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The saber-toothed cat *Homotherium latidens* (Owen, 1846) from the lower Pleistocene locality Dafnero, Western Macedonia, Greece

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Memorial Stéphane Peigné – Carnivores of the Cenozoic –

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The saber-toothed cat *Homotherium latidens* (Owen, 1846) from the lower Pleistocene locality Dafnero, Western Macedonia, Greece

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This article is dedicated to the memory
of our good friend Stéphane Peigné

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ABSTRACT

The homotheres, although known from the Greek fossil record since the beginning of the 1930's, have only been recorded from fragmentary material, sometimes undescribed and with questionable determinations. In 2017, the discovery of an almost complete cranium and a fairly complete humerus of a machairodontine in Dafnero-3, a lower Pleistocene site from Western Macedonia (Greece), confirm the presence of homotheres in Greece. The Dafnero-3 material is described and compared with Eurasian specimens. We conclude that in morphology and size the Dafnero-3 specimen coincides with *Homotherium latidens* (Owen, 1846). The taxonomy, geographic and stratigraphic distribution of *Homotherium* Fabrini, 1890 is also discussed. A biostratigraphic revision gives the distribution of the genus in Greece. *Homotherium* is referred from six Greek localities and its distribution covers the time span from the early Villafranchian (early Villafranchian, locality Milia, Western Macedonia; MN16, 3.0-2.5 Ma) to the middle Pleistocene (locality Tourkovounia near Athens, *c.* 0.4 Ma).

KEY WORDS
Carnivora,
Machairodontinae,
Homotherium,
Early Pleistocene,
Greece.

RÉSUMÉ
Le félin à dents de sabre Homotherium latidens *(Owen, 1846) de la localité pléistocène inférieure de Dafnero, Macédoine occidentale, Grèce.*
Les homotherinés, bien que connus depuis 1930 dans le registre fossile grec, sont représentés par des restes fragmentaires, parfois non décrits, et dont l'attribution taxinomique reste incertaine. En 2017, la découverte d'un crâne quasi-complet et d'un humérus complet d'un félin machairodotiné sur le site du Pleistocène inférieur de Dafnero-3 en Macédoine occidentale (Grèce) confirme la présence des homothérinés en Grèce. Le matériel de Dafnero-3 est décrit et comparé avec les spécimens eurasiatiques. Nous concluons que la crâne de Dafnero-3 coïncide en taille avec et est semblable à *Homotherium latidens* (Owen, 1846). La taxonomie, la distribution géographique et stratigraphique sont également discutées. Une révision biostratigraphique renseigne la distribution du genre en Grèce. *Homotherium* Fabrini, 1890 est présent sur six localités réparties depuis le Pléistocène inférieur (Villafranchien ancien, localité de Milia, Macédoine occidental, MN16, 3.0-2.5 Ma) au Pléistocène moyen (localité de Tourkovounia, près Athènes, *c.* 0.4 Ma).

MOTS CLÉS
Carnivora,
Machairodontinae,
Homotherium,
Pleistocène inférieur,
Grèce.

INTRODUCTION

The studied carnivoran material originates from the lower Pleistocene locality Dafnero in the Grevena Basin (Western Macedonia, Greece). Dafnero is situated in one of the deep ravines cutting the eastern bank of Haliakmon River, near the homonymous village. Three fossiliferous sites have been recognized in this locality. Dafnero-1 (DFN), discovered in 1990, providing a quite rich mammalian fauna (Koufos *et al.* 1991; Koufos 2001). The other two fossiliferous sites, Dafnero-2 (DFN2) and Dafnero-3 (DFN3), were discovered in 2010 during a new series of excavations in the area carried out by the Laboratory of Geology and Paleontology of the Aristotle University of Thessaloniki, Greece (LGPUT) and the Laboratoire Paléontologie, Evolution Paléoécosystémes, Paléoprimatologie, Université de Poitiers, France (PALEVOPRIM, CNRS-INEE) and continuing up to the present time. The fossiliferous sites are located near the base of a thick series (*c.* 60 m) of fluvio-terrestrial deposits, unconformably overlying the molassic palustrial sediments of the Tsotylion Formation in the Mesohellenic trough (Fountoulis *et al.* 2001 and references therein). The fossiliferous sites Dafnero-1 and Dafnero-3 belong to the same fossiliferous horizon, exposed on opposite slopes of an erosional crest. Biochronological evidence from Dafnero-1 and preliminary magnetochronology from Dafnero-3 suggest a middle Villafranchian age (post-Olduvai Matuyama Chron, between 2.5-2.0 Ma) (Koufos *et al.* 1991; Koufos & Kostopoulos 2016; Kostopoulos *et al.* 2018, 2019).

The fossiliferous site Dafnero-1 (DFN) has yielded a fauna including the taxa *Paradolichopithecus* aff. *arvernensis*, *Ursus etruscus* Cuvier, 1823*, Nyctereutes megamastoides* (Pomel, 1842), *Vulpes alopecoides* (Major, 1875), *Chasmaporthetes lunensis* (Del Campana, 1914), *Baranogale* aff. *B. helbingi* Kormos, 1934, *Equus stenonis vireti* Prat, 1964, *Palaeotragus inexpectatus* (Samson & Radulesco, 1966), *Eucladoceros ctenoides* (Nesti, 1841), *Metacervoceros rhenanus* (Dubois, 1904), *Gazellospira torticornis* (Aymard, 1854), *Gallogoral meneghinii* Guérin, 1965, *Gazella bouvrainae* Kostopoulos & Athanassiou, 1997*,* and Antilopinae indet. (Koufos & Kostopoulos 1997; Koufos 2001; Kostopoulos & Athanassiou 2005). To date, the fossiliferous site Dafnero-3 has yielded several mammalian fossils, which indicate a rich fauna. During the field trip of 2017 the cranium and humerus of a machairodontine were unearthed and they are described in this article. As Villafranchian machairodonts are rarely known in Greece, this cranium is very interesting and will offer a better understanding of this mammalian group in the eastern Mediterranean region.

MATERIAL AND METHODS

The studied material is stored in the LGPUT. The measurements were taken with digital caliper and are given in mm with an accuracy of 0.1 mm. The software PAST (Hammer *et al.* 2001) has been used for the diagrams.

ABBREVIATIONS

DFN	Dafnero-1;
DFN2	Dafnero-2;
DFN3	Dafnero-3;
FSL	Collections de Géologie de la Faculté des Sciences de l'Université de Lyon;
LGPUT	Laboratory of Geology and Paleontology of the Aristotle University of Thessaloniki;
MNHN.F	Muséum national d'Histoire naturelle, Paris, Palaeontology collections;
PALEVOPRIM, CNRS-INEE	Laboratoire de Paléontologie, Évolution Paléoécosystémes et Paléoprimatologie, Université de Poitiers.

SYSTEMATIC PALAEONTOLOGY

Order CARNIVORA Bowdich, 1821
Family FELIDAE (Fischer von Waldheim, 1817)
Subfamily MACHAIRODONTINAE Gill, 1872

Genus *Homotherium* Fabrini, 1890

Homotherium Fabrini, 1890: 161.

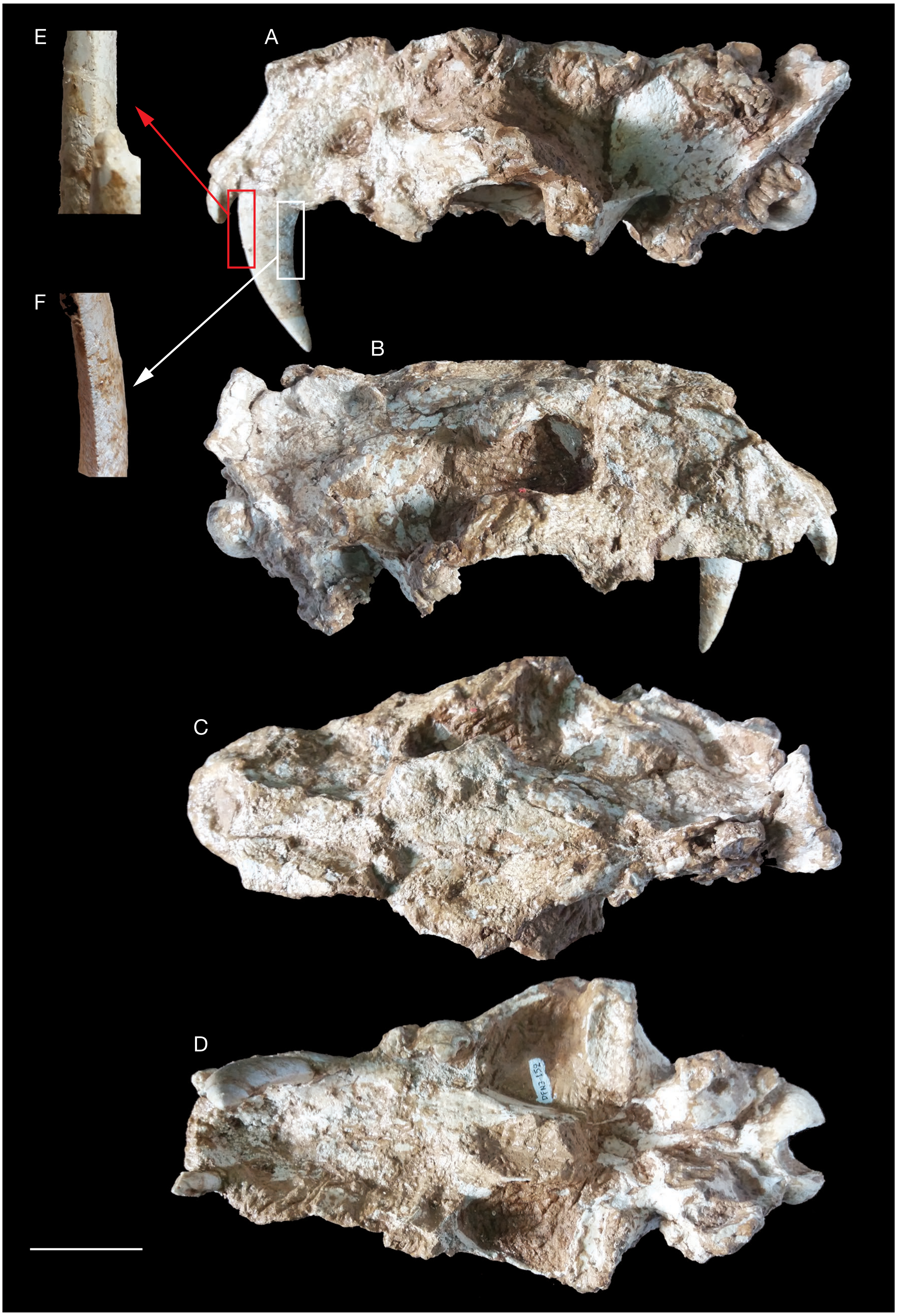

Fig. 1. — *Homotherium latidens* (Owen, 1846), Dafnero 3, Macedonia Greece, middle Villafranchian, cranium DFN3-152, in: **A**, left lateral; **B**, right lateral; **C**, dorsal; **D**, ventral; **E**, detailed canine views. Scale bar: 5 cm.

Table 1. — Cranial measurements of *Homotherium latidens* (Owen, 1846) from various Eurasian localities. Data sources: Theilhard de Chardin (1936), Ballesio (1963), Bonis (1976) and Galobart *et al.* (2003). *****, measurements taken from the casts.

	Dafnero	**Incarcal**			**Senèze**	**Perrier**	
Cranium	**DFN3-152**	**IN- I-929**	**IN- I-825**	**IN- II-37**	**FSL 210-991**	**MNHN.F. PET2000a**	**China**
1. Basal length (Bashion-Prosthion)	251.5	305.0	287.0	260.0	275.0	300.0	234.0
2. Maximal breadth at the zygomatic arches	?140	?175	195.0	?170	?185	200.0	141.0
3. Vertical diameter of the infraorbital foramen	19.1	21.3	20.0	16.0	14.0	16.0*	–
4. Transverse diameter of the infraorbital foramen	27.1	11.3	9.1	7.0	12.0	11.0*	–
5. Height of the nasal cavity	40	42.7	47.0	–	44.0	40.0*	–
6. Breadth of the nasal cavity	45	40.5	37.9	51.0	40.0	50.0*	–
7. Maximal distance of the occipital condyles	?52.6	60.4	64.5	–	61.0	70.2*	53.0
8. Maximal height of the occipital condyles	30.5	32.4	30	–	30.0	33.9*	–
9. Palatal breadth at the level of the canines	55.3	–	54.3	42.4	44.0*	49.0*	–
10. Idem at the level of the carnassials	84.9	–	95.6	?82	93.0*	97.8*	–
11. Diastema C-P3	16.0	22	?17	5.0	17.0*	23.1*	–

Fig. 2. — *Homotherium latidens* (Owen, 1846), Dafnero 3, Macedonia Greece, middle Villafranchian, humerus DFN3-153 in: **A**, anterior; **B**, posterior; **C**, lateral; **D**, medial views. Scale bar: 5 cm.

Homotherium latidens (Owen, 1846)

Machairodus latidens Owen, 1846: 179.

Homotherium latidens – Galobart *et al.* 2003: 99-141.

Holotype. — The upper canine described and figured as *Machairodus latidens* by Owen (1846: fig. 69). In total there are five upper canines and two I3 from Kent's Cave; the holotype, numbered 443/103 in the Museum of the Royal College of Surgeons, is that described by Owen, but it was destroyed during bombing in 1941 (Barnett 2014).

Type locality. — Kent's Hole, Torquay, England.

Locality. — Dafnero-3, DFN3, Grevena Basin, Western Macedonia, Greece.

Age. — Early Pleistocene (middle Villafranchian); 2.5-2.0 Ma.

Material. — Cranium, DFN3-152; left humerus, DFN3-153.

Measurements (in mm). — The measurements of the cranium and humerus are given in Tables 1 and 2. The dental measurements are: I3 dex = 12.1 × 11.3; I3 sin = 12.5 × –; C = 24.8 × 11.9; P4 = 36.2 × –.

Description

Cranium

The cranium DFN3-152 is dorsoventrally compressed, deformed and damaged in the occipital region (Fig. 1). The dentition preserves both I3, the left canine and part of the left carnassial. The worn incisors and carnassial indicate an old individual. The premaxillae are well developed and projected rostrally to protrude the large incisors. The incisor row is semicircular as in the Senèze (France) cranium FSL-210 991 (Ballesio 1963: fig. 11d) and the Incarcal (Spain) crania IN-I-929 and IN-II-37 (Galobart *et al.* 2003: figs 3, 4). The incisor row of the Perrier cranium of *Homotherium* (MNHN.F.PET2000) is less convex than that of DFN3-152, while that of IN-I- 825 from Incarcal is straight (Bonis 1976; fig. 3; Galobart *et al.* 2003: fig. 1). Between the canine and I3 of DFN3-152, there is a short diastema (4.3 mm) as in the Senèze (FSL-210 991; 9.0 mm), (Ballesio 1963) and Perrier crania (7.7mm; MNHN.F.PET2001). In the Incarcal crania the diastema varies greatly; it is long in IN-I929 and absent in IN-I-825 and IN-II-37 (Galobart *et al.* 2003). A large diastema (16.0 mm) also exists between the canine and the P3 in DFN3-152, as in the Senèze cranium and the Incarcal crania IN- I-1929 and IN-I-825 (Table 1).

The maxillary bones are relatively small and have a swelling that corresponds to the strong root of the upper canine. The nasals are rectangular, like in all machairodontines; their posterior margin is almost straight and their suture with the frontals is a straight line, which coincides with the line connecting the anterior margins of the orbits. This feature is clear in the Senèze and Perrier crania (Ballesio 1963: fig. 11d; Bonis 1976: fig. 9a). The nasal cavity is large, sub- rectangular and higher than wide; the index height/breadth of the nasal cavity is 89, versus 91 for the Senèze and 81-95 for the Incarcal crania (Galobart *et al.* 2003).

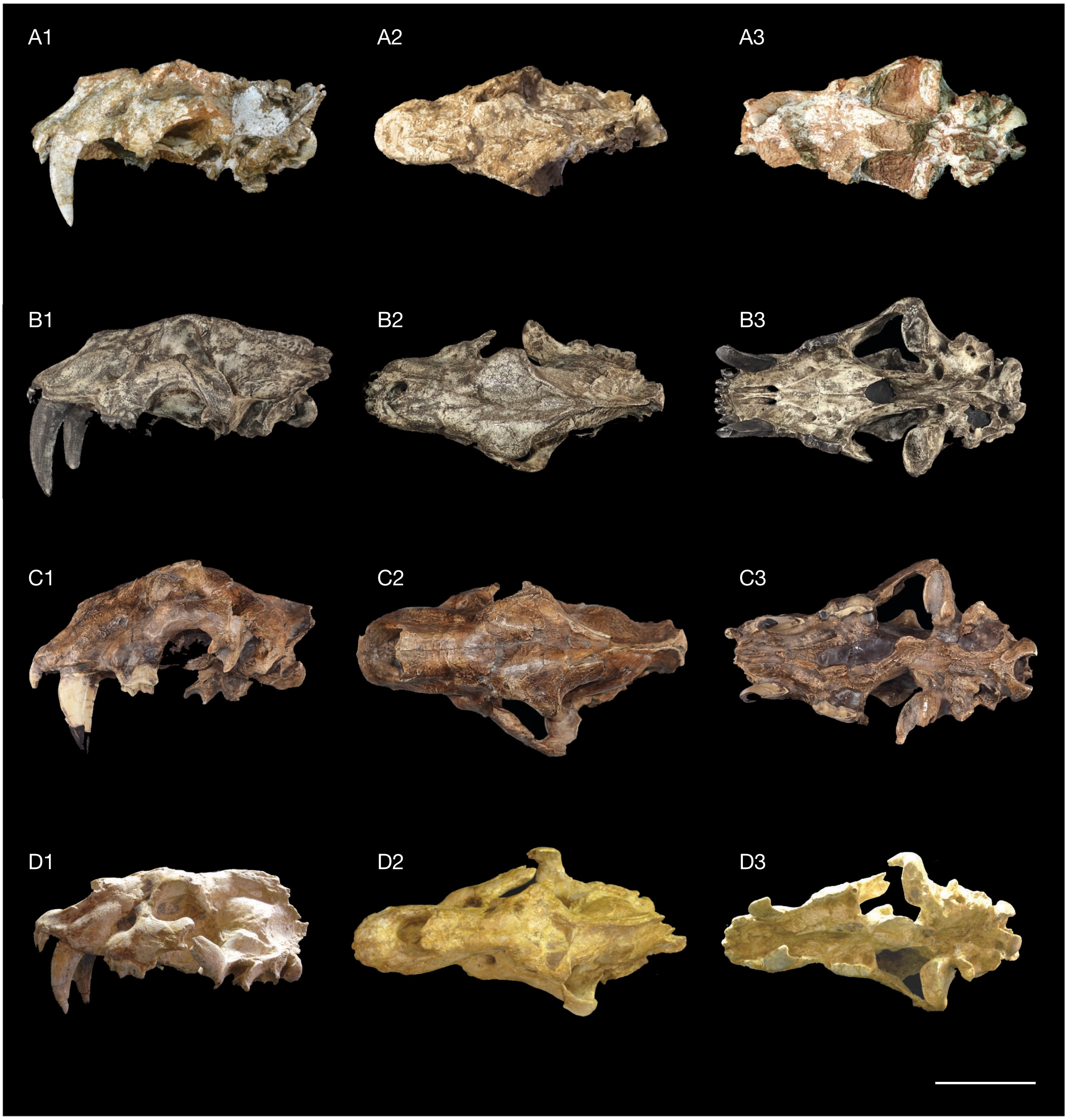

FIG. 3. — Comparison of the crania of *Homotherium latidens* (Owen, 1846): **A**, DFN3-152 from Dafnero-3; **B**, MNHN.F.PET2000 (cast); **C**, Perrier (France), Senèze (France), FSL-210 991 (cast); **D**, IN-I 929 from Incarcal (Spain). Views: **1**, lateral; **2**, dorsal; **3**, ventral. Scale bar: *c.* 10 cm.

The right orbit is better preserved and not deformed; it is rounded, with its anterior margin above the distal end of the carnassial. The infraorbital foramen is very large (Fig. 1A; Table 1). Its anterior margin is situated above the mesial part of the P3, while the posterior margin is above the parastyle of the carnassial. The zygomatic arches are small, relatively low and close to the braincase, starting just behind the distal end of the carnassial and directed slightly externally to connect with the glenoid fossa. The frontals are compressed and deformed; however, the groove between them and its continuity with the nasals is clearly distinguished. The sagittal crest is poorly preserved but based on its remnants seems to be thick and high. Although the development of the sagittal crest varies in the known material of *Homotherium* as a result of sexual dimorphism (Galobart *et al.* 2003), it is impossible to determine the sex of DFN3-152.

The palate is elongated, wide and bears two strong crests running mesio-distally (Fig. 1D). The choanae are poorly

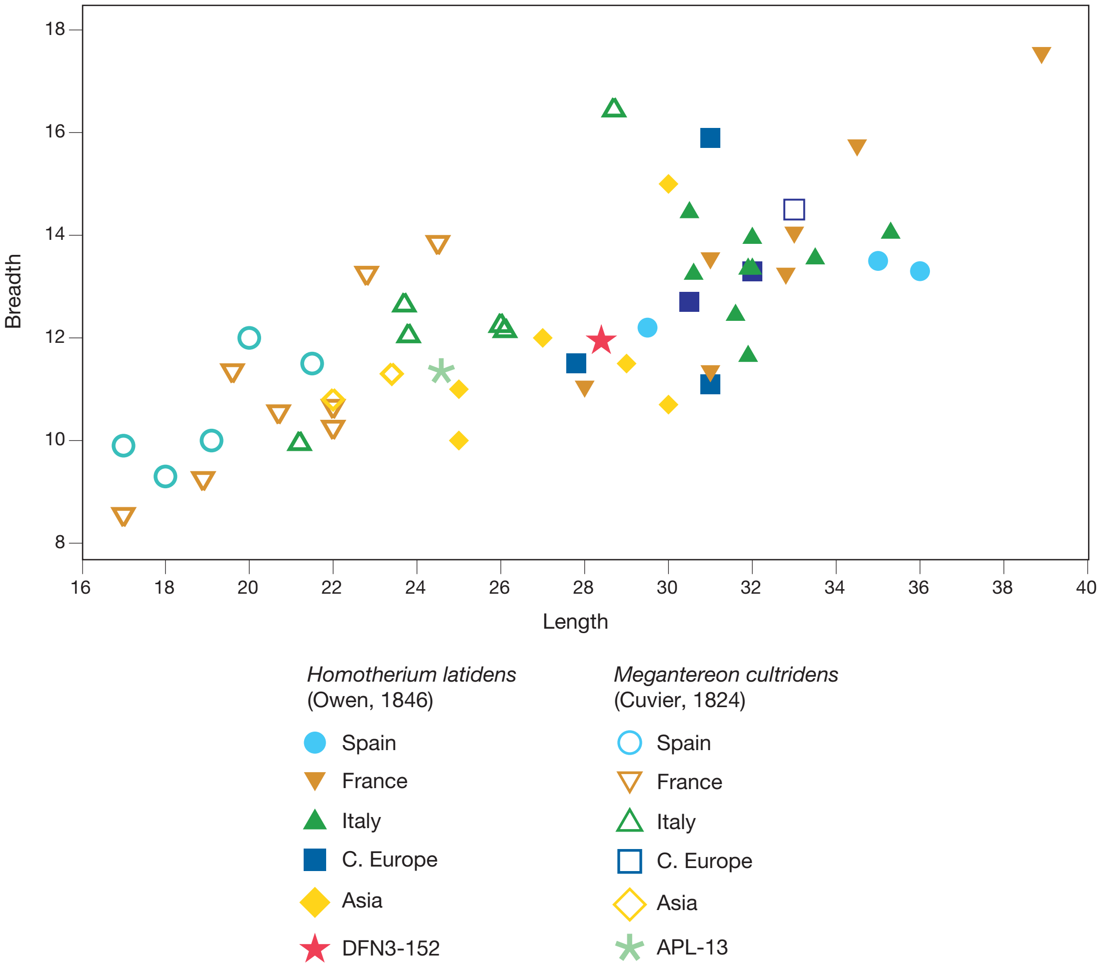

FIG. 4. — Scatter diagram comparing the upper canine dimensions of *Homotherium* Fabrini, 1890 and *Megantereon* Croizet & Jobert, 1828 from various Eurasian localities. Data sources: Bonis (1976), Koufos (1992), Galobart *et al.* (2003), Palmqvist *et al.* (2007) and Sardella & Iurino (2012).

preserved, deep and their anterior margin is situated behind the distal end of the carnassials. The mandibular fossa is long, with strong retroarticular process. The retroarticular foramen is situated in a large and deep fossa between the mandibular fossa and the tympanic bulla. The right part of the occipital is well preserved, having a rounded shape with strong nuchal and external occipital crests; the distal margin of the occipital bone does not exceed the level of the occipital condyles.

Dentition

The third incisors are worn and partially broken (Fig. 1D). They are large, canine-like, slightly inclined distally, with almost rounded occlusal outline, and bear a small lingual cusp. The canine is well preserved, long, narrow, sharp, inclined distally, like a double-edged knife. Although the wear is advanced, clear serration can be distinguished on its mesial and distal borders, like in *Homotherium* (Fig. 1E, F). The canine is strongly compressed laterally; the breadth/length index is 42. The root is very strong and elongated, running parallel to the margin of the nasal cavity to the end of the nasal bone. There is no trace of the P2, while there is a clear alveolus for the P3; its dimensions are 10.5 × 5.1 mm. The P4 is damaged and only the paracone and the worn metacone are preserved. The carnassial is elongated and relatively narrow. Although it is damaged there is evidence of a pre-parastyle, and the paracone is strong and high. There is no apparent protocone but as the tooth is very worn the presence of a small one as in all *Homotherium*, but totally worn down, cannot be ruled out.

Humerus

The humerus DFN3-153 is complete but the epiphyses are badly preserved (Fig. 2). The articular surface of the humerus caput is flattened, as in *Homotherium* from Incarcal (Anton *et al.* 2005). The major tubercle is well developed, and the articular head is wide and projected, like in the Incarcal *Homotherium* material. The intertubercular groove is wide. The diaphysis is long and straight; the deltoid ridge is strong and is not projected laterally. The distal epiphysis is wide and bears a large trochlea, and the olecranon fossa is deep.

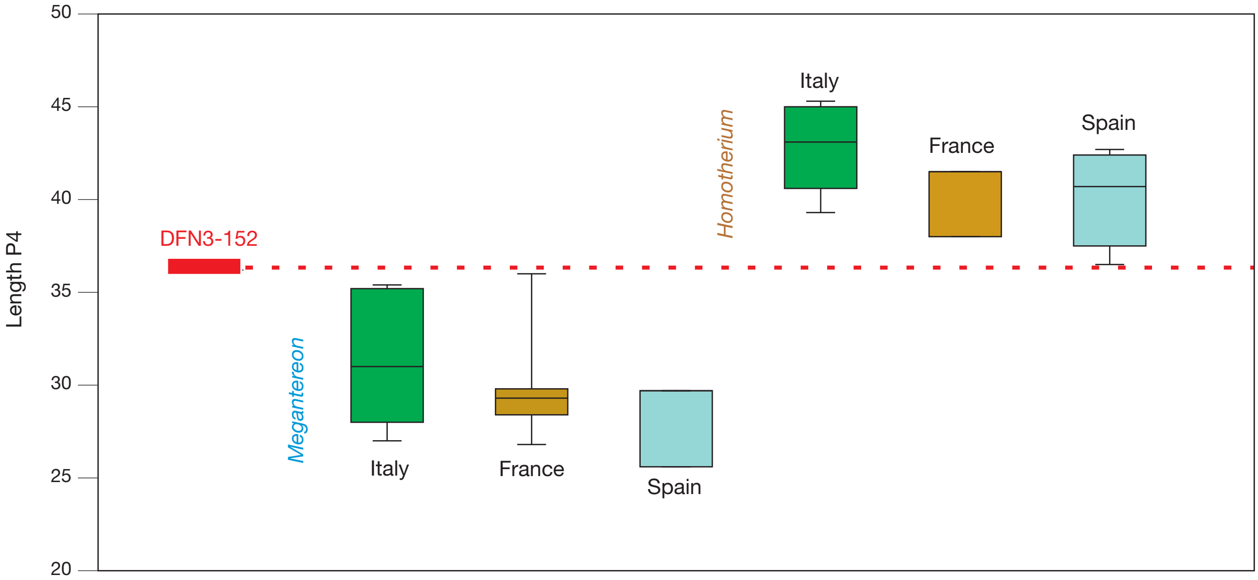

FIG. 5. — Box-plot diagram comparing the upper carnassial length of *Homotherium* Fabrini, 1890 and *Megantereon* Croizet & Jobert, 1828 from various European localities. Data sources as in Fig. 3.

DISCUSSION

REVIEW OF *HOMOTHERIUM* TAXONOMY

The taxonomy of the homotheres is still controversial and several opinions and hypotheses have been published. The genus *Homotherium* was erected by Fabrini (1890) on some material from Valdarno, Italy. However, Owen (1846) had already described a few isolated canines and incisors from Kent's Cave, Britain, as *Machairodus latidens*, which was later recognized as belonging to *Homotherium*. Fabrini (1890) studied the Italian material of machairodonts and recognized two large machairodontines *H. nestianum* and *H. crenatidens*. Woldřich (1917) described the new species *Machairodus moravicus* (synonym of *H. moravicum*) from the Pleistocene of Bohemia (Czech Republic). Later, Viret (1954) studied the Saint-Vallier (France) material and proposed the inclusion of most of the European material of homotheres in a single species, *H. crenatidens*. However, Bonis (1976) re-described the Perrier (France) cranium and suggested *H. nestianum* as a valid species. A few years later, Ficcarelli (1979) included all Villafranchian homotheres of Europe in the species *H. crenatidens*, but he retained the species *H. latidens* for the middle-late Pleistocene material. Turner & Antón 1997), opining that the differences separating *H. latidens* from *H. crenatidens* are not valid, synonymized them. The discovery of a rich collection of *Homotherium* remains in the lower Pleistocene Spanish locality Incarcal supported the monospecific character of the Villafranchian material of Europe. Thus, Pons-Moyà & Moyà-Solà (1992) referred it to *H. crenatidens*, but later Galobart *et al.* (2003) included all late Pliocene-late Pleistocene material of Europe in the single species *H. latidens* (Owen, 1846), which has the priority. The oldest, late Pliocene material from the Odessa Catacombs (Ukraine) with some primitive characters, like those of the Kvabebi (Georgia) material, was described as *H.* cf. *davitasvilii* by Sotnikova (2004). Some cranial and postcranial remains from Tajikistan were described as *H. crenatidens* because of their similarity with the Senèze *Homotherium*, (Sotnikova 1989; Antón *et al.* 2014). Sotnikova & Titov (2009), describing the Taman (northern Black Sea, Russia) homotheres accepted the name *H. latidens* for the post-Villafranchian material. The species *H. ultimus* is reported from the early-middle Pleistocene of China, next to Beijing at 40°N (Teilhard de Chardin 1936, 1939). The same species is also recorded from the Pleistocene deposits of Java, Indonesia (Koenigswald 1974; Hertler & Volmer 2008). Recently Antón *et al.* (2014) included all known Eurasian material in the single species, *H. latidens* and recognized some more advanced features in the anterior pocketing of the masseteric fossa in the younger material. This character is clear in the American material, allowing the separation of two species but for the Eurasian populations more material is necessary for such a distinction. Recent phylogenetic analyses based on craniodental characters, strongly support the monophyly of *Homotherium,* which along with *Amphimachairodus* and *Xenosmilus* comprise a monophyletic clade of tribal taxonomic status (Homotherini) within Machairodontinae (Christiansen 2012, Werdelin & Flink 2018). Homotherini appear as the sister group of *Smilodon* (Christiansen 2012) or *Smilodontini* (Werdelin & Flink 2018), from which they diverge before *c.* 18.0 Ma, based on ancient-DNA evidence (Paijmans *et al.* 2017; Barnett *et al.* 2005).

COMPARISONS

The morphological characters (premaxillae, nasal cavity, infraorbital foramen, nasal bones) of the cranium DFN3-152 coincide with those of the crania from Perrier, Senèze and Incarcal (Fig. 3) and its dimensions are into the range of variation of this sample (Table 1). The well-preserved upper canine with serrated margins

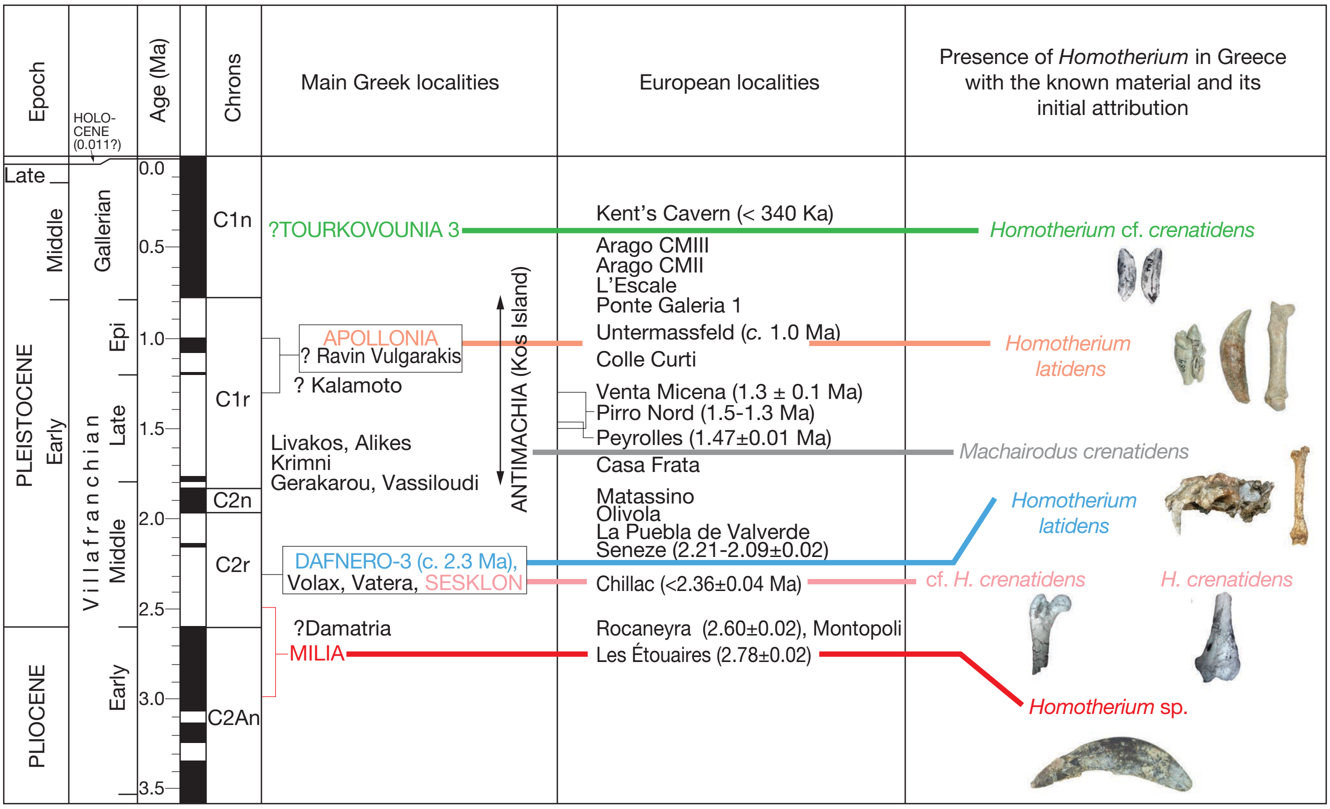

FIG. 6. — Biostratigraphic table including the main *Homotherium*-bearing mammal localities of Greece and Europe with the known Greek material and its original attribution. The absolute ages for the European localities were taken from Wiegank (1997), Napoleone *et al.* (2003), Palmqvist *et al.* (2003), Proctor *et al.* (2005), Nomade *et al.* (2014), and Palombo (2016).

and strong transverse compression indicates that DFN3-152 should be assigned to *Homotherium*. The breadth/length index of the canine is 42, which is within the range of variation for European *Homotherium* (36-45; according to the data provided by Galobart *et al.* [2003] and Sardella & Iurino [2012]). The size of the upper canine also falls within the range of Eurasian *Homotherium* (Fig. 4). The poor preservation of the upper carnassial does not allow for a full comparison, but its large size and the absence of the protocone resemble features seen in *Homotherium*. The measured length of the upper carnassial is between the mean values for *Homotherium* and *Megantereon* (Fig. 5). Keeping in mind that both mesial and distal parts of the carnassial are broken its length should be slightly longer and thus likely closer to *Homotherium*.

An almost complete and well preserved cranium from Loc. 13 of Choukoutien (China) was described as *Machairodus ultimus* or *M. (Epimachairodus?) ultimus* by Teilhard de Chardin (1936, 1939) and Teilhard de Chardin & Leroy (1945). Later, it was transferred to *H. latidens* by Antón *et al.* (2014 and references therein). The morphological characters of the Chinese cranium (medium size, elongated cranium, V-shaped and wide palate, absence of canine fossa, high zygomatic arches, flattened and serrated on both sides upper canine, reduced P3, blade-like carnassial with small pre-parastyle and absence of protocone) coincide with those of DFN3-152. Moreover, its cranial and dental dimensions are also close to those of DFN3-152, confirming their similarities (Fig. 4; Table 1).

The cranial and dental differences of *H. latidens* from the other Villafranchian machairodont of Europe, *Megantereon cultridens*, are clear as the size of the previous species is quite larger (Figs 4; 5). Concerning the humerus, the well-developed major tubercle, the flattened humeral head, the wide and projected articular head, the straight diaphysis, the large olecranon fossa, the medially projected medial epicondyle and the wide supracondyloid foramen of DFN3-153 are similar to those of the *Homotherium* humeri described from Senéze and Incarcal (Ballesio 1963; Galobart *et al.* 2003); its size is also within the range of variation for this material (Table 2). Two distal fragments of humeri known from the Greek localities Milia and Sesklon have similar morphology and dimensions as DFN3-153 (Athanassiou 1998; van Logchem *et al.* 2010) (Table 2).

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION

Although homotheres are distributed world widely, their known material is often fragmentary and cannot allow clear comparisons for taxonomic and evolutionary conclusions (Turner & Antón 1997; Werdelin & Peigné 2010). During the last two decades more material has been discovered in various Eurasian sites, enriching the known sample and allowing better comparisons and results. The earliest occurrence of homotheres is known from the late Pliocene Odessa Catacombs and they are recorded until the late Pleistocene in some fossiliferous sites of England and Germany (Turner & Antón 1997; Sotnikova & Titov 2009). The African records

Table 2. — Humeral measurements of *Homotherium latidens* from various European localities. Data sources: As in Table 1, plus Athanassiou (1998) and Tsoukala & Bonifay (2004). *, measurements taken from the casts.

	Dafnero	Sesklon			Incarcal		Ceyssaguet		
Humerus	**DFN3-153**	**Σ-708**	**Senèze**	**Perrier**	**IN-1195**	**IN-V310**	**CEY-7834**	**CEY-2309**	**CEY-1166**
Length	360.0	–	354.0	–	318+	320.0	–	–	–
DTproximal	63.0	–	64.0-65.0	67.5	65.0	64.8	–	–	–
DAPproximal	–	–	97.0	92.0	86.5	89.0	–	–	–
DTcaput	59.5	–	65.0	62.5	58.5	59.5	–	–	–
DTdiaphysis at the middle	[36]	–	–	–	–	–	[30]	[24.4]	[32]
DAPdiaphysis at the middle	[35]	–	–	–	–	–	[42.2]	[42.1]	[45]
DTdistal	76.0	81.4	85.0-86.0	–	77.3	72.8	[76.2]	–	–
DAPdistal	–	57.2	57.0	–	57.5	50.3	[50.8]	–	–
DTmaximal of the trochlea	55.3	58.0	56.0-57.0	–	58.0	52.0	–	–	–

of *Homotherium* are mainly known from the Pliocene to early Pleistocene of Eastern Africa (Werdelin & Peigné 2010) but it is also reported from the early Pleistocene of Tunisia and Morocco (Geraads 2002). In North America it is identified in several localities and recently it was recognized in Venezuela, South America (Turner & Antón 1997; Rincón *et al.* 2011).

As the earliest known evidence of *Homotherium* is both from Asia (Odessa Catacombs, MN 15, *c.* 4.0 Ma; Vangengeim *et al.* 1998) and Africa (Lonyumun Member of the Koobi Fora Formation, Kenya, Early Pliocene,4.3-4.1 Ma; Werdelin & Sardella 2006), it is impossible to identify the geographical origin of the genus. *Homotherium*, after its first occurrence in the Pliocene, shows a wide distribution in the Pleistocene all over the world. The genus disappeared from Africa during early Pleistocene but in Eurasia and America survived until the late Pleistocene. For a long time, the last evidence of *Homotherium* in Eurasia was from the middle Pleistocene at *c.* 300 000 years B.P., but the discovery of a mandible in the North Sea, dated at *c.* 28 000 years B. P. (Reumer *et al.*, 2003), challenged this datum, indicating that *Homotherium* survived in Eurasia until the late Pleistocene, unless it went extinct and reimmigrated from North America in the late Pleistocene. Mol *et al.* (2008) refers that in America *Homotherium* disappeared at *c.* 11 500 years B. P., while Ewald *et al.* (2017) refers the presence of *Homotherium* in Canada at 12 715-12 655 years.

Presence of *Homotherium* in Greece

The genus *Homotherium* was originally recognized in Greece in the ?middle Pleistocene fissure filling Tourkovounia 3, near Athens. The available material includes a poorly preserved lower canine described as *H.* cf. *crenatidens* (Symeonidis & de Vos 1977). The given dimensions of the Tourkovounia 3 lower canine are 14.0 × 9.8 mm and they are within the range of variation of the European homotheres (Koufos 2018: fig. 14a). The earliest occurrence of *Homotherium* in Greece has been found at the localities Milia-1a, 2a, 5 (Western Macedonia, Greece; Vlachos *et al.* 2018) which are biochronologically dated to the early Villafranchian, between 3.0-2.5 Ma. The Milia material includes an upper canine, a distal part of the humerus, a tibia and a navicular, which are reported as *H. crenatidens*. Based on the illustration of van Logchem *et al.* (2010: fig. 1), the Milia upper canine has serrated margins and its size is close to that of DFN3-152. Athanassiou (1998) described a distal humerus and a proximal femur from the middle Villafranchian fauna of Sesklon (Thessaly, Central Creece) as *H. crenatidens* and cf. *H. crenatidens,* respectively. The morphology and size of the distal humerus are close to those of DFN3-153 and the known European sample of *Homotherium* (Table 2). Recently, a lower canine, a distal fragment of the p4 and a second metacarpal from the Epivillafranchian fauna of Apollonia have been described as *H. latidens* by Koufos (2018). The genus is also mentioned, without description, from an unknown locality near the village Antimachia in Kos Island (Aegean Sea, Greece), (Desio 1931). Hitherto, the known *Homotherium* material is very fragmentary and the determinations doubtful, and thus its occurrence in Greece, could be challenged. The sixth occurrence of the genus is that from Dafnero-3 and it includes the most complete material from Greece so far. The described cranium from Dafnero provides clear evidence for the presence of the genus *Homotherium* in Greece and confirms the early occurrence of its presence. The genus is recorded across the whole area of Greece and its stratigraphic/temporal distribution (Fig. 6) covers the period from the early Villafranchian to the late Pleistocene (*c.* 3.0-*c.* 0.4 Ma).

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Conflict of interest

There is no conflict of interest.

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