

Carnivora

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ABSTRACT

The locality of Küçükçekmece has yielded a unique carnivoran fauna representing one of the rare fossil assemblages comprising both marine and terrestrial species. The studied sample comprises thirty-four specimens belonging to three different collections at the Technical University of Istanbul (ITU), Geology Museum of the Istanbul University (IU) and at the National Museum of Natural History of Paris. This low number of fossil remains contrasts with the relatively great taxonomic richness of the fauna, since six families and at least nine species are identified: the ursid *Indarctos arctoides* (Depéret, 1895), the mustelid *Sivaonyx hessicus* (Lydekker, 1884), the phocids *Cryptophoca* sp. and Phocidae gen. et sp. indet., the percrocutid *Dinocrocuta senyureki* (Ozansoy, 1957), the hyaenid cf. *Thalassictis* sp., the felids *Machairodus aphanistus* (Kaup, 1832), *Pristifelis* sp. cf. *P. attica* (Wagner, 1857) and Felidae gen. et sp. indet. medium size. A tenth species, a small mustelid identified as *Mustela pentelici* Gaudry, 1861 by Malik & Nafiz (1933), was probably present. However, the figured (and only?) specimen was destroyed during the 1942 fire at Istanbul University. Most of the species are documented by one or a few specimens, while the phocid material is the most abundant and represents more than half of the described fossils, with many postcranial remains. The list of Carnivora of Küçükçekmece suggests a late Miocene age for the fauna of this site.

KEY WORDS

Miocene,
Turkey,
Carnivora,
Ursidae,
Mustelidae,
Phocidae,
Hyaenidae,
Percrocutidae,
Felidae.

RÉSUMÉ

Carnivora.

La localité de Küçükçekmece a livré une faune originale de Carnivora représentant l'un des rares assemblages associant à la fois des espèces marines et terrestres. L'échantillon étudié comprend trente-quatre spécimens appartenant à trois collections conservées à l'Université Technique d'Istanbul, au Musée de Géologie de l'Université d'Istanbul et au Muséum national d'Histoire naturelle de Paris. Ce faible nombre de restes contraste avec la richesse et la diversité relativement grandes de la faune, puisque 6 familles et au moins 9 espèces sont identifiées : l'ursidé *Indarctos arctoides* (Depéret, 1895), le mustélidé *Sivaonyx hessicus* (Lydekker, 1884), les phocidés *Cryptophoca* sp. et *Phocidae* gen. et sp. indet., le percrocuté *Dinocrocuta senyureki* (Ozansoy, 1957), le hyénidé *Thalassictis* sp., les félidés *Machairodus aphanistus* (Kaup, 1832), *Pristifelis* sp. cf. *P. attica* (Wagner, 1857) et un *Felidae* gen. et sp. indet. de taille moyenne. Une dixième espèce, un petit mustélidé identifié comme *Mustela pentelici* Gaudry, 1861 par Malik & Nafiz (1933), était probablement présente. Cependant, le spécimen figuré (et unique ?) fut détruit lors de l'incendie de 1942 à l'Université d'Istanbul. La plupart des espèces ne sont documentées que par un ou quelques spécimens ; au contraire le matériel de phocidés est le plus abondant et représente même plus de la moitié des fossiles décrits, avec notamment de nombreux restes post-crâniens. La liste des Carnivora de Küçükçekmece suggère un âge miocène supérieur pour la faune de ce site.

MOTS CLÉS

Miocène,
Turquie,
Carnivora,
Ursidae,
Mustelidae,
Phocidae,
Hyaenidae,
Percrocutidae,
Felidae.

INTRODUCTION

Although it was discovered in the early 1930's, the site of Küçükçekmece remains poorly known in the scientific community, with only a handful of recent work discussing or reporting on this locality (e.g., Rückert-Ülkümen & Kaya 1993; Koufos 2006). Of the twenty or so mammalian taxa that are present in the first faunal list published by Malik & Nafiz (1933), about one-third are of the order Carnivora: the mustelids *Mustela pentelici* Gaudry, 1861 and *Lutra* sp., the ursid *Ursavus* sp., the hyaenid *Ictitherium* sp., the machairodontine felid *Paramachairodus orientalis* (Kittl, 1887) (named *Machairodus orientalis* in their contribution) and the phocid *Phoca* sp. Sayar (1953) added *Machairodus aphanistus* (Kaup, 1832) to this list, but Yalçınlar (1954) and Ozansoy (1957) did not list this species and proposed the same faunal list as in Malik & Nafiz (1933). By comparison, Nicolas (1978) provided a somewhat different faunal list based on his own discoveries: the mustelids *Lutra pontica* Nordmann, 1858 and *Sivaonyx hessicus* (Lydekker, 1884), the percrocuté *Percrocuta senyureki* (Ozansoy, 1957), the hyaenid *Ictitherium* sp. cf. *I. orbigny* (Gaudry & Lartet, 1856), the ursid *Indarctos arctoides* (Depéret, 1895), the felids *Machairodus aphanistus* (Kaup, 1832) and *Felis* sp. aff. *F. prisca* Kaup, 1833, indeterminate mustelids and viverrids, and the phocids *Phoca maeotica* Nordmann, 1860 and *Phoca vindobonensis* Toulou, 1898. The carnivorans from Küçükçekmece have never been described in detail and are infrequently mentioned in the literature, with one notable exception, however: the dental remains of the ursid were studied and assigned to *Indarctos arctoides* by Petter & Thomas (1986). The objectives of this paper are to describe in details the material from Küçükçekmece assigned to the Carnivora and to discuss its significance in the context of the late Miocene faunas of Europe and western Asia.

MATERIAL AND METHODS

The material from Küçükçekmece studied in this paper comes from three distinct collections. The specimens stored at the Muséum national d'Histoire naturelle, Paris (MNHN) were collected by the late Father Jean Nicolas between 1957 and 1967 (Nicolas 1978). Nicolas (1978) collected this material along the southwestern cliffs of the Küçükçekmece Lagoon and the adjacent shores of the Marmara Sea. In the present study this locality is called Küçükçekmece West and the specimens are labelled TRQ. The material housed at the Technical University of Istanbul (ITU) and at the Geology Museum of the Istanbul University (IU) issued from the excavations of Malik & Nafiz (1933) and later discoveries at the original Küçükçekmece locality, which is situated on the southeastern bank of the Küçükçekmece Lagoon. This locality is here called Küçükçekmece East, and the specimens are labelled KÇ and IU, respectively. The 1942 fire at the Geology Institute of Istanbul University, where the collection of Malik & Nafiz (1933) was preserved, destroyed most of the specimens studied and/or figured by these authors (see Sen 2016). Both localities (Küçükçekmece East and West) are in the sandy-conglomeratic horizon of the Çukurçesme Formation, and thus considered of the same age (see Lom *et al.* 2016; Sen 2016).

Lower case is used for lower teeth, upper case for upper teeth. All measurements are in mm and, unless otherwise noted, were taken with vernier callipers to the nearest 0.1 mm. Estimated measurements are labelled 'es' in tables and text. Anatomical nomenclature follows FIPAT (2011).

ABBREVIATIONS

TLMd	total length of mandible;
Lp1-4	length of p1-4;
DMp2-3	lingual depth of the dentary between p2 and p3 (or between any other teeth);
TMp3/m1	thickness of the dentary across p3/m1;

L	maximum length;
W	maximum width;
TWm1	maximum width of talonid;
H	height (from the tip to the dentine-enamel junction on the labial face of teeth);
HPrm1	height of the protoconid of m1;
TLim1	trigonid lingual length of m1;
TLam1	trigonid labial length of m1;
LMeP4	length of the metastyle of P4;
LPaP4	length of the paracone of P4.

MEASUREMENTS

See Peigné & Heizmann (2003) for precise definitions of measurements.

BIOSTRATIGRAPHIC REFERENCES

Biostratigraphic references used herein is the European Land Mammal Mega-Zone (i.e. Vallesian, Turolian) defined by Steininger (1999), and the MN-Zones (for “Mammal Neogene”; e.g., MN9, MN10) defined by BiochroM’97 (1997), Mein (1999) and Steininger (1999).

INSTITUTIONAL ABBREVIATIONS

AMPG	Athens Museum of Palaeontology and Geology;
BMNH/NHM	Natural History Museum, London;
BSP	Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich;
EUNHM	Ege Üniversitesi Natural History Museum, Bornova, Izmir;
FCPT	Fundación Conjunto Paleontológico de Teruel-Dinópolis;
FFSD	Fürstlich Fürstenbergische Sammlungen, Donaueschingen;
FSL	Collections Université Claude-Bernard Lyon I, Villeurbanne;
GSI	Geological Survey of India, Calcutta;
GSP	Geological Survey of Pakistan, Quetta;
HLMD	Hessisches Landes-Museum, Darmstadt;
IPS	Collections from the Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona;
ITU	Istanbul Technical University (specimens from Küçükçekmece East, labelled KÇ in the text);
IU	Istanbul University Geology Museum (material from Küçükçekmece East, labelled IU in the text);
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing;
MACA	Museum of Anatolian Civilizations in Ankara;
MGL	Musée géologique de Lausanne;
MHNL	Centre de conservation du Musée des Confluences, Lyon;
MNCN	Museo Nacional de Ciencias Naturales, Madrid;
MNHN.F	Muséum national d’Histoire naturelle, Paris, Palaeontology collection;
TRQ/MAR/PIK	MNHN.F, fossil collections of Turkey (abridged TRQ in the text), Maragheh (MAR), Piskermi (PIK);
MTA	Natural History Museum in Ankara;
NHMW	Naturhistorisches Museum, Vienna;
NMB	Naturhistorisches Museum, Basel;
NMNH	National Museum of Natural History, Sofia;
PAS	Polish Academy of Sciences, Cracow;
PNT	material from Pentelofos, Greece, stored in the University of Thessaloniki;
SMF	Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt/Main;
SMNK	Staatliches Museum für Naturkunde, Karlsruhe;
UM-MTN	University of Montpellier, collections from Montredon.

SYSTEMATIC PALAEONTOLOGY

Order CARNIVORA Bowdich, 1821
Suborder CANIFORMIA Kretzoi, 1943
Family URSIDAE Fischer, 1817

Genus *Indarctos* Pilgrim, 1913

TYPE SPECIES. — *Indarctos salmontanus* Pilgrim, 1913, by original designation.

Indarctos arctoides (Depéret, 1895)
(Fig. 1A, B)

Ursavus sp. – Malik & Nafiz 1933: 109, pl. 12, fig. 6.

Indarctos arctoides – Petter & Thomas 1986: 579, figs 1-5.

REFERRED MATERIAL FROM KÜÇÜKÇEKMECE. — MNHN.F.TRQ947, subcomplete left hemimandible with the root of the canine, the root of p1, the alveolus of p2, the fused roots of p3, p4-m2, and the root of m3.

DESCRIPTION

Mandible (Fig. 1A, B)

The hemimandible is slender and low compared to other specimens of *I. arctoides* (for example, the holotype from Montredon, Depéret & Lluca 1928: pl. 9, figs 3, 4; the hemimandible from Yulaflı, Geraads *et al.* 2005: fig. 2). However, it does not display any obvious pathology. The depth of the mandibular body is rather constant below p1-p4 (DMp2-3 = 39.3; DMp3-4 = 40; DMp4-m1 = 41), then increases slightly from m1 and posteriorly (DMm1-2 = 43.8; DMm2-3 = 46). Thickness of the dentary across p3 and m1 is 17.6 mm. The coronoid process is not preserved; the masseteric fossa has its dorsal part missing, is approximately 75-mm long and shallow. The anterior margin of the fossa is situated below the distal border of m3. The ventral margin of the fossa is marked by a crest, which continues posteriorly to the tip of the angular process. The latter is short and extends medially by a small, dorsoventrally flat process. The process displays an additional, ventral crest marking the lateral extension of the internal pterygoid muscle insertion. This insertion is particularly visible in the lingual face of the mandible, where it occupies a dorsally curved, oval-shaped area of 35-mm length. The anterior limit of this area is marked by a conspicuous tubercle located ventrolaterally on the mandibular body.

Dentition (Fig. 1A, B)

The p1, p2, p3 and m3 are not preserved. The p1, p2 and m3 are single-rooted, with alveolar length of 9, 8.6 and 13 mm, respectively; the p3 has two roots that are mostly fused, for a total alveolar length of 12 mm. The tooth row is 125.5-mm long, from the mesial margin of the alveolus of p1 to the distal margin of the alveolus of m3. There is no distinct diastema between cheek teeth but a small one between p2 and p3 (L = 3 mm). The premolar row (L = 52 mm, measured at alveolar level) is much shorter than the molar row (L = 74 mm, measured at alveolar level). The teeth are lightly worn.

TABLE 1. — Measurements (in mm) of *Sivaonyx hessicus* (Lydekker, 1890) from Küçükçekmece compared with other *Sivaonyx* Pilgrim, 1931 species. Symbols: *, type specimen; 1, from Pickford (2007); 2, cast of GSI D 156. See Material and methods for abbreviations.

		<i>Sivaonyx hessicus</i>		<i>S. bathygnathus</i> (Lydekker, 1884)				<i>S. gandakasensis</i> Pickford, 2007			
		KÇ 83	BMNH 27486*	GSI D 33* ¹	NHM M 16929 ²	GSI D 250 ¹	IVPP V 6886.8 ¹	GSP 4225 ¹	GSP 117023 ¹	GSI D 249 ¹	NHM M 13175
m1	L	14.7	16	17.1	15.6	16.4	15.9	15	13.9	14.4	15.6
	W	7.9	8.3	9.7	9	9.1	9	7.9	7.9	8.6	8.6
	TLam1	10.1	10.8		10.8						10.4
	TLim1	9.6	10.2		10.3						
Dmp4-m1		16.1	17	19.2est	19	18.8		15.5est		18.1	19

The main cuspid of the p4 (L = 17.7; W = 9.4) is broken off and a small, mesiolingual fragment of the crown is missing. Distal and mesial accessory cuspids are vestigial; the talonid is long, narrow, and marked by a central, longitudinal crest; it is bordered distally by a distinct cingulid. The m1 (L = 33; W = 15.7; TLim1 = 22.4) is elongated and low, especially the trigonid cuspids. The protoconid is the tallest trigonid cuspid, the paraconid and metaconid being approximately of equal height. The paraconid and protoconid have an orientation parallel to that of the long axis of the body of the mandible. The metaconid is located distolingually to the protoconid and is visible in labial view. The labial face of the tooth is marked by a pronounced concavity at the trigonid/talonid junction. The talonid is much wider than the trigonid and the labial cingulid is particularly developed; its lingual (and not labial, contra Petter & Thomas 1986: 575) crest bears two low cuspids, an entoconid distally, and a slightly larger and mesially located entoconulid. The *crista obliqua* is low and diverges distad to the hypoconid, which is the only labial cuspid. The talonid basin is shallow. The m2 (L = 25.3; W = 17.6; TWm1 = 16.6) is rectangular in outline, with a trigonid slightly longer and, especially labially, wider than the talonid. The trigonid is composed of a horseshoe-shaped basin outlined mesially by a circular crest and distally by a transverse crest connecting protoconid and metaconid. The lingual margin of the talonid bears two vestigial cuspids, the entoconulid being the most developed one. The hypoconid is partly broken and/or worn. The m3 is not preserved but its root is long and narrow.

COMPARISONS AND DISCUSSION

The genus *Indarctos* is a typical member of the late Miocene Holarctic faunas. In Eurasia, its species content is still disputed, with 2 to 5 species (see, for example, Hunt 1998; Baryshnikov 2002; Geraads *et al.* 2005). In Europe, three species are generally recognized, with evolution from MN9, *Indarctos vireti* Villalta & Crusafont, 1943, to MN12-13, *Indarctos atticus* (Weithofer, 1888), through the intermediate species *I. arctoides* (MN9-MN11). The first description and detailed comparison of the dentition of MNHN.F.TRQ947 were made by Petter & Thomas (1986), who assigned TRQ947 (KUC 1 in their paper) to *Indarctos arctoides*. The main difference from their description that is worth noting here is the alveolar length of p1, 0.4 mm in Petter & Thomas (1986), a value difficult to reconcile with my measurement, 9 mm. The specific as-

signment of Petter & Thomas (1986) is based on the overall size of teeth (compared with the Turolian *Indarctos atticus*), and the single-rooted p2, especially compared with *Indarctos vireti* from Can Llobateres. In their study of *Indarctos arctoides* from the site of Yulafli (9.3-9.4 Ma, late Miocene, Thrace, Turkey) Geraads *et al.* (2005) also assigned the specimen from Küçükçekmece to *Indarctos arctoides*. In their discussion, they underline how difficult species demarcation is in this genus, but they conclude that *Indarctos arctoides* occurs only in the late Vallesian-early Turolian, while *I. atticus* is known from later Turolian sites. There is little I can add here to support this assignment. A major contribution to the knowledge of *I. arctoides* will certainly come when the extraordinary sample from the Vallesian site of Batallones-3, Spain, which yielded approximately 2000 bones of this species representing a minimum of 16 individuals (Abella *et al.* 2013) is published.

The M2 assigned to *Ursavus* sp. figured by Malik & Nafiz (1933: fig. 6) probably belongs to the same species (see discussion in Petter & Thomas 1986). This specimen was part of the collection stored at the Geology Institute of Istanbul University and was probably destroyed by the fire of 1942.

Family MUSTELIDAE Fischer, 1817

Genus *Sivaonyx* Pilgrim, 1931

TYPE SPECIES. — *Sivaonyx bathygnathus* (Lydekker, 1884) by original designation.

Sivaonyx hessicus (Lydekker, 1890) (Fig. 1C-E; Table 1)

Lutra sp. — Malik & Nafiz 1933: 32, 66, 109. — Yalçınlar 1954: 112. — Ozansoy 1957: 33.

REFERRED MATERIAL FROM KÜÇÜKÇEKMECE. — KÇ 83, fragment of right hemimandible with m1.

DESCRIPTION

A small portion of the dentary is preserved (Fig. 1C-E); at the level of the carnassial it is thick and deeper than the length of the m1.

The carnassial is typical of lutrines. It is robust, elongated though low and wide. The trigonid cuspids are low and of approximately equal height; the metaconid is strong and slightly



FIG. 1. — **A, B**, *Indarctos arctoides* (Depéret, 1895): MNHN.FTRQ947, subcomplete left hemimandible with p4-m2 in labial (**A**) and occlusal (**B**) views; **C-E**, *Siv-aonyx hessicus* (Lydekker, 1890): KÇ 83, fragment of right hemimandible with m1 in lingual (**C**), occlusal (**D**), and labial (**E**) views; **F-H**, *Cryptophoca* sp.: KÇ 101, fragment of left hemimandible in occlusal (**F**), lingual (**G**), and labial (**H**) views. Scale bars: 10 mm.

TABLE 2. — Measurements (in mm) of the dentary of *Cryptophoca* sp. from Küçükçekmece and comparisons with some Miocene phocids from Europe. Symbols: 1, from Koretsky & Ray (1994); 2, from Koretsky (2001). Numbers between brackets indicate sample size. See Material and methods for abbreviations.

	<i>Cryptophoca</i> sp.	<i>C. maeotica</i> (Nordmann, 1860) ¹	<i>Praepusa pannonica</i> Kretzoi, 1941 ²	<i>P. vindobonensis</i> (Toula, 1897) ²	<i>Leptophoca lenis</i> True, 1906 ²
Lp1-m1	KÇ 101 48	60est	range 31.5-38 (2)	juvenile 34	range 47-51 (9)

distal to the protoconid; the paraconid is large, triangular in occlusal shape, and occupies nearly the entire mesial half of the trigonid; its distal face is transversely oriented. A prominent crest (= protoconulid, in Morales & Pickford 2005; = post-protoconid cusplet, in Pickford 2007) is present at the distal base of the protoconid; faint notches separate this crest from the protoconid and the hypoconid crest of the talonid. The trigonid basin is deep and opened lingually so that the paraconid and metaconid are deeply separated. A strong cingulid is present on the labial side of the crown and on the lingual side of the paraconid. The talonid is wide and rounded, with a shallow basin; the hypoconid crest is wide (the lingual slope occupies one-half of the talonid width) and tall relative to the lingual ridge. The hypoconid is poorly individualized, but is slightly prominent relative to the distal rim of the talonid. The tooth has its maximum width approximately at the trigonid/talonid boundary.

COMPARISONS AND DISCUSSION

The generic assignment of the material is based on a comparison with most of the late Miocene and Pliocene species of lutrines. Besides the robustness of the dentary, which is hard to estimate here, species of *Sivaonyx* are characterized by “an m1 with a low trigonid with cuspids of approximately equal height, deeply separated paraconid and metaconid, a talonid wider than the trigonid, a large hypoconid crest, a shallow talonid basin, a low but distinct entoconid crest, a cingulid marked on the labial side that may extend on to the lingual side of the paraconid” (Peigné *et al.* 2008: 795). These features are present in KÇ 83. An additional diagnostic feature of the species of *Sivaonyx* mentioned by Pickford (2007) is mandibular depth greater than m1 length, which is also observed in KÇ 83, but this may also be the case in non-bunodont otters such as *Lutra* spp. (personal observations). The specimen from Küçükçekmece differs from *Vishnuonyx* Pilgrim, 1932 (and extant genera such as *Lutra* Brisson, 1762) in having an m1 that is more bunodont and with a lower trigonid relative to the talonid, and from more bunodont taxa (e.g., *Enhydriodon* Falconer, 1868, *Djourabus* Peigné *et al.* 2008) in having an m1 that is less bunodont and a more slender dentary. Many species of *Sivaonyx* have been described, especially from Africa and southern Asia (Morales & Pickford 2005; Pickford 2007; Peigné *et al.* 2008; Werdelin & Peigné 2010). Most of these species have an m1 with a wider talonid and, generally, a larger size than the specimen from Turkey described here (Table 1). In addition, according to Pickford (2007), *S. gandakasensis* Pickford, 2007 has also a shorter trigonid (57–64%) than in *S. hessicus*.

The specific assignment is based on a comparison with the holotype and single specimen of the European species originally described as *Lutra hessica*, BMNH 27486. This specimen is a fragment of right hemimandible with a fragment of p4 and m1 from the German locality of Eppelsheim (MN9, late Miocene). The geographic and stratigraphic proximity of the specimens of Eppelsheim and Küçükçekmece, in addition to their morphological similarity, support their assignment to the same species. Additional material is required to confirm this hypothesis. Because the specimen from Eppelsheim displays the diagnostic features of the genus *Sivaonyx* mentioned above, I propose to name this species *Sivaonyx hessicus*, an hypothesis already suggested by Morales & Pickford (2005) and, especially, by Pickford (2007). As noted by Pickford (2007), however, there is not much difference between *Sivaonyx hessicus* and the type species of the genus, *S. bathygnathus*. The species from Germany and Turkey may prove to be synonymous with this Asiatic species when more material is known. In his review of the Pliocene and Quaternary European otters, Willemsen (1992) concluded that the morphology of the m1 of *Lutra hessica* suggested a closer relationship to Lutrini (i.e. *Lutra*, *Lutrogale* Gray, 1865, *Pteronura* Gray, 1837 and their fossil relatives; see Willemsen 1992: 114), but his comparison was biased since he did not compare *Lutra hessica* with the species of *Sivaonyx*, of which many species have been described since then.

Family PHOCIDAE Gray, 1821

Genus *Cryptophoca* Koretsky & Ray, 1994

TYPE SPECIES. — *Cryptophoca maeotica* (Nordmann, 1860), by original designation.

Cryptophoca sp.
(Figs 1F–H, 2, 3, 4A, B; Tables 2, 3, 4)

Phoca sp. – Malik & Nafiz 1933: 110, pl. 13, figs 1–3. Uncertain synonymy.

REFERRED MATERIAL FROM KÜÇÜKÇEKMECE. — KÇ 101, fragment of left hemimandible with roots of p2–4; MNHN.F.TRQ930, proximal two thirds of right humerus; TRQ933, proximal fragment of left humerus; TRQ935, distal half of right humerus; TRQ927 distal half of left radius; TRQ925, proximal half of left ulna; TRQ926, proximal fragment of right ulna; TRQ944, left femur without epiphysis; TRQ945 distal fragment of left femur without epiphysis; TRQ913, distal fragment of right tibia; TRQ916, distal fragment of left tibia; TRQ917, distal fragment of left tibia; TRQ918, distal fragment of left tibia; TRQ928, subcomplete left astragalus.



FIG. 2. — Postcranium of *Cryptophoca* sp., forelimb: **A, B**, MNHN.F.TRQ930: proximal fragment of right humerus in posterior (**A**) and proximal (**B**) views; **C-E**, TRQ935: distal fragment of right humerus in medial (**C**), posterior (**D**), and anterior (**E**) views; **F, G**, TRQ925: proximal fragment of left ulna in anterior (**F**) and lateral (**G**) views; **H, I**, TRQ927: distal fragment of left radius in lateral (**H**) and distal (**I**) views. Numbers refer to grooves on the lateral face of the radius, which are assigned to the tendon for the *M. abductor pollicis longus* (1), the *M. extensor digitorum communis* and/or the *M. extensor carpi radialis* (2), the *M. extensor digitorum lateralis* (3), and *M. extensor pollicis longus* (4). Scale bar: 10 mm.

TABLE 3. — Measurements (in mm) of the forelimb bones of *Cryptophoca* sp. from Küçükçekmece and comparisons with other Miocene phocids from Europe. Measurements follow Koretsky (2001: fig. 5). Symbols: 1, from Koretsky & Ray (1994); 2, from Koretsky (2001); 3, from Koretsky *et al.* (2015); 4, from Koretsky (2003); 5, from Koretsky & Grigorescu (2002). Abbreviations: **delto**, deltopectoral crest; **prox**, proximal; **dist**, distal; **T**, thickness; **trochl**, trochlea; **AP**, antero-posterior; **ML**, mediolateral; **olec proc**, olecranon process. Numbers between brackets indicate sample size. Specimens TRQ are from MNHN.F Collection. See Material and methods for additional abbreviations.

				<i>C. maeotica</i> (Nordmann, 1860) ¹	<i>Monachopsis pontica</i> (Eichwald, 1850) ²	<i>Praepusa vindobonensis</i> (Toula, 1897) ²	<i>P. boeska</i> Koretsky, Peters & Rahmat, 2015 ³	<i>P. magyarus</i> Koretsky, 2003 ⁴	<i>Pontophoca sarmatica</i> (Aleksseev, 1924) ⁵	
Humerus	<i>Cryptophoca</i> sp.									
	TRQ 933	TRQ 935	TRQ 930		males (range)	females (range)				
				range			range	range	range	
W head	14.5	–	–	23-28 (4)	18-23 (9)	15-19 (32)	17-22.5 (30)	19.4	20-22 (2)	23.-27.5 (5)
H head	14.5	–	16.6	24-28 (4)	18-23 (8)	15.5-19 (31)	15-24 (29)	18.6	17-19(3)	25.5-28 (5)
L delto	–	–	51.5	73-80 (5)	58.5 (1)	44.5-58 (21)	52-73 (19)	50.4	62.5	64-73 (7)
prox ML W	21.5	–	24.3	29-38.5 (7)	28.5-35 (7)	20-26 (24)	–	23.5	27.5-30 (2)	28-38 (7)
prox AP T	26	–	–	33.8-46 (7)	34.5-36.5 (4)	24-29.5 (22)	–	22.9	31-31 (2)	37.3-43 (7)
ML W	–	11.3	–	18-20 (4)	12.5-13 (2)	10.5-14 (17)	14.5-18 (28)	14.6-18.7 (5)	18-18.5 (3)	20-24 (5)
trochl dist										
dist ML W	–	20.6	–	30-45 (5)	27-28 (3)	21-26.5 (19)	26.6-31.1 (30)	21.2-32.7 (5)	27-29.5 (3)	30.1-47 (7)
dist AP T	–	11.5	–	–	–	–	–	–	–	–
Ulna				<i>Cryptophoca</i> sp.	<i>P. vindobonensis</i> ²			<i>P. magyarus</i> ⁴		
				MNHN.F.TRQ925	MNHN.F.TRQ926	juvenile	range adult	range		
AP L olec proc				34.2	20.7	25	35-38 (2)	36-39 (3)		
ML W olec proc				11.4	7.5	7	19-23 (2)	24-29.5 (5)		
Radius	<i>Cryptophoca</i> sp.			<i>P. vindobonensis</i> ²						
				MNHN.F.TRQ927	range juvenile	range adult				
dist ML W				13.1	12.5-13.5 (3)	11-15 (9)				
dist AP T				26.8	20.5-25.5 (3)	22-27 (7)				

DESCRIPTION

Mandible (Fig. 1F–H; Table 2)

The dentary is broken off approximately one cm posterior to the distal alveolus of m1 and also lacks a small part in the anterior extremity (the canine alveolus is not completely preserved). The mandibular body is overall thick, but its ventral rim is pinched. Dentary depth reaches its maximum below p4–m1 (DMp4–m1 = 18.6), where the ventral rim of the body shows a marked convexity. This convexity has various names in the literature: digastric apophysis (Grigorescu 1976), mental protuberance (Koretsky & Ray 1994), chin prominence (Koretsky & Grigorescu 2002). In the specimen from Küçükçekmece East, the mental protuberance is present though not marked. From this protuberance the dentary tapers off anteriorly and its ventral rim becomes oblique relative to the alveolar border. The symphysis is short and does not extend beyond the level of the mesial alveolus of p2; its surface is rugose only in its anterior part. On the labial face there are many mental foramina below p2 and partly coalescent ones below p3 and the diastema between p3 and p4. According to the preserved alveoli the p1 was large (nearly as large as the canine) and single-rooted, and the p2, p3, p4, m1 were biradicate. Alveolar lengths indicate an increasing length from p2 to m1. The greatest diameter of the alveolus of p1 nearly reaches the p2 alveolar length. Diastemata are short, a few mm long, but they are present between all teeth; the longest diastema is the one between p4 and m1 (L = 4 mm). The tooth row (p1–m1, alveoli) is 48-mm long. The tooth

row is not set strictly parallel to the long axis of the dentary, but it is slightly twisted, the p1 being set labially and the m1 being set more linguallly.

Postcranium

Anatomical descriptions are based on the description of extant phocids (Howell 1929; Piérard 1971) and middle-late Miocene taxa of Europe (Koretsky 2001; Koretsky & Grigorescu 2002; Berta *et al.* 2015).

Humerus (Fig. 2A–E; Table 3). The humeri are robust and, though none is complete, they are complementary: MNHN.F.TRQ930 and TRQ933 preserve the proximal part of this bone and TRQ935 preserves the distal two-thirds. The greater and lesser tubercles are greatly enlarged and projected far from the shaft. The greater and lesser tubercles extend proximal to the head. The humeral head is rounded, with mediolateral and anteroposterior (dorsoventral) diameters of similar size. The lesser tubercle is projected essentially to the medial and posterior sides. The intertubercular sulcus (or bicipital groove) is deep and has a maximum width of 7 mm. The deltopectoral crest is strongly developed and thick, especially at maximum crest height, where the deltoid tuberosity is prominent and slightly swollen laterally in TRQ933 and TRQ935; the crest is long and extends distally to approximately 10 mm from the distal articular surface. The epicondylar crest is prominent and anteroposteriorly thick, though not as developed and long as the deltopectoral crest. Nevertheless, it



FIG. 3. — Postcranium of *Cryptophoca* sp., hind limb: **A, B**, MNHN.FTRQ944: left femur in anterior (**A**) and posterior (**B**) views; **C, D**, TRQ945: distal fragment of left femur in anterior (**C**) and posterior (**D**) views; **E-H**, TRQ918: distal fragment of left tibia in medial (**E**), posterior (**F**), anterior (**G**), and distal (**H**) views. Scale bar: 10 mm.

TABLE 4. — Measurements (in mm) of the hindlimb bones of *Cryptophoca* sp. from Küçükçekmece and comparisons with some Miocene phocids from Europe. Measurements follow Koretsky (2001: fig. 5). Symbols: 1, from Koretsky (2001); 2, from Koretsky & Ray (1994); 3, from Koretsky & Grigorescu (2002); 4, from Koretsky (2003). Abbreviations: **prox**, proximal; **dist**, distal; **T**, thickness; **trochl**, trochlea; **AP**, anteroposterio; **ML**, mediolateral; **great tro**, greater trochanter; **max**, maximal. Numbers between brackets indicate sample size. See Material and methods for additional abbreviations.

Tibia	<i>Cryptophoca</i> sp.				<i>Praepusa vindobonensis</i> (Toula, 1897) ¹	<i>Leptophoca lenis</i> True, 1906 ¹
	MNHN.F. TRQ913	MNHN.F. TRQ916	MNHN.F. TRQ918	MNHN.F. TRQ917	range	range
prox ML W tibia	—	—	—	—	28-34.5 (8)	44-58 (16)
prox AP T tibia	—	—	—	—	—	—
dist ML W	17.8	15.8	17.2	18	17-21 (10)	25-33 (7)
dist AP T	17.7	16	16.4	17.3	—	—

Femur	<i>M. pontica</i> (Eichwald, 1850) ¹	<i>P. vindobonensis</i> ¹	<i>S. sintsovi</i> Koretsky, 2001 ¹	<i>C. maeotica</i> (Nordmann, 1860) ²	<i>Pontophoca sarmatica</i> (Aleksseev, 1924) ³	<i>P. magyaricus</i> Koretsky, 2003 ⁴
	males (range)	range	range	range	adults (range)	range
L	65-70 (5)	63-82.5 (22)	89.5-94.5 (2)	93-138 (23)	76.5-96 (16)	—
prox ML W	29.5-36 (14)	32-38 (29)	43	44.3-64.2 (23)	36-44 (13)	—
prox AP T	—	—	—	—	—	—
L great tro	18-21 (18)	18-22.5 (29)	26-26 (2)	25-33.5 (23)	25-30 (15)	—
dist ML W	30-38 (15)	30-39 (30)	47.5-48 (2)	47-62.3 (25)	54.5-66 (19)	31.5-40 (5)
dist AP T	—	—	—	—	—	—

Astragalus	<i>Cryptophoca</i> sp.
	MNHN.F. TRQ928
max ML W	20

extends proximal to the distalmost point of the deltopectoral crest. The epicondylar crest projects mainly posteriorly and poorly laterad; the lateral rim of its anterior face is marked by attachments for the extensor muscles of the manus. It is not possible to compare directly the distal and the proximal epiphysis, but TRQ933 and TRQ935 appear to be adequately complementary, hence providing a good idea of the complete bone. The distal epiphysis is narrow, probably narrower than the proximal epiphysis, or of approximately equal width. The medial epicondyle is broad and anteroposteriorly flattened. An entepicondylar foramen is present. The olecranon fossa is nearly flat and the coronoid fossa is shallow. In anterior view, the capitatum is much wider than the trochlea.

Ulna (Fig. 2F-G; Table 3). The olecranon process is extremely expanded posteriorly and narrow in MNHN.F.TRQ925, much more so than in TRQ926, which probably belongs to a juvenile specimen. The olecranon crest is convex in lateral view. In anterior view, the proximal surface of the process is medially flared, with an anconeal process projected medially. The medial surface of the olecranon is depressed. The coronoid process of the trochlear notch is prominent, while the one of the radial notch is not. The trochlear notch is as tall as it is wide, while the radial notch is taller than wide. The shaft is broken off 3 cm distal to the radial notch; at this level it is reduced in diameter, oval in cross section.

Radius (Fig. 2H, I; Table 3). Only the distal articulation and a part of the shaft are preserved in MNHN.F.TRQ927. The shaft is strongly flattened mediolaterally and expanded anteroposteriorly. The anterior rim of the expanded region

is convex, while the posterior rim is slightly concave. At least four grooves are present on the lateral surface for the tendons of extensor muscles of the manus. I interpret these grooves following the anatomical descriptions of Howell (1929) and Piérard (1971). The groove that obliquely crosses the distal region of the lateral side of the radius in a posteroproximal to anterodistal direction is particularly deep in the anterodistal corner. The position and the course of this groove indicate that this is the one for the tendon of the *M. abductor pollicis longus* (see Piérard 1971: fig. 20; Fig. 2H). A wide, smooth groove located just posterior to it is interpreted as the groove for the *M. extensor digitorum communis* and/or that for the tendon of the *M. extensor carpi radialis*; these two tendons are very close one to another but are not always associated with a groove in extant phocids (Piérard 1971). In the proximal part of TRQ927 this groove is visible along the anterior rim of the radius; distally it crosses the groove for the tendon of the *M. abductor pollicis longus*. A wide and low ridge separates this groove from two distinct grooves that are certainly for the tendons of the *M. extensor digitorum lateralis* and, more posteriorly, the *M. extensor pollicis longus*, as in extant phocids (Howell 1929: fig. 10). A small facet for the scapholunar occupies the distal epiphysis; it is concavoconvex and, in distal view, figure-8 shaped. Distally, the posterior side is flattened and occupied by the facet for the ulna, which is elliptical and slightly depressed.

Femur (Fig. 3A-D; Table 4). The two specimens from Küçükçekmece West do not preserve the epiphysis and certainly belong to juvenile or young adult individuals. The absence of a deep trochanteric fossa in MNHN.F.TRQ944



FIG. 4. — **A, B**, *Cryptophoca* sp.: MNHN.F.TRQ928, subcomplete left astragalus in ventral (**A**) and dorsal (**B**) views; **C-H**, Phocidae gen. et sp. indet.: **C, D**, TRQ932, proximal fragment of right humerus in anterior (**C**), proximal (**D**), and lateral (**E**) views; **F-H**, TRQ946, left tibia and proximal fragment of fibula in proximal (**F**), posterior (**G**), and anterior (**H**) views. Scale bars: 10 mm.

is most probably a juvenile feature, hence has no pertinent taxonomic value. The lesser trochanter is absent. The greater trochanter is large, anteroposteriorly flattened and extended proximal to the femoral head. Its proximomedial part extends posteriorly above the trochanteric fossa (nearly absent/not yet developed? in TRQ944). The neck is short. The shaft is strongly anteroposteriorly flattened and has a lateral and, especially, a medial rim that is particularly thin at mid-length. The intercondyloid fossa is shallow. The main difference between TRQ944 and TRQ945 is that the latter shows a greater medial expansion of the medial epicondyle of the distal epiphysis. As TRQ945 belongs to a larger individual this difference may result from an ontogenetic difference. Indeed Koretsky (2001: 25) mentioned that juveniles tend to have limb bones where the proximal and distal epiphyses are not much different, while in adults the distal epiphysis is “distended considerably” compared to the proximal epiphysis.

Tibia (Fig. 3E-H; Table 4). The four distal extremities assigned to *Cryptophoca* sp. have nearly the same size and proportions, MNHN.F.TRQ917 being slightly larger. They all have similar morphology, except in the length of the preserved portion of the shaft. In its proximalmost part, the shaft is triangular in cross-section, then becomes more quadrangular distally. Distally on the medial face, there is a flattened, elongated triangular area corresponding to the surface of contact with the fibula. The medial side of the posterior face is marked distally by two grooves, interpreted here as those for the tendon of the M. flexor digitorum longus and, more medially, for the tendon of the M. tibialis posterior (Piérard 1971: fig. 32). The grooves are well distinct in TRQ916 and TRQ913, but less so in TRQ917 and TRQ918, where only one groove is clearly identified. Lateral to these grooves, the tibia is convex and slightly bulged. The anterior face is marked by a wide groove, assigned to the one for the tendons of Mm. tibialis anterior and extensor hallucis longus. The anterior distal rim of the tibia extends distally to the level of the medial malleolus. The distal epiphysis is occupied almost entirely by the facet for the astragalus, which is strongly concave. Laterally the articular surface is inclined proximally, contrasting with the medial malleolus, which extends distally.

Astragalus (Fig. 4A, B; Table 4). The bone is poorly preserved. The calcaneal process is broken off and the articular facets are not well visible. The superior facet is proximodistally convex and mediolaterally flat. The neck is long and poorly deviated medially. The head, with an articular facet for the navicular, is flat distally and convex ventrally: the facet extends along the ventrolateral face of the neck. The facets for the calcaneus are not well distinct; the sustentaculum facet is narrow, convex and connected to the distal facet (for the navicular); the ectal facet is concave, wider, and separated from the sustentaculum facet by a shallow groove where a minute foramen is visible. The facet for the fibula occupies the entire lateral face of the body.

COMPARISONS AND DISCUSSION

Malik & Nafiz (1933: pl. 13, figs 1-3) figured and briefly described a craniodental material that was much more complete than that available today. Since their study, a fire destroyed all the specimens figured. The material found by Nicolas (1978) includes only post-cranial, mostly incomplete, elements.

Fossil phocids are abundant in late Miocene localities of Central Europe and the western and northern Black Sea region. In her review of the Miocene Phocinae Gray, 1821 of Europe Koretsky (2001: table 1) mentioned the species *Monachopsis pontica* (Eichwald, 1850) from Turkey, though no detail regarding the locality is mentioned. Among the many fossil Phocinae present in the middle and late Miocene of Europe, less than ten are known in eastern Europe, especially in the Black Sea region: *Praepusa pannonica* Kretzoi, 1941, *P. vindobonensis* (Toula, 1897), *P. magyaricus* Koretsky, 2003, *Sarmatonectes sintsovi* Koretsky, 2001, *Histriophoca alekseevi* Koretsky, 2001, *Monachopsis pontica* and *Cryptophoca maeotica*. The taxonomic nomenclature follows Koretsky (2001). I also include in the comparisons *Pontophoca sarmatica* (Alekseev, 1924), known from late Miocene strata of the same Black Sea region; Koretsky (2001) assigned this species to the Monachinae Gray, 1869.

There is a great variability of body size among these late Miocene species. *Cryptophoca* sp. from Turkey is a rather small species though a part of the material probably belongs to juveniles. Nevertheless I do not consider size as a pertinent character for taxonomic assignment. Pinnipeds generally show a marked sexual size (and morphological) dimorphism, but this is partly due to relative development of soft tissue (muscles, fat). Sexual dimorphism of bones does exist, and deals not only with size but also with the anatomy, which is worth knowing in the present context. In fossil seals, sexual dimorphism is generally not documented due to a lack of pertinent material. However, Koretsky (2001) provides differential measurements and traits for (supposed) males and females of *Monachopsis pontica*, which is one of the best-known late Miocene species. *Praepusa vindobonensis* also shows a great size variability (Koretsky 2001). Below I therefore discuss chiefly anatomical differences rather than size differences.

Dentary

Morphologically the hemimandible from Küçükçekmece East closely resembles that of *Cryptophoca maeotica* illustrated by Koretsky & Ray (1994: fig. 1) and Koretsky (2001: fig. 33): same development and position of the mental protuberance, large-sized and single-rooted p1, presence of diastemata between cheek teeth, development and length of the symphysis (straightness of the ventral rim, expansion not posterior to p2 mesial alveolus). The features that may represent autapomorphies for KÇ 101 and *C. maeotica* are the large size of the single-rooted p1 and the morphology of the anterior part of the dentary (symphysis length, ventral border straight). In these features these taxa differ from the species assigned to *Praepusa* Kretzoi, 1941, *Histriophoca* Gill, 1873, *Monachopsis* Kretzoi, 1941 and *Pontophoca* Kretzoi, 1941. KÇ 101 differs from *C. maeotica* in being smaller in size (by approximately 20%, based on illustrations of the tooth row of *C. maeotica*; Koretsky & Ray 1994: fig. 1; Koretsky 2001: fig. 33) and in having an m1 longer than p4 (based on alveolar length).

Postcranium

Comparison with *C. maeotica*. The humerus (MNHN.F.TRQ930, TRQ933, TRQ935) also fits the description of the same element in *C. maeotica* by Koretsky & Ray (1994) and Koretsky (2001): deltopectoral crest strong and long (though not reaching the coronoid fossa), lesser and greater tubercles at the same level and higher than the head, epicondylar crest reaching the distal part of the deltopectoral crest proximally. The fragmentary femora (TRQ944, TRQ945) belong to juveniles. They have a greater trochanter that is much higher than the head and a distal epiphysis that is only slightly wider than the proximal epiphysis, like in *Cryptophoca maeotica* (Koretsky 2001: fig. 35).

Comparison with *M. pontica*. The description of the humerus from Küçükçekmece West also fits with that of the humerus of *Monachopsis pontica*. Given the sexual dimorphism observed in the latter (Koretsky 2001) the distinction between the humeri of these species is not easy. According to the diagnosis of *M. pontica* provided by Koretsky, the humerus fragments from Turkey differ from the humerus of *M. pontica* in the absence of dorsoventral compression of the head and a shorter deltopectoral crest. However, the compression of the head in *M. pontica* is a highly variable, sexually dimorphic trait: the males have a dorsoventrally compressed humeral head, while the females do not (Koretsky 2001: tables 2, 6). Koretsky (2001: fig. 17, table 7) describes the strong morphological and metrical sexual dimorphism of the femora of *M. pontica*. Juvenile characters may add to this dimorphism. The femora from Küçükçekmece West cannot readily be distinguished from those of *M. pontica*. A single astragalus of *M. pontica* has been described (Grigorescu 1976: fig. 6). The description does not allow distinction from MNHN.F.TRQ928 but the figures show that the distal region of the astragalus of *M. pontica* (neck and head especially) are much more robust and wider relative to the body than in TRQ928.

Comparison with *Praepusa* spp. Compared to the material from Küçükçekmece West *Praepusa* spp. have a more slender humerus with a dorsoventrally compressed head, a sharper deltopectoral crest, a lesser tubercle that is less protruding (and elongated along the shaft axis) and a distal epiphysis that is wider relative to the proximal epiphysis (Koretsky 2001: figs 24, 28; Koretsky 2003), an ulna with a shaft that is more mediolaterally compressed and an olecranon process that is much less developed anteroposteriorly (Koretsky 2001: fig. 26), though *P. magyarus* has an ulna with a similar development of the olecranon (Koretsky 2003: fig. 2). Koretsky does not describe the radius and tibia of *P. vindobonensis* in detail, but their measurements and proportions do not differ markedly from the same elements from Küçükçekmece West (Koretsky 2001: figs 27, 28, 31, tables 10, 12).

Comparison with *P. sarmatica*. Based on Koretsky & Grigorescu (2002) and Koretsky *et al.* (2014), the material from Küçükçekmece differs from *Pontophoca sarmatica* (and this is also true for *P. jutlandica* Koretsky, Rahmat & Peters, 2014

TABLE 5. — Measurements (in mm) of Phocidae gen. et sp. indet. from Küçükçekmece. Measurements follow Koretsky (2001: fig. 5). For comparisons and abbreviations, see Table 4.

	MNHN.F. TRQ932	
Humerus		
ML W head	22.4	—
H head	19.8	—
prox ML W	30	—
prox AP T	41.4	—
	MNHN.F. TRQ946	MNHN.F. TRQ922
Tibia		
L	172.5	—
prox ML W prox (tibia + fibula)	49.2	—
prox ML W tibia	42	—
prox AP T tibia	22.8	—
dist ML W	23.3	23.3
dist AP T	20.3	20.2
	MNHN.F. TRQ923	
Mt I		
prox ML W	14.3	—
prox AP T	14.1	—

though not from eastern Europe) in having a single-rooted p1, a humerus with a longer deltopectoral crest, a more reduced epicondylar crest, a distal epiphysis (probably) narrower than the proximal epiphysis, and a femur with a higher greater trochanter and a distal epiphysis that is proportionally narrower, though exceeding the width of the proximal epiphysis.

The ulnae, radii, tibiae and astragali from Küçükçekmece West cannot be compared with all the late Miocene phocids of Europe due to lack of comparative data; only some of these bones may be compared to one or several taxa (see above the comparisons with *Praepusa* spp. and *M. pontica*). They are provisionally assigned to the same species as the dentary, humeri and femora based on their size. Given the difficulty of generic assignment of fragmentary specimens, the material assigned here to *Cryptophoca* sp. may prove to represent more than one species.

Phocidae gen. et sp. indet.
(Fig. 4C-H; Table 5)

REFERRED MATERIAL FROM KÜÇÜKÇEKMECE. — MNHN.F.TRQ932, proximal fragment of right humerus; TRQ946, left tibia and proximal fragment of fibula; TRQ922, distal fragment of right tibia; TRQ923, proximal fragment of ? left Mt I.

DESCRIPTION

Humerus (Fig. 4C, D; Table 5).

MNHN.F.TRQ932 belongs to a much larger specimen than those represented by *Cryptophoca* sp. The tubercles are developed and slightly higher than the humeral head. The latter is less rounded than in the specimens of *Cryptophoca* sp. described above, showing dorsoventral compression.

Tibia-fibula (Fig. 4F-H; Table 5).

The tibia and fibula are fused proximally (MNHN.F.TRQ946). Both articular facets for the femoral condyles are well de-

TABLE 6. — Measurements (in mm) of *Dinocrocota senyureki* (Ozansoy, 1957) from Küçükçekmece compared with other Percrocutidae: lower dentition. Symbols: m, mean (of left and right sides); *, type specimen; 1, from Viranta & Werdelin (2003); 2, from Howell (1987); 3, from Schlosser (1903); 4, from Zhang (2005); 5, from Zhang & Xue (1996); 6, from Zheng (1982); 7, from Koufos (1995). Abbreviations: **pC diast**, post-canine diastema; **Küçük.**, Küçükçekmece; **Yass.**, Yassiören; **Pent.**, Pentalophos; **D. m.**, *Dinocrocota minor* (Ozansoy, 1965); **D. a.**, *D. algeriensis* (Arambourg, 1959). Specimens from Bou Hanifia are stored in the MNHN under the acronym “MNHN.F-1951.9-”; specimens **TRQ** are from MNHN.F Collection; specimens labelled ‘**AS**’ and ‘**S**’ are stored in the MACA. See Material and methods for additional abbreviations.

		<i>Dinocrocota senyureki</i>							<i>D. m.</i>	<i>D. a.</i>	<i>Dinocrocota gigantea</i> (Schlosser, 1903)					
		Küçük.	Yassiören				Sahabi	Yass.	Bou Hanifia		Shaanxi ³	Lantian ⁴	Fugu ⁵	Biru ⁴	Tianzhu ⁶	Pent. ⁷
		TRQ	TRQ	TRQ	AS.95.	AS.95.	S.89.	TRQ			IVPP	IVPP	IVPP	IVPP	IVPP	
		685	1010*	1009	318 ¹	280 ¹	138 ¹	2P28A ²	1011*	172	29	V13789	V1054	V5185	V6410	PNT 70
pC diast	L	15.5	13	8	—	—	—	—	9	10.5	—	—	—	—	—	—
p2	L	22.7	22.3est	24	22.9	—	—	21est	18.1	24.1	25	24	30.4	27.6	25.5	29.2
	W	13.9	14.8	15.9	16.3	—	—	15.5est	9.8	16.5	16.3	17.5	20.7	18.1	16	19.1
p3	L	26est	—	27.4	25.9	26.3	—	26.7	20.1	25.1	26.7	28	32	30.5	25.5	30.5
	W	15est	—	17	17.5	16.7	—	17.3est	12.8	17.3	18	19	21	19	17.5	21.3
		KÇ 58														
p4	L	28.3	32.5	30.7	26.4	29.9	31.2	29.1	22.8	28.3	—	34	36.1	34.5	30.5	34.3
	W	15.1	16.8	17.1	16.6	16.4	18.6	14.5est	12.6	16.2	—	19	20.7	19.4	17.5	18.4

finned and slightly concave. The lateral condyle is larger and more elliptical than the medial one. Just distally, and rather lateral, to the proximal epiphysis, there is a deep and short tibial fossa on the anterior and posterior faces. The anterior fossa is much shorter than the posterior fossa. The shaft is triangular in cross section; minimal diameters are measured slightly distal to mid-length (minimum mediolateral width is 14.6 mm, anteroposterior thickness is 13 mm at the same level). The distal part of the shaft and the distal epiphysis in TRQ922 and TRQ946 are not different from those of the specimens assigned to *Cryptophoca* sp. described above. The distal tip of the medial malleolus of TRQ922 is broken off. The grooves observed in the latter are visible in TRQ922, but in TRQ946 a single wide groove is distinct on the posterior face.

Approximately 30 mm of the distal fibula are preserved in TRQ946. The shaft is nearly T-shaped, with a posterior face divided by a sharp crest into two subequal parts. The anterior face of the shaft is slightly depressed by a fossa that may be the insertion area of the M. extensor digitalis lateralis, as in extant phocids (Piérard 1971). Relative to the proximal face of the tibia, the proximal face of the fibula is inclined laterally distad.

Mt I (Table 5)

MNHN.F.TRQ923 may represent the proximal half of an Mt I. This identification is based on the morphology of the proximal epiphysis, which shows a strong concavity that may correspond to the articulation with the medial cuneiform; a small apophysis extending proximally is also present in the ventrolateral corner. Laterally, the facet for the Mt II is hardly visible.

COMPARISONS AND DISCUSSION

The fragmentary humerus MNHN.F.TRQ932 belongs to a much larger specimen than those represented by *Cryptophoca* sp. Besides size, its morphology differs from that of TRQ930 and 933 by having a deltoid tubercle located

more proximally, a lesser tubercle oriented more medially, hence a much wider intertubercular sulcus, and a dorsoventrally compressed head. The latter character is also a characteristic of *Monachopsis pontica* and of some species of *Praepusa* (Koretsky 2001).

MNHN.F.TRQ946 and TRQ922 differ from those assigned to *Cryptophoca* sp. (TRQ913, TRQ916, TRQ917 and TRQ918) mainly by larger size (see Tables 4, 5). Fragmentary tibiae of *Cryptophoca* sp. are close in size to the tibiae of *Praepusa vindobonensis*, while TRQ922 and TRQ946 are of the size of *Leptophoca lenis* True, 1906 (Koretsky 2001: table 12). In addition, compared to the specimens assigned to *Cryptophoca* sp., TRQ922 and TRQ946 have a proportionally wider distal epiphysis.

I consider that the observed difference in size and anatomy between the humeri and tibiae of these two species cannot be attributed to sexual dimorphism and/or ontogeny.

Both the anatomical and taxonomic assignments of MNHN.F.TRQ923 are judged to be provisional.

Suborder FELIFORMIA Kretzoi, 1945
Family PERCROCUTIDAE Werdelin & Solounias, 1991

Genus *Dinocrocota* Schmidt-Kittler, 1976

TYPE SPECIES. — *Dinocrocota algeriensis* (Lydekker, 1884) by original designation.

Dinocrocota senyureki (Ozansoy, 1957)
(Figs 5, 6; Tables 6, 7)

Machairodus aphanistus – Sayar 1953: fig. 1.

REFERRED MATERIAL FROM KÜÇÜKÇEKMECE. — MNHN.F.TRQ685, fragment of left hemimandible with p2-3; KÇ 58, right p4; KÇ 60, fragment of right maxilla with P2; TRQ948, proximal half of left ulna, lacking most of the olecranon.

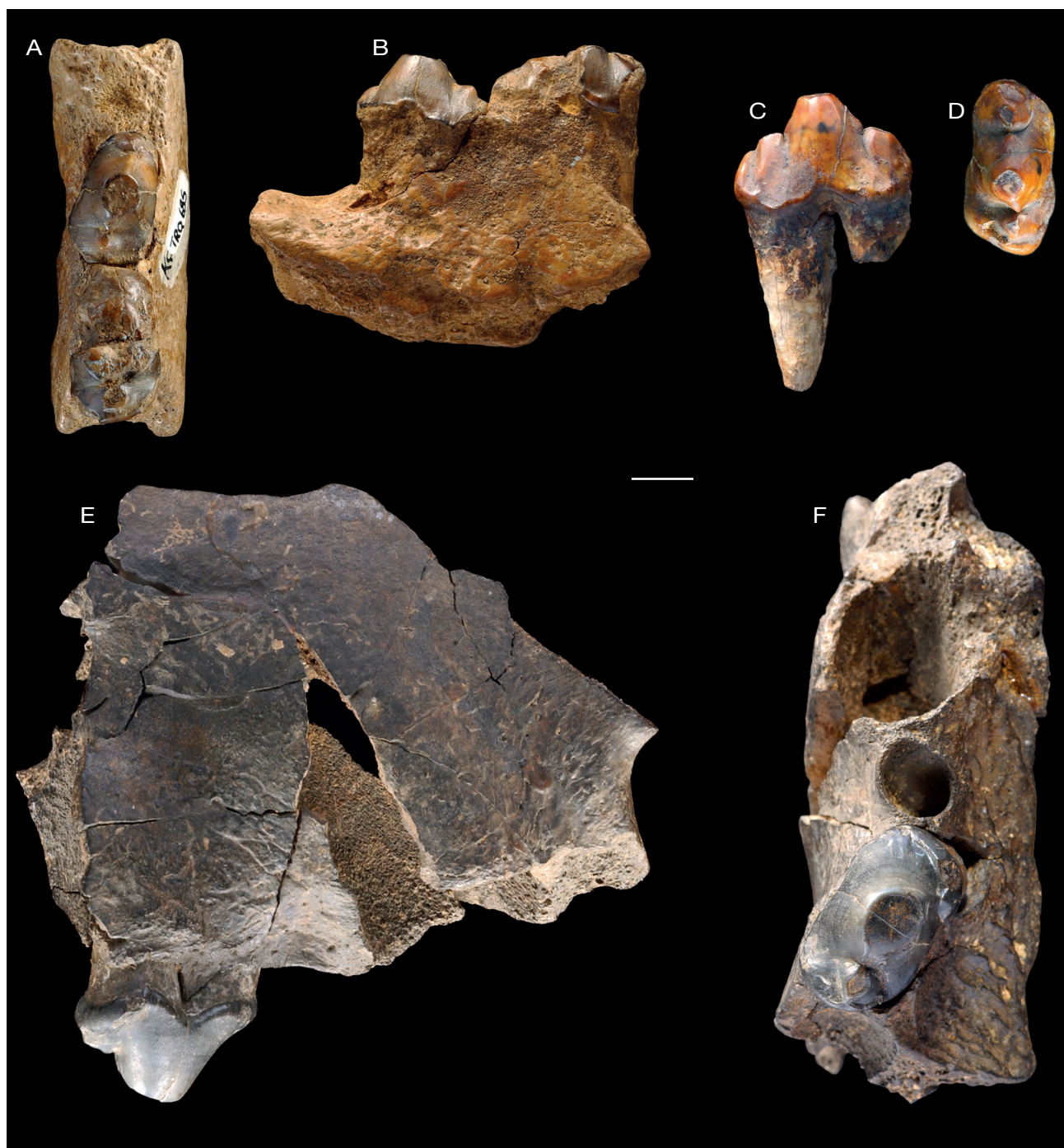


FIG. 5. — *Dinocrocuta senyureki* (Ozansoy, 1957), dental remains: **A, B**, MNHN.F.TRQ685: fragment of left hemimandible with p2-p3 in occlusal (**A**) and labial (**B**) views; **C, D**, KÇ 58: right p4 in labial (**C**) and occlusal (**D**) views; **E, F**, KÇ 60: fragment of right maxilla with P2 in labial (**E**) and occlusal (**F**) views. Scale bar: 10 mm.

DESCRIPTION

Mandible (Fig. 5A, B; Table 6)

Only an anterior fragment of the dentary is preserved, but it is thick (TMp3 = 23 mm) and robust. The post-canine diastema is long and there is no alveolus for a p1.

Dentition

Lower dentition (Fig. 5A-D; Table 6). The two premolars preserved in MNHN.F.TRQ685 display a moderate, hori-

zontal wear pattern, the p2 being less heavily worn than the p3. The p2 is set slightly obliquely in the dentary and relative to the p3 (see Fig. 5A). A major part of the mesial root is visible well above the dorsal rim of the dentary so that in lateral view the tooth seems to be oriented backwards. It bears a strong, but not particularly bulbous, main cuspid; the crown width increases distad; the mesial accessory cuspid is small, slightly lingual, and displays a small wear facet; the distal accessory cuspid is slightly more prominent than

TABLE 7. — Measurements (in mm) of *Dinocrocota senyureki* (Ozansoy, 1957) from Küçükçekmece compared with other Percrocutidae: upper dentition. Symbols: *, type specimen; 1, from Viranta & Werdelin (2003); 2, from Howell (1987); 3, from Zhang & Xue (1996). Abbreviation: **Küçük.**, Küçükçekmece; ^m, mean. Specimens labelled ‘**AS**’ and ‘**S**’ are stored in the MACA. See Material and methods for additional abbreviations.

<i>Dinocrocota senyureki</i>						<i>D. algeriensis</i> (Arambourg, 1959)	<i>D. gigantea</i> (Schlosser, 1903)
		Küçük.	Yassiören			Bou Hanifia	Fugu ³
			MNHN.F. TRQ1007	MNHN.F. TRQ1008	AS.95.413 ^{m1}	MNHN.F-1951. 9-174*	IVPP V 1052
P2	L	31	26.3	26.3	23.6	24	29.7
	W	17.9	—	16	14.2	16.3	20.5

the mesial one, centrally located, and is followed by a short cingulid. The p3 is both worn and damaged so that it is not possible to assess the relative development of the accessory cusps. However, the tooth does not show the bulbous morphology of the p3 of durophagous species such as *Adcrocuta* spp. On the contrary, p3 appears to be an enlarged version of the p2. The isolated p4 KÇ 58 is moderately worn. It differs from the p2 and p3 by a more slender main cuspid and more developed accessory cusps, where the mesial cuspid is larger than the distal cuspid. The distal accessory cuspid is followed by a short cingulid. The distal rim of the tooth is curved distally but rectilinear more mesially along the contact with the carnassial (see Fig. 5D).

Upper dentition (Fig. 5E, F; Table 7). The fragmentary right maxilla KÇ 60 preserves the P2. Only the alveoli of the I3, canine, and P1 are preserved. That of the I3 is not complete but indicates a tooth larger than the P1. The canine alveolus is oval, approximately 32 mm in length and 25 mm in width. The single, rounded alveolus of P1 indicates that it was relatively large (alveolus length is 13.9 mm, alveolus width is 12 mm). Very short diastemata separate the P1 from the adjacent teeth. The main cusp and distal accessory cusp of P2 display a moderate, horizontal wear pattern. The tooth is wide relative to its length; it has roughly the same width mesial to the main cusp as distal to that cusp. There is no mesial accessory cusp but a strong cingulum that is particularly prominent mesiolingually. Contrary to the p2, the distal accessory cusp of P2 is lingually located; the distal cingulum is very reduced.

Postcranium (Fig. 6)

A fragmentary ulna is the only postcranial bone from Küçükçekmece that might be assigned to *D. senyureki*. Unfortunately, the olecranon is not preserved. Overall the shaft is slender and the articular part is narrow compared to that of *Indarctos* and *Machairodus*, two genera also present at the site. On the anconeal process, the articular surface for the humerus extends proximally less than in the bears, felids, and hyaenids used in comparison (*Ursus* sp., *Indarctos arctoides*, *Panthera tigris* (Linnaeus, 1758) and *P. leo* (Linnaeus, 1758), *Machairodus aphanistus*, *Amphimachairodus giganteus* (Wagner, 1848), *Crocota crocuta* (Erxleben, 1777), *Hyaena hyaena* (Linnaeus, 1758)), especially on the lateral side. The morphology of the radial notch is typical of that

in hyaenids: the lateral extremity of the coronoid process is very short and poorly projected, the articular facet for the articular circumference of the radius forms a very thin surface, and a deep, marked area (presumably for ligament attachment at the proximal radioulnar joint) is present just distal to the radial notch. Overall MNHN.F.TRQ948 looks very like the ulna of roughly contemporaneous hyaenids such as *Adcrocuta eximia* (e.g., MNHN.F.PIK3247, proximal fragment of right ulna from Pikermi, late Miocene of Greece) and that of extant hyaenas (*Crocota crocuta*, *Hyaena hyaena*) though the shaft of the fossil specimen is clearly more robust than in the extant taxa.

COMPARISONS AND DISCUSSION

We follow previous authors by recognizing the family Percrocutidae as distinct from the Hyaenidae Gray, 1821 (see Werdelin 1996, for a historical background). Here I restrict comparisons to the late Miocene middle and large-sized percrocutids, i.e. the species of the genus *Dinocrocota*. Sayar (1953: fig. 1) figured KÇ 60 as a maxilla fragment of the sabre-toothed felid *Machairodus aphanistus*, but the premolar preserved and the size of the alveoli indicate a clear distinction from those of a sabre-toothed cat. This specimen (KÇ 60, Fig. 5E, F) is assigned to *Dinocrocota senyureki* based on the overall size of the dentition, the morphology of P2, with its distinctive mesial cingulum, and the presence at the site of additional specimens of the same species. *Dinocrocota senyureki* was erected by Ozansoy (1957) and described in detail later (Ozansoy 1961, 1965) based on specimens from Yassiören (MN9, late Miocene, Turkey). The syntype content is not clear in 1957 but is detailed in 1961. Some of the specimens listed by Ozansoy (1961) are stored in the MNHN and comprise: MNHN.F.TRQ1010 (= Yas 62 in Howell & Petter 1985; Ozansoy 1957: pl. 2; Ozansoy 1961: pl. 2, figs 3, 4), a fragment of left hemimandible with p2, fragmentary p3, p4-m1; TRQ1009 (= Yas 59 in Howell & Petter 1985; Ozansoy 1961: figs 4, 5, pl. 2, figs 1, 2; Ozansoy 1965: pl. 3, figs 3, 4), a fragment of right mandible with c-m1; TRQ1008 (= Yas 60 in Howell & Petter 1985; Ozansoy 1961: figs 2, 3, pl. 1, figs 1-3; Ozansoy 1965: pl. 3, figs 1, 2), a fragment of left maxilla with P2-M1; and TRQ1007 (= Yas 61 in Howell & Petter 1985), a fragment of right maxilla with P3-4 belonging to the same individual; a few additional, more fragmentary specimens (see Ozansoy 1961, 1965). In his publications Ozansoy did not clearly

select a type specimen, however. Howell & Petter (1985) regarded TRQ1010 (the only specimen figured by Ozansoy in 1957) as the type specimen of *Dinocrocutea senyureki*. This specimen is a lectotype, by subsequent designation (Howell & Petter 1985). The material from Küçükçekmece is fragmentary, but the assignment of this material to *Dinocrocutea senyureki* is well supported by the comparison with specimens from the type locality. I did not find any difference between the lectotype TRQ1010 (Yassiören) and TRQ695 (Küçükçekmece). Both specimens share the absence of p1, the oblique orientation on the dentary and the morphology of p2, the absence of marked bulbous morphology on p3. In the upper dentition, the distinct mesiolingual cingulum around the crown basis of P2 has the same development in TRQ1007 from Yassiören and KÇ 60 from Küçükçekmece. This is also true for the p4 KÇ 58 from the latter site, which shows cuspids and cingulum as developed as in the p4 of the specimens from Yassiören listed above. Additional specimens from the Sinap were collected more recently and described by Viranta & Werdelin (2003). This sample comes from Loc. 108 (10 Ma in age; Kappelman *et al.* 2003) and Loc. 12 (9.6 Ma in age; Kappelman *et al.* 2003), both in the MN9 (early Vallesian) biostratigraphic level and from Loc. 37, MN10 (late Vallesian). These localities yielded a few postcranial bones and many dental remains (Tables 6, 7). Among this new sample from Yassiören the elements that also are known from Küçükçekmece are morphologically very similar. In addition to the type locality, *D. senyureki* has been described from the Turkish sites of Eşme Akçaköy (MN9, early Vallesian), Kayadibi (MN11, early Turolian) and İnönü (MN10-11, late Vallesian-early Turolian), which yielded dental elements that are not comparable with those from Küçükçekmece (Schmidt-Kittler 1976). Elsewhere, the species is also known at Sahabi (late Miocene, Libya) from right and left hemimandibles of a single individual, an isolated P2 (Howell 1987: fig. 4), and several postcranial specimens. There are differences in proportions or size of teeth or between teeth (Table 6), but the intraspecific variability of the sample from Yassiören alone indicates great variability in size of *D. senyureki*. The P2 from Küçükçekmece is larger than in the other specimens of the species, but this is the sole difference and the known sample is limited. Therefore the material from Küçükçekmece is assigned to the same species.

Other species of *Dinocrocutea* are known from late Miocene sites in the Old World, especially *D. minor* (Ozansoy, 1965), *D. salonicae* (Andrews, 1918), although generic assignment of this species is still debated (Koufos 1995; Zhang 2005), *D. gigantea* (Schlosser, 1903) and *D. algeriensis* (Arambourg, 1959). The morphological distinction between the species of *Dinocrocutea*, which has been discussed elsewhere (e.g., Howell & Petter 1985; Spassov & Koufos 2002; Zhang 2005), is not easy. The main reason to assign the material from Küçükçekmece to *D. senyureki* rather than to *D. minor* is the size, with *D. minor* being much smaller based on the holotype (by monotypy) and probably single known specimen of this species (but see Viranta & Werdelin 2003: 182),



FIG. 6. — *Dinocrocutea senyureki* (Ozansoy, 1957), postcranium: MNHN.FTRQ948, fragment of left ulna in medial (A), anterior (B), and lateral (C) views. Scale bar: 10 mm.

MNHN.FTRQ1011 (fragment of left hemimandible with i1-m1 = Yas 58 in Howell & Petter 1985; Ozansoy 1965: pl. 4, fig. 1). The p2 of the holotype of *D. minor* is narrower distally than in *D. senyureki*, but it is hard to tell whether this difference is significant considering the limited samples. Except size, one of the diagnostic features of *D. senyureki* is the presence on P3 of a strong mesial accessory cusp, but this tooth is not preserved in the material from Küçükçekmece. According to Zhang (2005), compared to *D. senyureki*, *D. gigantea* is much larger and has proportionally larger p2/P2. The specimens from Küçükçekmece fit this picture and show a more reduced p2 compared to p3 than in most specimens of *D. gigantea*. *Dinocrocutea algeriensis* is based on a sample from Oued el Hamman (= Bou Hanifia; late Miocene, Algeria; Arambourg 1959: fig. 8A, 9D, 10C, 11, 12D, pl. 2, pl. 3, fig. 1-4) representing at least three individuals, two (young) adults (the holotype MNHN.F-1951.9-174, the paratype MNHN.F-1951.9-172, MNHN.F-1951.9-29, MNHN.F-1951.9-75, MNHN.F-1951.9-76) and one juvenile (MNHN.F-1951.9-19 and a couple of isolated, unnumbered teeth). An isolated P3 (MNHN.F.AMA9) from Menacer (= Marceau in Arambourg 1959) is also assigned to this species. Like *D. gigantea*, *Dinocrocutea algeriensis* differs from our material by a enlarged p2, especially relative to p3, and a thicker P2.

MNHN.FTRQ948 is an important specimen because percrocutid postcranial remains are rare (Howell 1987; Zhang & Xue 1996; Viranta & Werdelin 2003). Nevertheless, it is far too fragmentary to address morphological distinction between the skeleton of hyaenids and percrocutids.

TABLE 8. — Measurements (in mm) of cf. *Thalassictis* sp. from Küçükçekmece compared with other species of *Thalassictis* Gervais, 1850 ex Nordmann MS. Symbols: *, type specimen; **, type specimen of *T. chinjiensis* (Pilgrim, 1932), junior synonym of *T. proava* (Pilgrim, 1910); m, mean; 1, from Kurtén (1982); 2, from Morlo (1997); 3, from Beaumont (1986); 4, from Villalta & Crusafont (1943); 5, from Crusafont & Petter (1969); 6, from Viranta & Werdelin (2003); 7, from Heizmann & Kubiak (1992); 8, from Schmidt-Kittler (1976); 9, from Mayda *et al.* (2015); 10, from Semenov (1989); 11, from Bonis (2005); 12, from Viret (1951); 13, from Pilgrim (1932). Abbreviations: **Küçük.**, Küçükçekmece; **Host.**, Hostalets de Pierola; **S. Q.**, San Quirze; **Prz2**, Przeworno 2; **Yeni Esk.**, Yeni Eskihsar; **Akk.**, Akkasdağı; **LGSA**, La Grive Saint-Alban. Specimens labelled 'AS' and 'S' are stored in the MACA. See Material and methods for additional abbreviations.

		<i>T. robusta</i> Gervais, 1850 ex Nordmann MS			<i>T. montadai</i> (Villalta & Crusafont, 1943)				
cf. <i>Thalassictis</i> sp.		Küçük.	Kishinev ^{1m}	Dorn- Dürkheim ²	Host. ⁴	S. Q. ⁵	Sinap ⁶	Prz2 ⁷	Yeni Esk. ⁸
				SMF DD 3495	IPS-2074		AS.92.463 & 464m	PAS MF/1992/91	BSP1967 VI 772m
m1	L	22.10	17.4	16	20.5	20	23.1	20.3	23.3
	W	10.40	7.98	7	9	10	10.3	10	10.15
	TLim1	18.20	13	—	—	16.7	—	—	—
	TLam1	17.60	—	—	—	—	—	—	—
		cf. <i>T.</i> <i>montadai</i>	<i>T. spelaea</i> (Semenov, 1988)	cf. <i>Thalassictis</i> sp.	<i>T. certa</i> (Major, 1903)	<i>T. proava</i>			
		Çandir ⁹	Gritsev ^{10m}	Akk. ¹¹	LGSA ¹²	Chinji ¹³	Chinji ¹³		
		EUNHM PV-2675		MTA AKK 114	MTA AK7 107	MHNL LGr 1330	MHNL LGr 1332	GSI D 126*	GSI D 233**
m1	L	23.94	17.29	18.6	21.1	17.8	17.7est	15.6	16.5
	W	9.22	8.52	8.8	9.5	8.9	—	8.1	7.8
	TLim1	—	12.82	13.7	14.4	—	—	—	—
	TLam1	—	—	—	—	—	—	—	—

Family HYAENIDAE Gray, 1821

Genus *Thalassictis* Gervais, 1850 ex Nordmann MS

TYPE SPECIES. — *Thalassictis robusta* Gervais, 1850 ex Nordmann MS by subsequent designation of Palmer (1904).

cf. *Thalassictis* sp. (Fig. 7A-C; Table 8)

Ictitherium sp. — Malik & Nafiz 1933: 67, pl. 12, fig. 5. — Yalçınlar 1954: 140. — Ozansoy 1957: 33. Uncertain synonymy.

REFERRED MATERIAL FROM KÜÇÜKÇEKMECE. — Kadi Mezarligi Quarry unnumbered: right m1.

DESCRIPTION

The tooth (Fig. 7A-C) is complete except for the distal root. The paraconid and protoconid blades and the hypoconid tip show slight wear. The crown is low relative to its length. The paraconid blade is horizontal and similar in length to the protoconid one; the paraconid is lower than the protoconid. The metaconid is strongly reduced and lower than the paraconid; in occlusal view, it is slightly distal to the protoconid. The talonid is short (approximately 20% of m1 length; Table 8) and narrow, and displays only two cuspids of approximately equal height, although the hypoconid (a little worn here) probably was taller than the entoconid. The hypoconid crest is individualized and well distinct from the basal cingulid; mesially it starts between the metaconid and protoconid and becomes taller and cuspid-like distally. Mesially, the entoconid crest is very low and emerges in the middle of the metaconid distal side. It then runs obliquely

and distally forms a small cuspid that is less individualized than the hypoconid. The distal margin of the talonid is nearly transversely oriented and no cuspid is present: the hypoconulid is clearly absent/vestigial in this tooth. A developed cingulid is present on the labial side of the crown and extends slightly on the lingual side of the paraconid.

COMPARISONS AND DISCUSSION

The Hyaenidae is one of the most diverse carnivoran families in Europe during the Miocene. This family experienced a diversification and geographic expansion during the late Miocene (Vallesian and early Turolian), before decreasing in diversity toward the end of the Turolian (Werdelin & Solounias 1996). Morphologically (reduced metaconid and talonid, medium size), the carnassial from Küçükçekmece resembles that of species assigned to genera that are classified in the third ecomorph proposed by Werdelin & Solounias (1996), comprising *Ictitherium* Wagner, 1848, *Thalassictis*, *Hyaenotherium* Semenov, 1989 and *Hyaenictitherium* Kretzoi, 1938. Given their probable close relationships with the genera mentioned above and/or their similar m1 (see Werdelin 1988; Werdelin & Solounias 1991: fig. 38), I consider that *Miohyaenotherium* Semenov, 1989 and *Palinhyana* Qiu, Huang & Guo, 1979 also belong to this ecomorph. The definition and specific content of these taxa have known many changes in the past (Werdelin & Solounias 1991, 1996) and even recent authors do not always agree regarding their taxonomy (compare, e.g., Viranta & Werdelin 2003; Bonis 2004, 2005; Tseng & Wang 2007; Özkurt *et al.* 2015). It is beyond the scope of this paper to discuss this topic. In the context of this study, I have first considered the type species of each of these genera. Among



FIG. 7. — A-C, cf. *Thalassictis* sp.: Kadi Mezarligi Quarry unnumbered, right m1 in labial (A), occlusal (B), and lingual (C) views; D-N, *Machairodus aphanistus* (Kaup, 1832): MNHN.F.TRQ1214, right p4 in occlusal (D) and labial (E) views; TRQ1213, right m1 in labial (F) and occlusal (G) views; TRQ1215, right P4 in occlusal (H), lingual (I), and labial (J) views; TRQ694, fragment of right Mt III in proximal (K) and anterior (L) views; TRQ700, proximal fragment of proximal phalanx in proximal (M) and anterior (N) views. Scale bars: 10 mm.

TABLE 9. — Measurements (in mm) of *Machairodus aphanistus* (Kaup, 1832) from Küçükçekmece compared with specimens from European localities. Lower dentition. Abbreviations: **Höw.**, Höwenegg; **Char.**, Charmoilles; **Zill.**, Zillingdorf; **LVF**, Los Valles de Fuentidueña; **Sob.**, Soblay; **Kemik.**, Kemiklitepe; **DD**, Dorn-Dürkheim; **Mah.**, Mahmutgazi; **unn**, unnumbered. Symbols: *, type specimen; ^m, mean; ¹, from Beaumont (1988); ², from Monesillo *et al.* (2014); ³, from Spassov & Koufos (2002); ⁴, from Madurell-Malapeira *et al.* (2014); ⁵, from Bonis (1994); ⁶, from Beaumont (1986); ⁷, from Morlo (1997); ⁸, from Schmidt-Kittler (1976). See Material and methods for additional abbreviations. Specimens TRQ are from MNHN.F Collection.

MN9																		
Küçükçekmece					Eppelsheim ¹		Höw. (cf.) ⁶		Char. ⁶		Zill. ⁶		LVF					
					HLMD-Din													
unn					1132*		BMNH 49967c		FFSD Hö 141		NMB Cm 244		NHMW		MNCN 32000		MNCN 46552	
p4	L	–	–	24.7	27.3	25.6	24.8	25.5	–	22.7	24.6							
	W	–	–	10.6	12	11.8	10.8	12.6	–	10.1	10.7							
m1	L	–	25.5	–	30.3	30	–	27-28	30.6	24.7	–							
	W	10.9est	11.6	–	14.2	14.3	–	12.9	13.9	10.9	–							
TLim1	–	23.8	–	–	–	27.4	–	–	–	23.5	–							
MN10																		
												MN11						
					Montredon									DD				
					(cf.) ¹		Sob. ¹	Batallones ²		Nessebar ³	Vallès-Penedès (IPS-) ⁴				Kemik. ⁵	DD (cf.) ⁷	Mah. ⁸	
					FSL	UM-										SMF		
					210.	MTN	NMB									DD	Ma	
nn					390	3173	TF 164	Bat-1 ^m	Bat-3 ^m	1505	62083 ^m	13167	13177	13165	KTD 63	4796	1/49	
p4	L	–	24.7	24.5est	–	–	25.11	24.24	–	23.1	21.5	22.3	–	–	29	25		
	W	–	10.6	12.5	–	–	11.44	10.64	–	10.45	9.9	10.4	–	–	12.3	11.9		
m1	L	25.5	–	–	31.7	30.6	30.46	29.58	30	27.8	–	–	26.5	30.8	–	31.8		
	W	10.9est	11.6	–	17.6	13.5	13.4	11.91	12.8	12.2	–	–	12.5	11	–	13.2		
TLim1	23.8	–	–	–	–	–	–	–	26.1	22.8	–	–	23.3	27	–	–		

TABLE 10. — Measurements (in mm) of *Machairodus aphanistus* (Kaup, 1832) from Küçükçekmece compared with specimens from European localities. Upper dentition. Symbols: ^m, mean; ¹, from Beaumont (1988); ², from Monesillo *et al.* (2014); ³, from Madurell-Malapeira *et al.* (2014); ⁴, from Schmidt-Kittler (1976). See Material and methods for additional abbreviations.

		MN10						MN11			
		Küçükçekmece		Montredon (cf.) ¹		Batallones ²		Vallès-Penedès ³			Mahmutgazi ⁴
		MNHN.F.TRQ1215	FSL 210.189	FSL 210.166	Bat-1 ^m	Bat-3 ^m	IPS13185 ^m	IPS13170	IPS13164	Ma 2/Gips 28	Ma 1/159
LP4		37.3	36.9	–	38.35	37.15	36.7	33.2	32.9	40.1	43.1
LPaP4		14.5	–	15.9	–	–	13.7	11.9	12.8	15.2	15.9
LMeP4		14.6	–	–	–	–	14.2	12.6	13.2	–	–

them only *Hyaenotherium wongii* (Zdansky, 1924) (type species of *Hyaenotherium*; = *H. magnum* Semenov, 1989), *Palinhyana reperta* Qiu, Huang & Guo, 1979 (type species of *Palinhyana*), *Hyaenictitherium hyaenoides* (Zdansky, 1924) (type species of *Hyaenictitherium*) and *Ictitherium viverrinum* Roth and Wagner, 1854 (type species of *Ictitherium*) were included in Werdelin & Solounias (1991) cladistic analysis. The character analysis performed by these authors includes only two characters applicable to the tooth from Küçükçekmece: the number of talonid cuspids (character 7 in Werdelin & Solounias 1991: 51) and the presence/absence of the metaconid (character 8 in Werdelin & Solounias 1991: 51). The latter is not informative as the metaconid is present in all the species considered here and in the tooth from Küçükçekmece. The number of talonid cuspids is more diagnostic as the latter specimen has only two cuspids in the talonid, the hypoconid and the entoconid; the hypoconulid is absent/vestigial. All the type species listed above retain the primitive feature, i.e. three cuspids in the talonid of m1 (see also Semenov 2008: fig. 6; analysis of Tseng & Wang 2007: Appendix 2, character 6). However two genera were not included in the cladistic analysis of Werdelin & Solounias (1991): *Miohyaenotherium* and *Thalassictis*. These authors placed

the species of these genera in a clade comprising *Hyaenotherium*, *Hyaenictitherium* and more derived genera (e.g., hunting hyaenas and bone-cracking taxa; Werdelin & Solounias 1991: fig. 38), considering, however, that the type and only species of *Miohyaenotherium*, *M. bessarabicum* Semenov, 1989, is a possible synonym of *Hyaenictitherium parvum* (Khomenko, 1914). In a recent analysis, Tseng & Wang (2007) considered the two latter species as synonyms of *H. wongii*. The close relationship of *M. bessarabicum* with *Hyaenictitherium* spp. and/or *Hyaenotherium wongii* suggest that it is distinct from the species from Küçükçekmece. The genus *Thalassictis* includes the type species *Thalassictis robusta* Gervais, 1850 ex Nordmann MS and according to Werdelin & Solounias (1991) perhaps also: *T. certa* (Major, 1903), *T. sarmatica* (Pavlov, 1908), *T. proava* (Pilgrim, 1910) (= *T. chinjiensis* (Pilgrim, 1932); see Werdelin & Solounias 1991: 35), *T. montadai* (Villalta & Crusafont, 1943) and *T. spelaea* (Semenov, 1988). *Thalassictis sarmatica* is based on a skull and not comparable to the material from Küçükçekmece. The m1 of the species of *Thalassictis* is described as having a protoconid taller than the paraconid, a reduced metaconid, and a short and low talonid with two or three cuspids. Generally, late Orléanian-Astaracian

(MN5-8) specimens have an m1 talonid with three cuspids (Villalta & Crusafont 1943; Viret 1951; Crusafont & Petter 1969; Schmidt-Kittler 1976; Kurtén 1982; Heizmann & Kubiak 1992; Mayda *et al.* 2015) and Vallesian and Turolian specimens (i.e. MN9-12) have only two cuspids (Viranta & Werdelin 2003; Bonis 2005). The only exceptions are late Miocene specimens from the Turolian of Dorn-Dürkheim (*T. robusta*; Morlo 1997) and from Chinji (*T. proava*; Pilgrim 1932; for age, see Werdelin & Solounias 1991) that have a three-cusped m1 talonid. In addition, intraspecific morphological variability of the relative development of talonid cuspids is observed in some species. For example, in *Thalassictis montadai* the m1 may have a tall hypoconulid associated with a tall entoconid (specimens from Spain and Poland; Villalta & Crusafont 1943; Heizmann & Kubiak 1992) or an entoconid smaller than the hypoconid, as in specimens from the Sinap (Viranta & Werdelin 2003).

The m1 from Küçükçekmece resembles *Thalassictis* species in having a protoconid taller than the paraconid, a reduced metaconid, and a short and low talonid with two cuspids. In fact in the number and relative development of the talonid cuspids, it differs from *T. proava* and *T. certa* and resembles late Miocene specimens assigned to *T. montadai* and *T. spelaea*. The m1 from Turkey differs from species of *Thalassictis* in having a longer paraconid relative to the protoconid (measured parallel to the alveolar margin) and a shorter talonid. Pending discovery of more material, I maintain the taxonomic assignment open.

Malik & Nafiz (1933: pl. 12, fig. 5) assigned to *Ictitherium* sp. an incisor and a p4 (L: 19 mm; w: 11 mm) that could belong the same species. This is reported in the published faunal lists of Küçükçekmece (e.g., Yalçınlar 1954; Ozansoy 1957). These specimens were destroyed by fire during the last century. Nicolas (1978) also listed *Ictitherium* sp. cf. *I. orbignyi*, which is now *Plioviverrops orbignyi*, but this species is clearly distinct from cf. *Thalassictis* sp. described here. In Nicolas' collection stored in the MNHN, there is no evidence supporting the presence of *P. orbignyi* or a closely related species.

Family FELIDAE Fischer, 1817

Genus *Machairodus* Kaup, 1833

TYPE SPECIES. — *Machairodus aphanistus* (Kaup, 1832) by subsequent designation of Pilgrim (1931). Matthew (1929: 500) supposed that *M. aphanistus* was “probably” the type species of the genus, but this cannot be considered as a clear designation.

Machairodus aphanistus (Kaup, 1832)
(Figs 7D-N, 8; Tables 9, 10, 11)

REFERRED MATERIAL FROM KÜÇÜKÇEKMECE. — Çukurçesme Quarry unnumbered, fragment of right m1; IU 01, distal half of a left humerus; MNHN.F.TRQ700, proximal fragment of proximal phalanx; TRQ694, fragment of right Mt III; TRQ1213, right m1; TRQ1214, right p4; TRQ1215, right P4. The two last specimens present the same colour and wear pattern and might belong to the same individual.



FIG. 8. — Distal fragment of right humerus (IU unnumbered) of *Machairodus aphanistus* (Kaup, 1832) in anterior (A) and posterior (B) views. Scale bar: 20 mm.

DESCRIPTION

Dentition

Lower dentition (Fig. 7D-G). The p4 (Fig. 7D-E) is very well preserved and nearly unworn. In occlusal view the crown forms roughly an elongated rectangular. The main cuspid is sharp, with a convex distal crest and a nearly rectilinear mesial crest. In labial view it is oriented somewhat distally relative to the crown-root junction. The accessory cuspids are large and sharp, the mesial cuspid being slightly larger than the distal cuspid. Both are separated from the main cuspid by deep notches. The distal cingulid is marked but short and extended lingually rather than labially. The crown of m1 (MNHN.F.TRQ1213, Fig. 7F-G; Çukurçesme unnumbered) and the mesial root (Çukurçesme unnumbered) are preserved. In both specimens it is heavily worn labially along the paraconid and protoconid crests at the level of the carnassial notch and on the distolabial face of the protoconid. The protoconid is taller and longer than the paraconid. In TRQ1213 there is no metaconid distinct from the talonid. The latter appears very short and sharp, and separated from the distal rim of the protoconid by a deep notch.

Upper dentition (Fig. 7H-J). The P4 presents a similar size and wear pattern as the p4 MNHN.F.TRQ1214 and could belong the same individual. The paracone tip and the protocone are broken off. The labial cusps are narrow and trenchant. The metastyle/metacone blade and the paracone are approximately the same length. The notches that separate the metacone, paracone and parastyle are deep. The parastyle is very large and tall. There is a small ectoparastyle (or ectostyle) mesial to the parastyle.

TABLE 11. — Measurements (in mm) of *Machairodus aphanistus* from Küçükçekmece compared with specimens from European localities. Postcranium. Abbreviations: **Küçük.**, Küçükçekmece; **Ph**, phalanx; **Hum**, humerus; **Dg.**, digit; **epi**, epiphysis; **art**, distal articulation; **prox**, proximal; **dist**, distal; **ML**, mediolateral; **AP**, anteroposterior; **T**, thickness; ¹, from Madurell-Malapeira *et al.* (2014); ², from Beaumont (1988); ³, from Salesa *et al.* (2012b); ⁴, from Roussiakis (2002). Material labelled '**PIK**' and '**MAR**' are from the MNHN. See Material and methods for additional abbreviations.

<i>Machairodus aphanistus</i> (Kaup, 1832)													
		Küçük.	Vallès-Penedès (IPS-) ¹						Montredon ²				
		MNHN.F. TRQ700	36058	15007	15015	15021	15022	13173	FSL 210191	FSL 210196	FSL 210172		
Ph	prox ML W	21.5	18.7	19.2	20.6	20.4	17.8	–	–	–	22est		
	prox AP T	17	14.7	12.8	13.9	13.9	12.9	–	–	–	–		
Hum	dist epi ML W	88.3	–	–	–	–	–	–	77est	–	–		
	dist art ML W	58.6	–	–	–	–	–	–	–	–	–		
MtIII	prox ML W	25.4	–	–	–	–	–	25.7	–	22.5est	–		
<i>Amphimachairodus giganteus</i> (Wagner, 1848)													
		Las Casiones (FCPT) ³			Pikermi (AMPG PG from ⁴ ; PIK from MNHN.F.)						Maragheh		
		K-504	K-505	K-506	AMPG PG 98/26	AMPG PG 2799/91	AMPG PG 3552/91	PIK 3358	PIK2973			MNHN.F. MAR3422	MNHN.F. MAR3410
									Dg. III	Dg. IV	Dg. V		
Ph	prox ML W	18.98	17.47	18.65	–	–	–	–	22.9	21.9	21.9	19est	–
	prox AP T	15.15	15.07	16.51	–	–	–	–	–	–	–	–	–
Hum	dist epi ML W	–	–	–	83.8	79.4	78.7	98.8	–	–	–	92	–
	dist art ML W	–	–	–	59.6	57.4	58.9	68	–	–	–	58	–
MtIII	prox ML W	–	–	–	–	–	–	–	–	–	–	–	–

TABLE 12. — Measurements (in mm) of *Pristifelis* sp. cf. *P. attica* from Küçükçekmece compared with late Miocene small felines from Europe. Symbols: *, type material; **, lectotype of '*Pseudaelurus*' *transitorius* Depéret, 1892. Abbreviations: **Küçük.**, Küçükçekmece; ¹, from Beaumont (1961); ², from Roussiakis (2002); ³, from Salesa *et al.* (2012b); ⁴, from Salesa *et al.* (2012a); ⁵, from Viranta & Werdelin (2003). See Material and methods for additional abbreviations.

		<i>Pristifelis</i> sp.	<i>Pristifelis attica</i> (Wagner, 1857)					<i>Styriofelis vallesiensis</i> Salesa, Antón, Morales & Peigné, 2012							<i>Styriofelis turnauensis</i> (Hoernes, 1882)						
		Küçük.	Pikermi			Las Casiones ³	Sam- os ¹	Batallones (BAT-/B-) ⁴					La Grive (MHNL LGr & BSP)					Sinap			
			BSP A 511.	AMPG PG	AMPG PG		MGL	1'03 D4-	1'02 D6-	1'01 D6-	2074 (45)	3319 left	1383**	1382	1205	1937- II-	1937- II-	MACA			
		KÇ 61	116* ¹	01/107 ²	01/108 ²	mean	482S	D6-37	265	57	65					13336	13328	S.89.1 ⁵			
p3	L	6.3	7.1	7.1	–	7.05	8	6.52	6.74	6.02	6.26	6.48	6.19	6.5	–	6.9	7.2	7	6.7		
	W	3.2	4.1	3.4	–	3.52	4	2.87	3.16	2.8	2.82	3.03	3.02	3.2	–	3.3	3.3	3.5	3.8		
	H	4.3			–	–	–	4.2	4.54	4.27	4.31	4.78	4.55	4	–	4.2	–	–	–		
p4	L	8.2	9.2	8.3	–	9.37	9.8	7.63	8.46	7.37	7.36	7.91	7.69	8.8	8.6	8.6	9	–	9.2		
	W	3.9	4.2	3.8	4est	3.98	4.2	3.66	3.85	3.22	3.29	3.44	3.58	4.4	4.1	4.3	4	–	4.4		
	H	5.3	–	–	–	–	–	5.33	5.41	4.91	5.23	5.29	5.29	5.8	5.8	6.1	–	–	–		
m1	L	9.3	11	10.2	10.3	10.3	11.1	9.39	10.48	9.41	9.28	9.38	9.46	11	10.5	11.4	11	–	11.2		
	H	3.9	5	4.3	4.3	4.43	4.4	3.94	4.12	3.94	3.93	3.96	4.06	4.9	4.9	5	4.7	–	4.8		
HPm1		5.3	–	–	–	–	–	–	5.67	5.74	5.44	5.51	5.82	7.5	6.6	6.8	–	–	–		
DMp4-m1		13	–	12.4	12.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–		

Postcranium (Figs 7K–N, 8)

Three postcranial specimens are assigned to *M. aphanistus*. IU 01 is a fragment of left humerus broken across the mid-diaphysis (Fig. 8). The shaft and the olecranon fossa are also damaged. The maximum width of the distal epiphysis is 88.3 mm and the maximum width of the articulation is 58.6 mm. The anteroposterior diameter of the medial part is 44.4 mm, while that of the lateral part is 49.5 mm. The overall morphology of this specimen is similar to that of specimens assigned to *Amphimachairodus giganteus* (Wagner, 1848) from Maragheh (MN11, Iran) and Pikermi that were used in comparison

(MNHN.F.PIK3358 and PIK3361, MNHN.F.MAR3410 and specimens figured in Roussiakis 2002) and to that of published material related to *M. aphanistus* from the Vallès-Penedès Basin (Madurell-Malapeira *et al.* 2014) and Montredon (Beaumont 1988: pl. 4, fig. 10). Our specimen is a little bit more robust, especially compared to the specimen from Pikermi figured by Roussiakis (2002: fig. 12-1). The medial epicondyle is medially and proximodistally more extended than in the specimen from Montredon (*M. cf. aphanistus*), but not especially more than in the compared specimens of *A. giganteus* that display great morphological variability regarding this feature.

MNHN.F.TRQ700 (Fig. 7M, N) is a proximal fragment of a proximal phalanx with a proximal mediolateral width of 21.5 mm and a proximal dorsoventral height of 17 mm. The phalanx is robust, with a dorsoventrally compressed shaft and a slightly asymmetrical proximal articulation. It is very similar to the proximal phalanges of the associated forelimb of *A. giganteus* MNHN.F.PIK3241 from Pikermi (see Table 11). The fragmentary Mt III (Fig. 7K, L) lacks the distal epiphysis and the ventral part of the proximal articular surface. The proximal width of the head is 25.4 mm. The fragment is approximately 110 mm long. In lateral view the diaphysis is curved dorsally.

COMPARISONS AND DISCUSSION

Machairodus aphanistus is a relatively common Vallesian-early Turolian (MN9-MN11) species of Europe, where it is known from a number of localities in Germany, Spain, France, Austria, Switzerland, Bulgaria, Hungary and Turkey (see Madurell-Malapeira *et al.* 2014). In Turkey, remains of the species are rare, however, and is known only from Kemiklitepe D (MN11) and Mahmutgazi (MN11). The dental material described here represents at least 3 individuals: two are represented by the m1 (MNHN.F.TRQ1213 and Çukurçesme unnumbered), and the third individual is documented by TRQ1214, a p4, and TRQ1215, a P4. The two first individuals are rather small and about the size of early Vallesian (MN9) specimens such as those from Los Valles de Fuentidueña (including specimens assigned to *M. alberdiae* Ginsburg *et al.*, 1981, a junior synonym of *M. aphanistus*; see Peigné *et al.* 2005), Höwenegg, and Can Llobateres (Table 9). The third individual is of average size for the species, with dental lengths within the range of populations such as that from Batallones (MN10, Spain; Monesillo *et al.* 2014; Tables 9, 10). I consider that the material from Küçükçekmece belongs to a single species displaying a large size variability that could be related to sexual dimorphism. *Machairodus aphanistus* was one of the most dimorphic known felids, together with the extant *Panthera leo* (Linnaeus, 1758) and *Panthera pardus* (Linnaeus, 1758) (Monesillo *et al.* 2014). Morphologically, the material from Küçükçekmece does not differ from that of the other sites where the species is known, especially the large sample from Batallones (Antón *et al.* 2004; Monesillo *et al.* 2014).

The fragmentary postcranial remains belong to different individuals also. The measurements of the humerus are within the range of those of the humerus of extant *P. leo* and *P. tigris* (Peigné *et al.* 2005: table 2), of *Amphimachairodus giganteus* from Pikermi and Maragheh (Table 11), and of *M. aphanistus* from Montredon and the Vallès-Penedès Basin. The mediolateral width of the proximal articulation of the Mt III and the size and proportions of the proximal phalanx are within the size range of specimens of *Machairodus aphanistus* and *Amphimachairodus giganteus* (Table 11). Specimens MNHN.F.PIK3278, PIK3279, PIK3280, PIK3240 and PIK3244 from Pikermi, described as metatarsals by Özkurt *et al.* (2015), are all metacarpals and therefore not comparable to the material from Küçükçekmece.

Genus *Pristifelis* Salesa, Antón, Morales & Peigné, 2012

TYPE SPECIES. — *Pristifelis attica* (Wagner, 1857) by original designation.

Pristifelis sp. cf. *P. attica* (Wagner, 1857)
(Fig. 9A, B; Table 12)

REFERRED MATERIAL FROM KÜÇÜKÇEKMECE. — KÇ 61, right hemimandible with p2-m1.

DESCRIPTION

Mandible (Fig. 9A, B; Table 12)

The dentary is broken across the middle of the masseteric fossa. The postcanine diastema is long (7 mm) and dorsally concave. There are two mental foramina, one large at the mid-length of the diastema and a smaller one beneath p3. The anterior rim of the masseteric fossa is at the level of the distal border of the m1.

Dentition (Fig. 9A, B; Table 12)

There is no premolar between the canine and p3. The p3 is short and low compared to p4. It has no mesial cuspid and a small distal accessory cuspid. The distal cingulid is long and extended lingually and labially. The tooth is much wider distally than mesially. There is a tiny diastema between p3 and p4. The p4 is taller than the m1 paraconid and of the same height as the m1 protoconid. The main cuspid has a straight mesial rim and a markedly convex distal rim. Accessory cuspids are large and similar in size. The distal accessory cuspid is located labially in the crown. It is separated from the main cuspid by a deep notch and its distal rim is vertical. The distal cingulid is more expanded than in p3. The carnassial is elongated and low compared to p4. Its paraconid is lower than the protoconid and approximately of the same length. The blade of these two cuspids forms an obtuse angle in labial view. The distal face of the protoconid is vertical. The talonid is short and the metaconid is not individualized.

COMPARISONS AND DISCUSSION

Late Miocene small-sized Felinae are not abundant in Europe. Two species are recognized in MN10-MN13 strata: *Styriofelis vallesiensis* from Batallones-1, Batallones-3 (type locality) in Spain and Maragheh in Iran, and *Pristifelis attica* from Pikermi (type locality), Samos, and, possibly, Vathyakkos-3 in Greece, Akkasdağı in Turkey and Las Casiones in Spain (Roussiakis 2002; Bonis 2005; Salesa *et al.* 2012a, b). Additional late Miocene similar-sized felines are Felinae indet. from Las Casiones (Salesa *et al.* 2012b) and the feline from Dorn-Dürkheim assigned to *P. attica* by Morlo (1997) but showing a distinct metaconid suggesting a different species (according to Roussiakis 2002: 714), such as *S. vallesiensis*.

The derived characters that support the assignment of the hemimandible from Küçükçekmece to *Pristifelis* sp. cf. *P. attica* are the absence of premolars anterior to p3 and a distally wide p3 lacking a mesial cuspid. The first character distinguishes the specimen from Küçükçekmece from *Styriofelis vallesiensis* (and

TABLE 13. — Measurements (in mm) of Felidae gen. et sp. indet. medium size from Küçükçekmece compared with late Miocene medium-sized felids from Europe. Abbreviations: **prox**, proximal; **dist**, distal; **ML**, mediolateral; **AP**, anteroposterior; **T**, thickness; ¹, from Salesa (2002); ², from Roussiakis *et al.* (2006). See Material and methods for additional abbreviations.

	<i>Promegantereon ogygia</i> (Kaup, 1832)			<i>Metailurus parvulus</i> (Hensel, 1862)	
	Küçükçekmece MNHN.F.TRQ701	Batallones (range) ¹		Kerassia (range) ²	
		Digit III & IV manus (range)	Digit III & IV pes	manus	pes
L	32.4	30.7-37.48	31.33-35.34	17.4-31.9	27.2-33.7
prox ML W	11.7	11.7-14.55	11.7-19.66	9.9-11.5	9.6-12.9
prox AP T	9.1	9.32-11.29	9.41-11.91	8.1-9.2	8.7-9.9
dist ML W	8.7	9.28-10.95	9-11.3	7.2-9	7.9-9.9

from the other species assigned to *Styriofelis*). The development of the mesial cuspid on the p3 is highly variable, especially in *P. attica* (Roussiakis 2002; Salesa *et al.* 2012b), but in KÇ 61 this tooth lacks a mesial cuspid and is wider distally than in the contemporaneous *S. vallesiensis*. The Turkish specimen differs from the Turolian *P. attica* (i.e. specimens included in the comparison: see Table 12) in having a less reduced talonid and in being smaller in size; it is, however, from a site that is several million years older.

Felidae gen. et sp. indet. medium size
(Fig. 9C, D; Table 13)

REFERRED MATERIAL FROM KÜÇÜKÇEKMECE. — MNHN.F.TRQ701, proximal phalanx.

DESCRIPTION

The phalanx (Fig. 9C, D) is relatively long (Table 13). It is relatively slender with a dorsoventrally compressed proximal articulation and a distal epiphysis that is narrower than the proximal one (Table 13).

COMPARISONS AND DISCUSSION

The length of MNHN.F.TRQ701 is much greater than the proximal phalanges of the known small felines from the late Miocene of Europe. On the other hand this phalanx fits with the size range of the proximal phalanges of species such as *Promegantereon ogygia* (Salesa 2002) or *Metailurus parvulus* (Hensel, 1862) (Roussiakis *et al.* 2006; for a discussion of the taxonomic status of this species, see also Spassov & Geraads 2015), although not for all measurements. In previous faunal lists of Küçükçekmece, *Paramachairodus orientalis* (Kittl, 1887), or *Machairodus orientalis* Kittl, 1887, was mentioned by Malik & Nafiz (1933) and Yalçınlar (1954) and *Machairodus* (*Paramachairodus*) *orientalis* by Ozansoy (1957). One of the specimens assigned to this species was figured by Malik & Nafiz (1933: pl. 12, fig. 7); the only descriptive information is the length of P3 (12 mm) and of the diastema between the canine and P3 (5 mm). Unfortunately this specimen was not recovered and was certainly destroyed by fire (see Sen 2016).

MNHN.F.TRQ701 described here and the specimen figured by Malik & Nafiz (see above) both support the presence of a third, medium-sized felid at Küçükçekmece. Both the size and the morphology of this felid exclude an assignment to either *Mach-*

airodus aphanistus or *Pristifelis* sp. cf. *P. attica* already identified from the site. In contrast, the size of the phalanx TRQ701 and/or that of the P3 figured by Malik & Nafiz (1933) fits well with that of the same elements in late Miocene felids such as *Paramachairodus orientalis*, *Promegantereon ogygia*, *Metailurus parvulus* and ‘*Felis pamiri*’ Ozansoy, 1965 from Yassören. Compared to these species, however, the P3 of the specimen figured by Malik & Nafiz (1933) is taller relative to its length. The phalanx is not diagnostic at the genus level.

DISCUSSION

The 1942 fire at the Geological Institute of Istanbul University destroyed most of the fossil specimens described by Malik & Nafiz (1933). Among Carnivora, this occurred for specimens assigned to *Mustela pentelici* and a (more or less important) part of the material assigned to the Phocidae, *Indarctos arctoides*, cf. *Thalassictis* sp. and Felidae gen. et sp. indet. medium size.

Nevertheless my study of the few specimens still stored at the ITU and IU and at the MNHN allows identification of 9 taxa of Carnivora at Küçükçekmece: the ursid *Indarctos arctoides*, the mustelid *Sivaonyx hessicus*, the phocids *Cryptophoca* sp. and Phocidae gen. et sp. indet., the percrocudid *Dinocrocuta senyureki*, the hyaenid cf. *Thalassictis* sp. and the felids *Machairodus aphanistus*, *Pristifelis* sp. cf. *P. attica*, and Felidae gen. et sp. indet. medium size. It is highly probable that a tenth species close to *Mustela pentelici* was present, but it is known today only from illustrations (Malik & Nafiz 1933: pl. 12, fig. 3). As a consequence, my work was mostly based on fossils found by Nicolas (1978) and stored at the MNHN. It is not surprising to find similarities between my faunal list and that which Nicolas proposed, though he did not provide any description nor illustration to support his assignments. Nicolas (1978) mentioned *Sivaonyx hessicus*, *Percrocuta senyureki*, *Indarctos arctoides* and *Machairodus aphanistus*. Except for the generic assignment of the percrocudid, I confirm the presence of these species (but *Sivaonyx hessicus* is based, in my study, on a single specimen stored at the ITU, not at the MNHN). However, contrasting with Nicolas’ faunal list, I did not find any evidence supporting the presence of *Lutra pontica*, *Ictitherium* sp. cf. *I. orbigny*, *Felis* sp. aff. *F. prisca* and indeterminate viverrids at Küçükçekmece. The faunal list of Nicolas also included two phocids, *Cryptophoca maeotica* and *Praepusa vindobonensis* (= *Phoca vindobonensis*). The material stored at the MNHN is probably not diagnostic at the species level, but I agree that it represents at least two species. One is probably close to *Cryp-*

tophoca maeotica, the other remains undetermined, as Phocidae gen. et sp. indet.

Considering the limited material available to me, the fauna from Küçükçekmece is relatively rich. Taxa are not equally documented though. Five species are known from a single specimen: *Indarctos arctoides*, *Sivaonyx hessicus*, cf. *Thalassictis* sp., *Pristifelis* sp. cf. *P. attica* and Felidae gen. et sp. indet. medium size. In contrast, the majority of the fossils (18 of the 34 specimens) belong to the family Phocidae. The sample from Küçükçekmece in fact represents the only published description of this family in the Neogene of Turkey. Isolated finds are mentioned by Koretsky & Rahmat (2013: 328) without precision and by Ozansoy (1957) from the sites of Ramiz and Osmaniye; *Phoca pontica* is mentioned but not described from Çanakkale (= Erenkoj; Ozansoy 1957).

Overall, the carnivoran fauna from Küçükçekmece indicates a late Miocene age for the locality. Many of the taxa have a range extending over several MN-zones. Thus, *Indarctos arctoides*, *Dinocrocuta senyureki* and *Machairodus aphanistus* are known from MN9 to MN11. One species, *Sivaonyx hessicus*, was previously known only from early Vallesian strata (MN9). The indeterminate species cf. *Thalassictis* sp. and *Pristifelis* sp. cf. *P. attica* show derived features that are more consistent with a late Vallesian or Turolian age (MN10-MN12). The phocid *Cryptophoca* sp. is related to a species that has a wide stratigraphic range (late Astaracian-early Turolian; Koretsky 2001: fig. 63).

The site Küçükçekmece has yielded a surprisingly rich fossil fauna of Carnivora. It is unusual in representing one of the rare fossil Miocene assemblages that include both marine and terrestrial taxa. Among the taxa identified, less than half can be assigned to species. The others are documented by too fragmentary remains. Unfortunately there is little chance to find more fossils at Küçükçekmece, which decades ago became a very dense urban area now part of the European part of Istanbul.

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Fig. 9. — **A, B**, *Pristifelis* sp. cf. *P. attica*: KÇ 61, right hemimandible with p2-m1 in labial (**A**) and occlusal (**B**) views. **C, D**, Felidae gen. et sp. indet. cf. *Paramachairodus orientalis*, MNHN.F.TRQ701, proximal phalanx in proximal (**C**) and anterior (**D**) views. Scale bar: 10 mm.

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