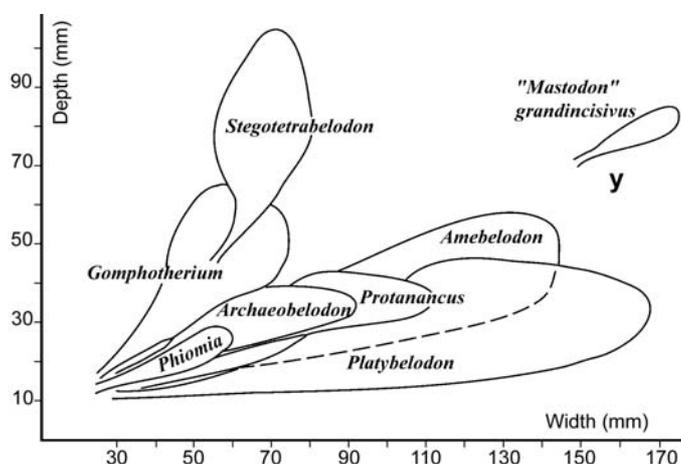


Fig. 9. Measurements of the cross-section of the lower i2s in various Proboscideans. From Tassy (1986: fig. 14) and y = Yulafli.

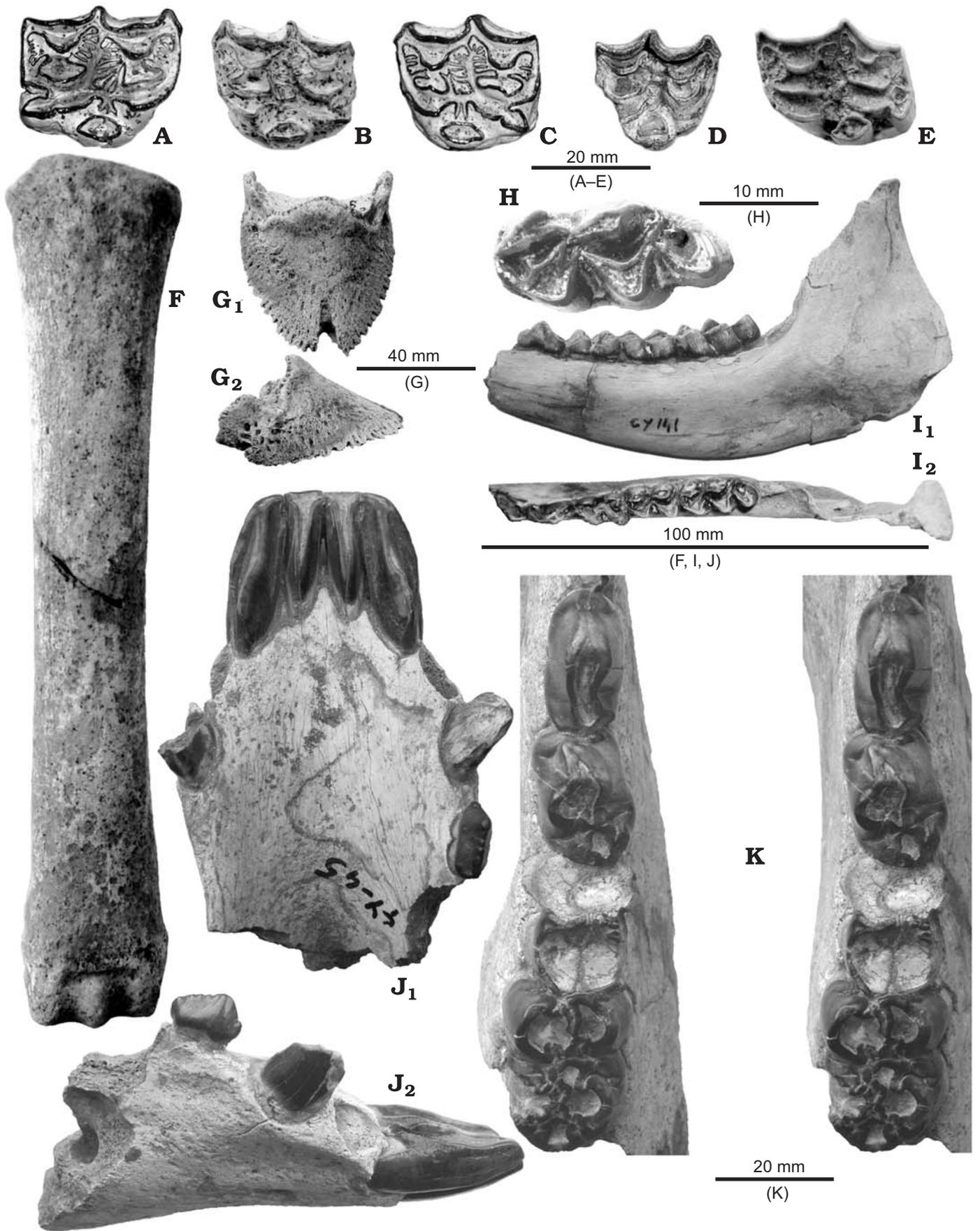


Table 3. Measurements of *Hippopotamodon cf. primigenium* from Yulaflı, in mm; A-P, antero-posterior.

Teeth	P3–4	M1–2			M3	m1–2	
Length	26.8	23.5	23.8	23.2	21.3	22.3	23
Width	22.9	20.3	21.1	19.4	18.7	17	12

Mc-III	TTMEU-CY-18	TTMEU-CY-200	Calcaneus	TTMEU-CY-118
(1) Maximum length	212	201	(1) Maximum length	107
(5) Proximal width	33	39	(3) Width of tuber	30
(6) Proximal diameter	27	26	(4) Diameter of tuber	42
(11) Distal articular width	30	31	(5) Maximum distal width	48
(12) Distal A-P diameter	24	25.2		
(13) Minimum distal diameter	21.5	22.3		

Astragalus	TTMEU-CY-19	TTMEU-CY-19a	Phalanges	phalange II TTMEU-CYA-4	phalange III TTMEU-CYA-9
(1) Maximum length	53	55	(1) Maximum length	36.3	58
(4) Maximum breadth	51	51	(3) Maximum width		51.5
(5) Distal articular width	39,5	39	(4) Proximal articular width	35.5	33
(6) Distal A-P diameter	(26)	30	(5) Proximal articular A-P diameter	22	19.5
			(6) Height		32

Hippotherium cf. primigenium (von Meyer, 1829)

Material from Yulaflı.—Five isolated upper cheek teeth, two isolated lower cheek teeth, three isolated incisors, two Mc-III (TTMEU-CY-18, CY-200), two astragali (TTMEU-CY-19, TTMEU-CY-19a), calcaneus (TTMEU-CY-118), phalanx-2 (TTMEU-CYA-4), phalanx-3 (TTMEU-CYA-9). Measurements: Table 3.

Description.—On the upper teeth (Fig. 10A–E), the protocone is lingually flattened, and more lingual than the hypocone. Its length varies from 7.5 to 6.1 mm. The hypocone is triangular and encircled by a deep hypoglyph. The upper cheek teeth have richly plicated enamel. The folds (24 on the molars) are deep, narrow, and almost parallel. The posterior wall of the postfossette is distinct. The pli caballin is complex or bifid. The lower teeth have a small protostylid at occlusal level, but no ectostylid, a triangular-rounded metaconid, and crenulated enamel in the flexids. The hypsodonty index (HI) can be calculated for a few teeth (for upper molars 181–217; for one upper premolar 186) and their values show moderately hypsodont teeth. The lower incisor ($I_1 = 15 \times 10.3$ mm) has crenulated enamel on the occlusal surface.

The Mc-III (Fig. 10F) is short and rather slender (Fig. 11), especially distally, with low robustness indices (11/1) of 141 and 154 for two Mc-IIIs. The keel index (12/13) is 111 and 113, respectively. The astragalus and calcaneus are of me-

dium size. The third phalanx (Fig. 10G) is well preserved with small splits around the sole.

Comparisons.—The *Hippotherium* remains from Yulaflı are too incomplete for precise specific identification. Their characters fit those of *H. primigenium* from Eppelsheim (Bernor et al. 1996), but they are smaller and the metacarpal is gracile and less massive (especially distally). The index (11/1) of Mc-III is smaller than those of *H. primigenium* from Eppelsheim (174) and Vienna Basin (165–194) (Sondaar 1974; Bernor et al. 1988), but closer to that (157) of Rudabánya (Bernor et al. 1993). *Hippotherium primigenium* from Ravin de la Pluie has some morphological similarities with that from Yulaflı, but the plication number is low (17 for M1–2) and the metacarpal III is short and robust (Koufos 1986). The teeth from Yulaflı are similar to those of *H. primigenium* from the Vallesian of Nesebar in Bulgaria, but the metacarpal III is slightly more massive (Forstén 1978). The maxillary teeth of *H. primigenium* from Dorn-Dürkheim 1 (Kaiser et al. 2003 pl. 1) share some morphological similarities with the Yulaflı material, but differ in their wider maxillary teeth, shallower hypoconal groove, and larger size.

The material of Yulaflı is similar to that of the Vallesian of Eşme-Akçaköy in the TTMEU Izmir, in having highly ornamented pre- and postfossette, a complex pli caballin, and a moderate hypsodonty. However, the latter differs from our sample by its larger size, the occurrence of a protocone spur,

← Fig. 10. A–G. *Hippotherium cf. primigenium*. A. TTMEU-CY-50, right P3–4. B. TTMEU-CY-123, left M1–2. C. TTMEU-CY-20, left M1–2. D. TTMEU-CY-51, right M1–2. E. TTMEU-CYA-7, left M3. F. TTMEU-CY-200, Mc-III in anterior view. G. TTMEU-CYA-9, Phalanx-III in dorsal (G_1) and lateral (G_2) views. H, I. *Dorcatherium cf. jourdani*. H. TTMEU-CY-139, left m3 in occlusal view. I. TTMEU-CY-141, left dentary in lateral (I_1) and occlusal (I_2) views. J, K. *Hippopotamodon antiquus*. J. TTMEU-CY-45, symphysis and front teeth in dorsal (J_1) and right lateral (J_2) views. K. TTMEU-CY-49, right tooth-row in occlusal view, stereo. All from Yulaflı, Turkey, Vallesian, late Miocene.

the deeper hypoconal groove, the confluent distal wall of the postfossette, and stouter metacarpals (Fig. 11). The Mc-IIIs from Yulaflı are also smaller and less massive than the Mc-IIIs from Eppelsheim and Rudabánya. The Yulaflı hipparion differs from both *Cormohipparion sinapensis* and "*H. ankyranum*" from Sinap Tepe (Ozansoy 1965; Bernor et al. 2003) in the following characters: the maxillary cheek teeth have highly ornamented pre- and postfossette, the protostylid is present in the lower teeth, and the metacarpal III is lightly built (Bernor et al. 2003: fig. 11.8). They share a lingually flattened protocone, a deep distal hypoconal groove, a complex or bifid pli caballin, and a distinct posterior wall of the postfossette. However, the Mc-IIIs from Sinap Tepe have very diverse proportions, and some specimens from Loc. 12 (early MN 10), conform well with our specimens in being short and slender (Fig. 11); they were referred by Bernor et al. (2003) to "*Hipparion*" sp. 1, while slightly stouter specimens from Sinap Loc. S01 were identified as aff. "*Hipparion*" *kecigibi*.

Our material is also distinct from the *H. aff. depereti* from Pentalophos (Koufos 2000), which has teeth with moderate enamel plications (19 for M1–2) and short massive metacarpals (the index 11/1 = 170). The teeth from Yulaflı certainly differ from the Turolian hipparions of Gülpınar and Kemiklitepe (TTMEU), where the enamel plication is simple, the protocone is rounded, and the pli caballin is simple. The keel index of Mc-IIIs is 111–113 indicating Vallesian forms (Sen et al. 1978; Staesche and Sondaar 1979) from that of the Turolian forms.

Similarities in dental morphology indicate that the Yulaflı hipparion is closer to Vallesian forms than to Turolian ones, but the Mc-IIIs are smaller and less massive. These characters suggest that it is more advanced than early Vallesian forms of *H. primigenium*.

Order Artiodactyla Owen, 1848

Family Suidae Gray, 1821

Genus *Hippopotamodon* Lydekker, 1877

(= *Limnostonyx* Ginsburg, 1988)

Type species: *Sus antiquus* Kaup, 1832; Eppelsheim, Germany, Vallesian, Miocene.

Hippopotamodon antiquus (Kaup, 1832)

Material from Yulaflı.—TTMEU-CY-45, symphysis with i1–i2 on both sides, bases of canines and right p1 (Fig. 10J); TTMEU-CY-49, right mandibular ramus with root of canine, and p3–m2 (Fig. 10K). Measurements are given in Table 4.

Description.—A slight overlap in the preserved parts of the dentaries show that the two specimens are not from the same individual.

Although the posterior border of TTMEU-CY-45 is missing, it is clear that the symphysis was short and stout. The incisors are inserted along a rather shallow arch, the line joining the alveoli of i1 and i3 being inclined at about 50° in respect to the sagittal line. There is a minute diastema between

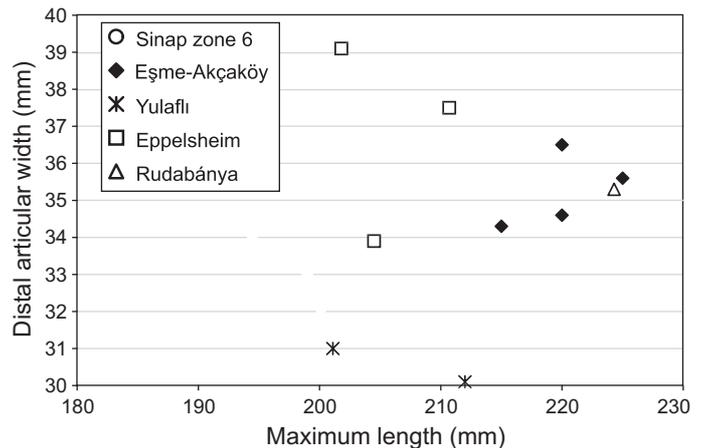


Fig. 11. Plot of length versus distal articular width of Mc-III in some hipparions.

i3 and the canine, itself separated from p1, which is present on the right side only, by a very short diastema.

The incisors are robust but quite short, although they are only slightly worn, at their tips and along the lingual (dorsal) ridge of i1. The i2 is much broader than i1, and its flange, laterally offset, overlaps the labial face. The third incisor is missing on both sides, but was intermediate in diameters between i1 and i2. The length and relative position of the incisors, as well as the lack of diastemata, clearly point to a suid with a shortened muzzle.

The canine, rather vertically inserted, is imperfectly preserved, but it has an oval cross-section and a clear demarcation between crown and root. The latter, not being visible at the break just behind p1, must have been quite short, in sharp contrast to that of the other specimen (TTMEU-CY-49), and TTMEU-CY-45 is likely from a female individual.

The p1 is small but not vestigial (Fig. 10J). It is strongly compressed transversally, with a main tubercle, plus an anterior cuspid and several small ones along the main cristid. There are two fused roots.

TTMEU-CY-49: this specimen is broken in front of p2. Posteriorly, the symphysis reached at least the level of p3, and perhaps even that of p4. Although there is no direct evidence of it, the shape of the dentaries TTMEU-CY-45 + TTMEU-CY-49 suggests that the diastema between p1 and p2 was short. The canine, of which a part is preserved inside the bone, is much larger than that of TTMEU-CY-45, and therefore likely from a male individual. The cross-section is of *verrucosus*-type, with the following approximate widths (in mm) of the three sides: lingual = 20; antero-labial = 15; postero-labial = 15. The former two sides are covered with enamel.

Table 4. Measurements of *Hippopotamodon* teeth from Yulaflı, in mm.

	TTMEU-CY-45				TTMEU-CY-49		
	i1	i2	c	p1	p3	p4	m2
mesio-distal diameter	10	17	15	15.5	23.4	22.8	30
dorso-ventral diameter	15.4	12.6	10	6.8	13.1	16.6	22.2

Only the posterior root of p2 is preserved; all that can be said is that this tooth was rather large. The other cheek-teeth are in medium wear, except m1, which is in late wear. The p3 is a large and robust tooth, being even slightly longer than p4. Its morphology is simple, without any evidence of division of the main cuspid, which is inflated, especially labially; the talonid is expanded disto-labially into a strong vertical buttress. In lateral view; the steep slope of the anterior wear facet shows that the anterior accessory cusp was low, but it is also buttressed on both the lingual and labial sides. The p4 is stout and broad. As on p3, the anterior accessory cuspid is broadened.

Comparisons.—The most common suid of the Mediterranean late Miocene is *Microstonyx*, whose systematics have long been debated. In the Turolian, in spite of the wealth of the material, recent reviews (Bonis and Bouvrain 1996; Kostopoulos et al. 2001) have highlighted the difficulty to recognise two or more taxonomic entities. The variation range of the Pikermi m3s encompasses those of most of the other samples, except some Greek ones (Vathylakkos, Kerassia, Perivolaki), and no clear metric trend through time is evident. Therefore, we will include all of them in *Microstonyx major*. This species differs from the one present at Yulaflı by a number of features:

- the anterior part of the dentary is much more elongated so that, even though the symphysis is much longer, it does not reach farther posteriorly than the level of p2, and usually remains more anterior. The i3 is more posterior relative to i1–i2; there is a diastema between i3 and the canine, and a very long one between the latter and p2.
- i1 and i2 are much longer, adding to the long slender aspect of the symphyseal area, which much contrasts with that of the Yulaflı specimen. This difference has also been mentioned by Made (2003). The i2 is not so broad relative to i1.
- the canine is much smaller (it may even be missing), the difference being more marked in the male.

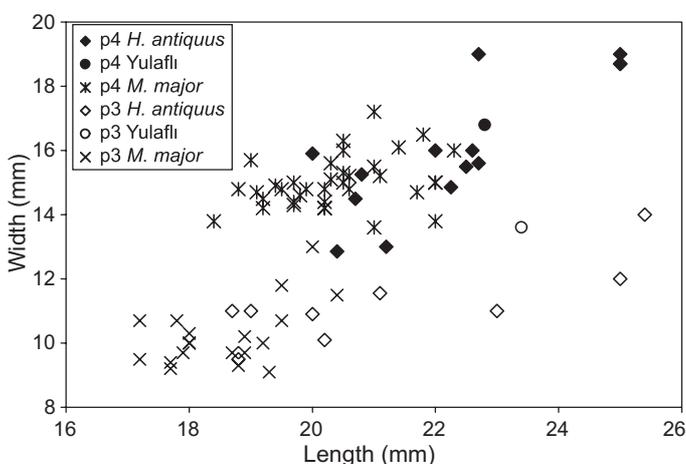


Fig. 12. Length vs. width plot of p3s and p4s in *Hippopotamodon antiquus* and *Microstonyx major*.

- p1 is always missing.
- p2 is smaller.
- the premolars are smaller, and p3 is shorter relative to p4 (Fig. 12), but its anterior accessory cuspid is higher and narrower.
- p4 is narrower, especially anteriorly, although some specimens approach the condition seen at Yulaflı. This tooth, which is rather variable in *M. major*, especially in the development of the “Innenhügel” does not significantly differ in other morphological features.

Therefore, the Yulaflı suid cannot be referred to *M. major*. It is much closer to the earlier species *antiquus*, often included in the same genus, or in *Hippopotamodon* Lydekker, or in *Limnostonyx* Ginsburg, of which it is the type-species. Following most recent authors, we will regard both latter generic names as synonymous, and include *antiquus* in it. Bonis and Bouvrain (1996) gave a clear account of this species, and we will follow their conclusions here. Besides the type locality, Eppelsheim, well-documented reports of this species are from Montredon in France (Ginsburg 1988) and perhaps from Sophades in Greece (Thenius 1955) although, as noted by Kostopoulos et al (2001) the teeth from Sophades are small. Bonis and Bouvrain (1996) also referred to this species some teeth from Akkirma, a site of unknown age near Ankara, and the anteriorly broadened premolars described by Senyürek (1952) support this identification. Further material of this species in Turkey includes a dentary MTA-2388 from Bayraktepe, and a dentary MTA-1964 from “Uşak”. The latter locality is very imprecise but, as this dentary is very different from those of Kemiklitepe, one of the main sites close to Uşak, Akçaköy is a more likely provenance. A few more specimens come from Sinap Tepe, near Ankara. MTA-1955 (or 1953) displays the lower incisors, set in a shallow arch, and without any diastema between them and the canines, which are large. In the MNHNP, the holotype of *Dicoryphochoerus metei* Ozansoy, 1965, from Yassiören, is a complete right dentary. The i2 is much larger than i1; there are only very short diastemata between i3 and the canine, and between p2 and p1, which is long and bi-rooted. The p3 is long, and p4 is broad. All these specimens, in contrast to *M. major*, share the features observed in the Yulaflı specimens.

These differences between *H. antiquus* (including the Yulaflı suid) and *M. major* far exceed those between any two Turolian samples of *Microstonyx*. Even if there is only one species of this genus in the Turolian, we find it difficult to include *antiquus* in the same genus, as the differences between the two species would be far greater than between two living suid species (e.g., *Sus scrofa*/*S. barbatus*, *Phacochoerus aethiopicus*/*P. africanus*), and we prefer to use *Hippopotamodon*. Indeed, pending detailed phyletic analysis, there is no evidence that *H. antiquus* and *M. major* form a monophyletic group. We agree with Bernor and Fessaha (2000) that “There is little data supporting its [*Microstonyx*] transition in MN10 from *Hippopotamodon antiquus*.”. In sharp contrast to *Indarctos*, for instance, no intermediate form is

known, and *Microstonyx* is more likely to be a Turolian immigrant into Europe and the Eastern Mediterranean.

In any case, there is a clear chronological distinction between both genera, *Microstonyx* being known only in Turolian-equivalent sites, while all sites with *H. antiquus* are earlier.

Family Tragulidae Milne-Edwards, 1864

Genus *Dorcatherium* Kaup, 1833

Type species: Dorcatherium naui Kaup, 1836; Eppelsheim, Vallesian, Miocene.

Dorcatherium cf. *jourdani* Depéret, 1887

Type locality and age: Lyon Croix-Rousse, Vallesian, Miocene.

Material from Yulaflı.—TTMEU-CY-139, dentary with slightly worn m3; TTMEU-CY-140, dentary with p4-m3, in middle wear; TTMEU-CY-141, dentary with p4-m1; TTMEU-CY-141, metatarsals III-IV, lacking distal ends.

Description.—TTMEU-CY-140 has the most complete tooth series, as it includes also the alveolus for p3, which was about as long as p4. The latter is a long narrow tooth, not very much broader across the talonid than across its anterior lobe, which is also relatively long. The morphology of m3 is best seen on TTMEU-CY-139 (Fig. 10H). The labial crescents are fully selenodont, and the tooth is not very brachyodont. The disto-labial wing of the protoconid meets the hypoconid, while its disto-lingual wing joins the mesial end of the entoconid, which is rather more labial than the disto-labial wing of the metaconid, which curves labially near its distal end. The third lobe is large and forms a complete loop; the lingual wall is thin but reaches the disto-lingual corner of the hypoconid. The ectostylid is weak, as on the other specimens, but it is larger on the m1 of TTMEU-CY-141, a dentary with the ascending ramus preserved (Fig. 10I). The labial cingulum is weak. Measurements are given in Table 5.

Table 5. Measurements of *Dorcatherium* teeth from Yulaflı, in mm.

	p4	m3	m1-m3
TTMEU-CY-139	–	20.0 × 9.8	–
TTMEU-CY-140	12.6 × 5.7	20.4 × 9.8	42.2
TTMEU-CY-141	11.7 × –	19.5 × –	42.0

Comparisons.—As acknowledged by most authors, systematics of *Dorcatherium* is not easy, because of dental uniformity and overlap of size ranges between species. Furthermore, the genus is not common in the Eurasian upper Miocene, and descriptions are very scarce. The m3s are larger than a Vallesian tooth from Sigindere (Alçitepe) near Gelibolu, in the TTMEU (length of m3 = 17.8), but slightly smaller than an m3 from Kozbaşı near Çanakkale, a locality which is probably also of Vallesian age, as shown by the occurrence of *Hippopotamodon antiquus*. They are also slightly larger than the teeth from Eppelsheim, whose length was given as 17–19 mm by Kaup (1832). Their dimensions are almost identical with those from the type locality of the

Vallesian, Los Valles de Fuentidueña, which were given by Morales and Soria (1981) as 12.1 × 5.4 and 20.1 × 8.8 for p4 and m3 respectively. However, the p4s from Yulaflı lack the disto-labial expansion of the hypoconid present in the illustrated tooth from Spain (Morales and Soria 1981: fig. 1C). Both the m3 and m1-m3 lengths at Yulaflı are similar to those of *D. jourdani* from Küçükçekmece. The latter measurement is given by Malik and Nafiz (1933) as 41 mm, and the length of the largest m3, which is similar to the Yulaflı teeth, is 20.5 mm (MNHN).

Dorcatherium puyhauberti Arambourg and Piveteau, 1929, from the Turolian of Northern Greece is slightly smaller (lengths of m3s: 17–18 mm), and further differs by the peculiar morphology of its lower molars, in which the postero-labial wing of the metaconid curves labially to fuse with the protoconid, while the entoconid remains more lingual.

Thus, the Yulaflı material differs from the Turolian species of the same area, and we prefer to compare it to the species most commonly mentioned in these levels, *D. jourdani*, first described from the Vallesian of France (Depéret 1887), keeping in mind that this identification is provisional, as the systematics of the late (and middle) Miocene European *Dorcatherium* is still confused.

Family Giraffidae Gray, 1821

Genus *?Palaeogiraffa* Bonis and Bouvrain, 2003

Type species: ?Decennatherium macedoniae Geraads, 1989; Pentelophos, Greece, Vallesian, Miocene.

?Palaeogiraffa cf. *macedoniae* (Geraads, 1989)

Material from Yulaflı.—Three complete metacarpals, one incomplete metatarsal, several distal humeri. No teeth have been found.

Description and comparisons.—This giraffid is a large form; the distal articulation of the humeri has the cylindrical shape of the largest members of the family. The three perfectly preserved metacarpals are very similar in size and morphology. Their proportions (Fig. 13) are quite unusual for the late Miocene of the Eastern Mediterranean, and indeed for the family as a whole. They are about as long as those of the most dolichopodial *Samotherium*, *S. sinense* from China (Bohlin 1926), but are more slender, and even more slender than a specimen from the Turolian of Gülpınar (a locality geo-

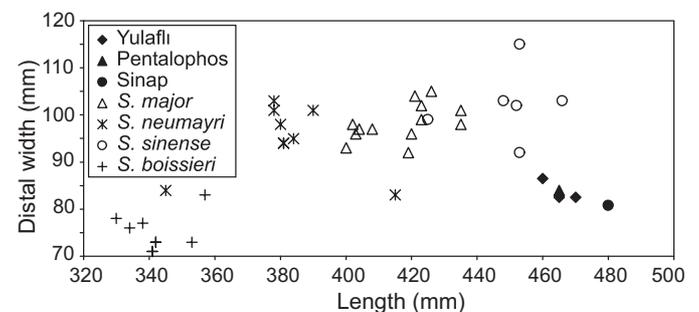


Fig. 13. Plot of length vs. distal width of the metacarpal of some large late Miocene Giraffidae. Black symbols are for “*Palaeogiraffa*”, others are for *Samotherium*.

graphically close to Yulaflı). Thus, the Yulaflı giraffid does not belong to *Samotherium*, the classic large turolian giraffid of the Turkish area. They are much shorter, however, than those of the giraffe-like *Bohlinia attica*, a close relative of the living form.

A few other giraffids from this area are more similar. Among the Sinap specimens, which document at least three species, the metacarpal MTA-1745 (very probably of Vallesian age) is only slightly longer and more slender. It is likely, but not quite certain, that it belongs to the species called *Samotherium pamiri* Ozansoy, 1965, which is probably the same as the Sinap species called *Decennatherium macedoniae* by Gentry (2003). Metacarpals from Pentalophos in Greece, type locality of the latter species, are also very similar. Bonis and Bouvrain (2003) erected the new genus *Palaeogiraffa* for it. They included in the same genus *S. pamiri* (referring as well the material from Xirochori to this species), and a new species from Ravin de la Pluie, that they called *P. major* (probably the same as the *Decennatherium?* sp. in Geraads 1989).

We agree with Bonis and Bouvrain (2003) that there is no strong argument for putting these Eastern Mediterranean forms in *Decennatherium*, known from Spain only, and that this assignment (Geraads 1978, 1989) was misleading, especially in terms of biogeography. Still, there is no argument either for thinking that they are very different, especially as, while the skull of *Decennatherium* is reasonably well-known (Morales 1985), evidence from the Eastern Mediterranean is scanty, and includes almost only teeth and limb-bones. The best collection comes from Pentalophos, and the binomen *Palaeogiraffa macedoniae* can be used for material from this locality. It is also true that these Vallesian Eastern Mediterranean forms (from Pentalophos, Ravin de la Pluie, Xirochori, and Sinap) are distinct from those of the classic Turolian sites, but we believe that referring them all to the same genus is far-fetched, especially as resemblances mostly rest upon primitive dental (mostly deciduous) features. Therefore, we prefer to compare the Yulaflı form with the best known of these taxa, rather than attempting to refer it to one of the evolutionary stages envisioned by Bonis and Bouvrain (2003), which need further substantiation.

Family ?Bovidae Gray, 1821

Genus indet.

The only remain of a non-giraffid pecoran from Yulaflı is a distal metacarpal of small size (DT = 23). The rarity of bovids is one of the most noticeable features of the Yulaflı fauna.

Discussion

Biochronology.—The fauna from Yulaflı includes at present the following species: *Testudo* sp., *Indarctos arctoides*, *Deinotherium giganteum*, *Tetralophodon longirostris*, *Choerolophodon anatolicus*, *Amebelodon grandincisivus*, *Aceratherium incisivum*, *Acerorhinus zernowi*, *Dihoplus*

schleiermacheri, *Hippotherium* cf. *primigenium*, *Hippopotamodon antiquus*, *Dorcatherium* cf. *jourdani*, ?*Palaeogiraffa* cf. *macedoniae*, ?Bovidae indet.

This faunal list is biased towards large animals, because many fossils were recovered during quarry works, and excavations have been of very limited extent. Still, this faunal association contains enough significant elements to allow comparison with some other upper Miocene faunas from Europe and the Near East.

Kaya and Heissig (2001) had suggested that the rhinoceroses of Yulaflı point to a Turolian (MN 11–12) age but, although the rhinos alone do not rule out such a possibility, it should be noted that the type localities of all three rhino taxa are of Vallesian age.

The suid is not *Microstonyx antiquus*, recorded in almost every Turolian site of the area, but *Hippopotamodon antiquus*, a Vallesian taxon. The *Dorcatherium* is distinct from the Turolian species of Northern Greece. The giraffid is also certainly distinct from the Turolian forms in this area, and more akin to the ones from Pentalophos, Xirochori, Ravin de la Pluie, and Sinap, all of Vallesian age.

Table 6 compares the distribution of the seven most characteristic taxa in those major late Miocene European sites that share at least four of these taxa with Yulaflı. None of these localities share all seven taxa, but four localities have six taxa in common, and many more have five or four. All localities with six common taxa belong to zones 9, 10 or 11, and localities from MN 12 with five common taxa have *I. atticus* instead of *I. arctoides*. There is no doubt, therefore, that Yulaflı is earlier than MN12. Against its belonging to MN9 is the large size of its *Indarctos*, which certainly does not belong to *I. vireti*, so that it almost certainly belongs to MN10 or 11. However, the only MN11 locality with six common taxa is Dorn-Dürkheim, the age of which could in fact be late Vallesian. Thus, the best fit is clearly MN10. This also fits the evidence provided by *Choerolophodon anatolicus*, which is restricted, among the well-dated localities of Sinap, to those that correlate with MN 10 (Locs 12, 49, and 83).

It is hard to refine the chronological placement of Yulaflı by comparison with other MN10 localities of the area. In Greece, Pentalophos and Ravin de la Pluie are rather different in faunal composition. They have several bovid taxa, but neither *Indarctos*, nor *Hippopotamodon* or *Dorcatherium* have been reported, and the Proboscidea have not been studied so far. However, they both have “*Palaeogiraffa*” and perhaps “*Acerorhinus*”, although the systematics of these rhinos is not firmly established.

In central Turkey, Sinap Loc.12, dated to 9.59 Ma., and Sinap Loc.49, dated to 9.13 Ma. (Kappelman et al. 2003) can both be correlated to MN 10. The former has *Indarctos vireti*, suggesting an age earlier than Yulaflı, while the latter has *Microstonyx major*, suggesting a later age. Thus, we can very tentatively estimate the age of Yulaflı at about 9.3–9.4 Ma.

Küçükçekmece is geographically close to Yulaflı, but its fauna has not been recently revised. The *Indarctos* is similar,

Table 6. Occurrences of the most significant taxa from Yulafli in some late Miocene European faunas.

<i>Indarctos</i>	<i>Aceratherium</i>	<i>Deinotherium</i>	<i>Tetralophodon</i>	<i>Hippopotamodon</i>	<i>Dorcatherium</i>	<i>D. schleiermachi</i>	number of common taxa	MN zone	Localities
	<i>A. incisivum</i>	+	<i>T. longirostris</i>	<i>H. antiquus</i>	+	+	6	9	Eppelsheim, Germany
<i>I. vireti</i>	<i>A. incisivum</i>	+	<i>T. longirostris</i>		+	+	6	9	Can-Llobateres, Spain
	<i>A. incisivum</i>	+	<i>T. longirostris</i>		+	+	5	9	Subsuelo-de-Sabadell, Spain
	<i>A. incisivum</i>	+	<i>T. longirostris</i>	<i>H. antiquus</i>	+		5	9	Wissberg, Germany
	<i>A. cf. incisivum</i>	+	<i>T. longirostris</i>		+	+	5	9	Charmoille, Swiss
	<i>A. incisivum</i>	+	<i>T. longirostris</i>	<i>H. antiquus</i>		+	5	9	Melchingen, Germany
<i>I. arctoides</i>		+	<i>T. longirostris</i>		+	+	5	9	Orignac, France
<i>I. arctoides</i>	<i>A. incisivum</i>	+	<i>T. longirostris</i>	<i>H. antiquus</i>			5	9	Westhofen, Germany
	<i>A. incisivum</i>	+	<i>T. longirostris</i>		+		4	9	Rudabánya, Hungary
	<i>A. tetradactylum</i>	+	<i>T. longirostris</i>		+		4	9	Castell-de-Barberá, Spain
	<i>A. incisivum</i>	+	<i>T. longirostris</i>		+		4	9	Los-Valles-de-Fuentidueña, Spain
<i>I. vireti</i>		+	<i>T. longirostris</i>		+		4	9	Can-Ponsic, Spain
<i>Indarctos</i> sp.	<i>A. incisivum</i>	+	<i>T. longirostris</i>		+	+	6	10	Terrassa, Spain
<i>I. arctoides</i>	<i>A. incisivum</i>	+		<i>H. antiquus</i>		+	5	10	Montredon, France
<i>I. arctoides</i>		+		<i>H. antiquus</i>	+		4	10	Küçükçekmece, Turkey
<i>Indarctos</i> sp.		+			+	+	4	10	Soblay, France
<i>I. vireti</i>	<i>A. incisivum</i>		<i>T. longirostris</i>			+	4	10	Villadecavalls, Spain
<i>I. arctoides</i>	<i>A. incisivum</i>	+	<i>T. longirostris</i>		+	+	6	11	Dorn-Dürkheim, Germany
<i>I. cf. arctoides</i>		+	<i>T. longirostris</i>		+	+	5	11	Crevillente-2, Spain
<i>I. atticus</i>	<i>Aceratherium</i> sp.	+	<i>T. atticus</i>		+		5	12	Pikermi, Greece
<i>I. atticus</i>	<i>A. incisivum</i>	+	<i>T. longirostris</i>			+	5	12	Cerro-de-la-Garita, Spain
<i>I. atticus</i>	<i>A. incisivum</i>		<i>T. longirostris</i>			+	4	12	Concud, Spain
<i>I. atticus</i>	<i>A. incisivum</i>	+				+	4	13	Baltavar, Hungary

but its p2 has only one root. This is a derived feature, but it might well result from individual variation. Detailed comparison must await revision of the Küçükçekmece fauna, but they are unlikely to be of very different ages.

The bias towards large mammals renders palaeoecological comparisons difficult, but the ecology of *Testudo*, the almost complete lack of bovids and the high frequency of *Dorcatherium* and *Deinotherium*, which were certainly browsers, definitely speaks in favour of wet forested environments, quite unlike those reported at that time in Greece and Anatolia.

Biogeography.—It has long been acknowledged (Bernor 1978; Bonis et al. 1979) that late Miocene large mammal faunas of Europe and the eastern Mediterranean belong to two main biogeographic provinces, chiefly distinct by their latitude, although the Iberian Peninsula (not discussed here) clearly falls into the northern one.

In the Vallesian, the North-Western Province (Fig. 14: 1) is documented by numerous sites in France (e.g., Montredon, Soblay), Germany (e.g., Eppelsheim, Höwenegg), Switzerland, Austria (e.g., Mariathal, Vienna Basin), and Hungary (e.g., Rudabánya). Documentation for the South-Eastern Province (Fig. 14: 3) is more sparse, but there is a good record from Greek Macedonia (review in Bonis and Koufos 1999), and central Anatolia (Fortelius et al. 2003). This South-Eastern Province corresponds in part to the Province-1 of Bernor (1978), the Sub-Paratethyan Province of Bernor (1984), the Greco-Iranian Province of Bonis et al. (1979) or the Balkano-Iranian Province of Spassov (2002), although they were all defined for the Turolian.

In Thrace, besides Yulafli, the known localities are Ramiz (Yalçınlar 1952) and Küçükçekmece (Malik and Nafiz 1933; Nicolas 1978), both within present-day Istanbul; from their geographic location, they could be expected to belong to the South-Eastern Province.

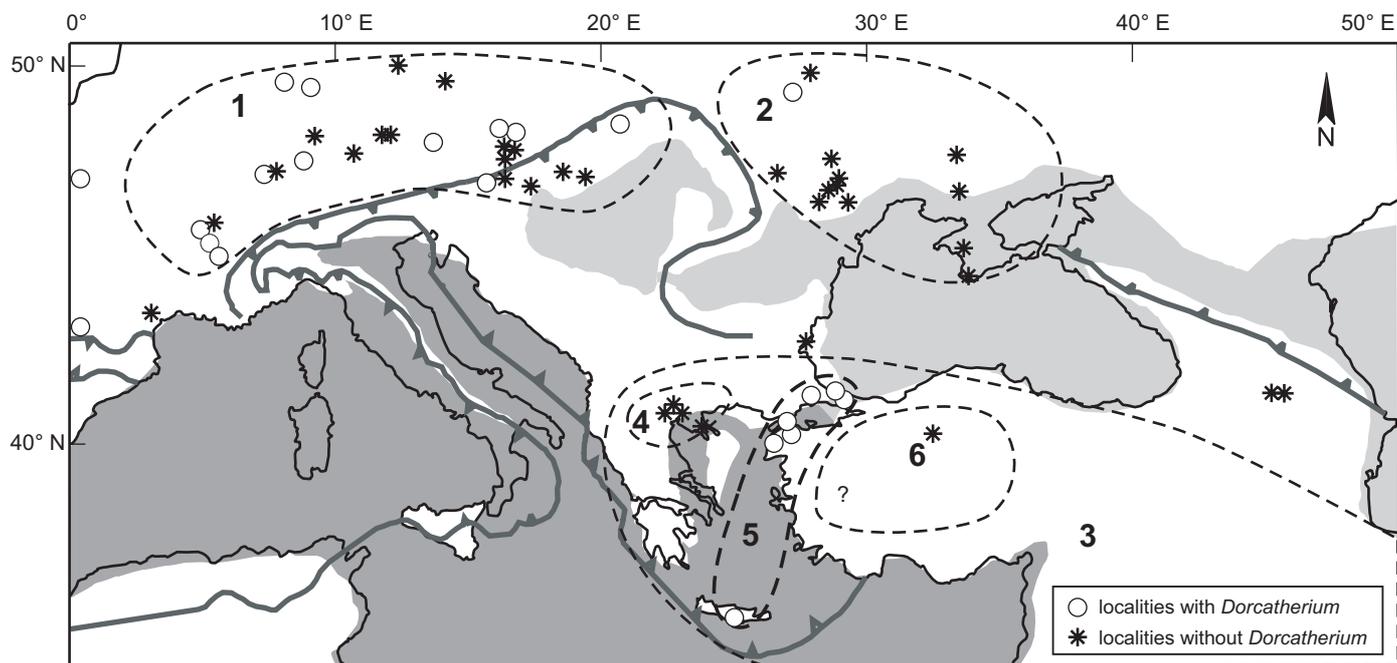


Fig. 14. Map (slightly modified from Vasiliev et al. 2004) of the Tethys (dark grey) and Paratethys (light grey) region in early late Miocene times, showing the main mammalian localities with and without *Dorcatherium*, and the tentative extent of the provinces discussed in the text. 1, North-Western Province; 2, North-Dacian Province; 3, Balkano-Iranian (= Sub-Paratethyan) Province; 4, Greek Macedonian Province; 5, Eastern Aegean Province; 6, Anatolian Province.

Two other biogeographical zones are intermediate in character. North of the Dacian Basin (a part of the middle Miocene Western Paratethys that became incorporated in the Eastern Paratethys in the late Miocene: Rögl 1999; Meulekamp and Sissingh 2003), several localities are known in Romania, Moldova, and southern Ukraine (Fig. 14: 2). South of the Caucasus, the localities of Eldar and Udabno, in spite of their position, do share similarities with the North-Western Province.

There are striking differences between the Vallesian faunas of these two main provinces. Although there is some overlap, especially in the intermediate zones, several significant taxa have distinct distributions.

Carnivores are poor biogeographic markers, but *Dinocrocota*, best recorded from the North-Dacian Province, is absent from the north-western province; by contrast, the Amphicyonidae survive there, but are extinct in the south.

Among the Proboscidea, *Choerolophodon* is restricted to the South-Eastern Province and intermediate zones, but wholly absent in the North-Western Province. There, the typical proboscidean association is *Deinotherium* + *Tetralophodon*, and is seldom found elsewhere.

In the present state of our knowledge, it is hard to draw conclusions about the distribution of the Rhinocerotidae, because a comprehensive systematic review of the late Miocene representatives of this group is still wanting, but it is likely that the forerunners of the Turolian *Chilotherium* arose

in the south-eastern part of this domain, as this genus is absent from the North-Western Province.

The difficult taxonomy of hipparionine horses also prevents the recognition of detailed patterns, but it is becoming clear that *Hippotherium*, with the common species *H. primigenium*, is restricted to central Europe (Bernor 1984; Bernor et al. 1996; Bernor and Armour-Chelu 1999). The same is true of *Anchitherium*, a survivor from the middle Miocene, and of the tapirs.

The suid *Hippopotamodon* has a wide range, but *Proppotamochoerus palaeochoerus* is the typical form of the North-Western Province, and is unknown elsewhere. Cervids are common components of this province and of the North-Dacian Basin, but are quite rare in the South. By contrast, giraffids are present in every southern sites, but absent in the north, except at Soblay (and in Spain). Northern bovids include only boselaphines and gazelles, whereas they are always more diverse in the south, announcing the Turolian diversity (Bouvrain 1997; Gentry 2003).

Last, hominoids of the north belong to the Pliopithecinae and Dryopithecinae, whereas the southern ones are *Ouranopithecus* and *Ankarapithecus*, both thick-enamelled forms.

The obvious meaning of these differences is that Western Europe and the western part of the Eastern Paratethys were more forested than the Sub-Paratethyan Province. There, a more open landscape was already in place in Vallesian times, if not earlier (Geraads et al. 2003). Solounias et al. (1999)

pointed out that it is probably incorrect to call it a savannah, since many ungulates were certainly partly browsers, but the difference with northern latitudes is nonetheless clear.

In the Eastern Mediterranean, Vallesian faunas are known from two major areas. To the West is Macedonian Greece (Fig. 14: 4), with the localities of Ravin de la Pluie, Pentaplophos, Xirochori (Bonis and Koufos 1999, and references therein); we doubtfully include the Nikiti-1 locality here, as it is certainly of later age, perhaps even early Turolian. To the East is central Turkey (Fig. 14: 6), with the Sinap area near Ankara (Fortelius et al. 2003). Eşme-Akçaköy in Eastern Turkey, also of Vallesian age, can be added to this latter area, but Çorakyerler, which has also yielded a hominoid, is definitely of Turolian age (Sevim et al. 2001). The age of the Greek localities is probably equivalent to MN 10, while the Sinap Tepe section is in the 10.9 to 9 Ma range, and thus covers most of the Vallesian (Kappelman et al. 2003).

However, in spite of sampling contemporaneous faunas (see chart in Koufos 2003, appendix 2), these two areas display major differences in their Vallesian faunal assemblages. Among the Proboscidea, *Choerolophodon* is represented by distinct species (*C. anatolicus* in Turkey, *C. pentelici* in Greece), and no other elephantoid is known in Turkey, whereas *Tetralophodon* is present in Greece. No hipparionine equid is common to both areas, with *Cormohipparion sinapensis* being restricted to Sinap and perhaps Eşme-Akçaköy (Bernor et al. 2003). Various suids have been reported or described from Turkey (Pickford and Ertürk 1979; Made 2003), but none from Greek Macedonia, and they were certainly quite rare there. Giraffids are hard to identify, because cranial remains are virtually unknown in this area for this period (see above, Systematic Palaeontology), but our examination of unpublished material in MTA confirms the absence from Sinap of any *Bohlinia*-like large long-limbed giraffid (Gentry 2003), which is present at Ravin de la Pluie, at least (Geraads 1978). Bovids are not easy to compare, not least because most of the Sinap material is fragmentary and remains incompletely studied (there is still a lot of unpublished material in MTA), but they include at least one endemic genus, *Sinapodorcas* Bouvrain et al., 1994. On the other hand, the Vallesian of Greek Macedonia has at least two endemic genera, *Mesembriacerus* Bouvrain, 1975, and *Helladorcas* Bouvrain, 1997, to which should perhaps be added *Ouzocerus* Bouvrain and Bonis, 1986 which has not definitely been recorded from Turkey. Last but not least, the hominoids *Ouranopithecus* in northern Greece and *Ankara-pithecus* in Turkey, both of them present in several localities in their respective areas (review in Bonis and Koufos 1999, and Kappelman et al. 2003), attest to the persistence, for a significant period of time perhaps equivalent to a whole MN zone, of two sub-provinces (Fig. 14: 4 and 6) characterised by several endemic taxa. Therefore, some ecological or geographical barrier must have been acting somewhere in the area of the present-day Dardanelles and Sea of Marmara. Most palaeogeographic reconstructions assume the existence there of a marine connection between the Aegean Sea and the

Paratethys in the early Tortonian (Rögl and Steininger 1983; Rögl 1999; Meulekamp and Sissingh 2003; Vasiliev et al. 2004), but detailed local studies (Sakıncı et al. 1999) suggest that this Marmara channel was not permanent, and definitely narrow. It is therefore quite unlikely that, in itself, it might have seriously hindered East/West mammalian migrations.

The large mammal assemblage from Yulaflı documents the occurrence in Thrace of an environment quite unlike those recorded West and East of it, in the sub-provinces of Northern Greece and Anatolia. The abundance of *Dorcatherium* and *Deinotherium*, together with the almost complete lack of bovids and of dolichopodial giraffids, are conclusive evidence of a wet and probably forested landscape, more like the one known in the North.

That this environment was not purely local, but had instead a rather large extent along the Eastern shore of the Aegean Sea (Fig. 14: 5), is shown by several other sites that share the same features, although they are less rich or have not recently been revised. Küçükçekmece (Malik and Nafiz 1933; Nicolas 1978) also has very few bovids, but *Deinotherium* and *Dorcatherium* are present. The latter is also present at Ramiz (Yalçınlar 1952), another site included in present-day Istanbul. Other localities along the Turkish Aegean coast have yielded mostly micromammals, but *Dorcatherium* is always common. It is present at Kozbaşı (together with *Hippopotamodon*) and Arikaşığı near Lapsecki, and is also present at Bayraktepe near Çanakkale (Tekkaya 1973). Fortelius (2004) mentions it at Eşme-Akçaköy but we could not find this record in the literature. It may have extended as far south as Crete, which was at that time connected to the mainland and had not yet drifted southwards. Made (1996) referred the tragulid from the late Miocene of Crete to cf. *Dorcabune*, but this is unlikely in terms of palaeogeography, as this genus is endemic to South-East Asia.

The localities of this "Eastern Aegean Province" (Fig. 14: 5) share with Macedonian and Anatolian contemporaneous localities some of the characteristic Vallesian taxa of the Balkano-Iranian/Sub-Paratethyan Province, such as giraffids or *Choerolophodon*. However, they also include, besides *Dorcatherium*, some taxa of northern affinities. Although these faunas are poor in macromammals, there is a cervid at Bayraktepe, Ramiz, and in Crete, an *Anchitherium* at Bayraktepe (Tekkaya 1973), and a cf. *Protopotamochoerus palaeochoerus* (Made 1996) in Crete, although the latter two are possibly from pre-Vallesian levels. These taxa definitely point to a humid/forested environment, and this Eastern Aegean Province indeed lack the open-country mammals found both east and west of it, in Anatolia and Greek Macedonia, dolichopodial giraffids and a diversity of bovids.

Some other lines of evidence confirm the prevalence of this type of environment in the area. For instance, the Vallesian micromammals from Bayraktepe II (Ünay and De Bruijn 1984) have a high proportion of castorids. Lefkon in eastern Greek Macedonia, correlated to MN 10 (De Bruijn 1989) has a significant proportion of petauristids (flying squirrels), indicating a woody environment, in accordance

with the high proportion of lignites in the deposits, indicating humid tropical conditions (Karistineos and Ioakim 1989). The early late Miocene of Samos (Ioakim and Solounias 1985) also had a dense vegetation under humid climate.

More evidence from neighbouring areas is needed to evaluate the extent of this closed environment. In the Struma Valley (Sandanski Graben) in southern Bulgaria, most of the localities are of Turolian age (Spasov et al. in press, and references therein), and the rest of this country is poorly known, but ongoing survey by Spasov et al. in the south-central part of this country might contribute to a better understanding of the possible connections between Thrace, the Dacian Basin and the north of the Paratethys in Vallesian times.

We believe that the differentiation, from some *Griphopithecus*-like ancestor, of the open-country apes *Ouranopithecus* in Greece and *Ankarapithecus* in Anatolia can be explained by the setting of this ecological barrier in the potential pathway between both areas, in parallel with the establishment of a marine connection between the Aegean Sea and the Euxinian Basin.

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