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A skull of *Machairodus* Kaup, 1833 (Felidae, Mammalia) from the late Miocene of Hadjidimovo (Bulgaria), and its place in the evolution of the genus

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A skull of *Machairodus* Kaup, 1833 (Felidae, Mammalia) from the late Miocene of Hadjidimovo (Bulgaria), and its place in the evolution of the genus

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ABSTRACT

The late Miocene locality Hadjidimovo in Southwestern Bulgaria has yielded a huge collection of mammalian fossils, including a complete skull of *Machairodus* Kaup, 1833, first described (in Bulgarian) by Kovachev (2002). We re-describe it here, compare it with other *Machairodus*, and review the evolution of the genus. We conclude that the transition from *M. aphanistus* (Kaup, 1832) to *M. giganteus* (Wagner, 1848) is gradual and mosaic, that assigning these species to different genera fails to reflect this relationship, and that the Hadjidimovo skull represents a rather late evolutionary stage of this lineage.

KEY WORDS
Bulgaria,
Late Miocene,
Machairodontinae,
saber-tooth felid.

RÉSUMÉ

Un crâne de Machairodus *Kaup, 1833 (Felidae, Mammalia) du Miocène supérieur de Hadjidimovo (Bulgarie), et sa place dans l'évolution du genre.*

La localité de Hadjidimovo dans le Sud-Ouest de la Bulgarie a livré une énorme collection de mammifères fossiles, dont un crâne complet de *Machairodus* Kaup, 1833, décrit (en Bulgare) par Kovachev (2002). Il est ici re-décrit, et comparé avec les autres *Machairodus,* genre dont l'évolution est revue. Nous concluons que la transition entre *M. aphanistus* (Kaup, 1832) et *M. giganteus* (Wagner, 1848) est graduelle et mosaïque, que de rapporter ces espèces à des genres distincts ne reflète pas cette relation, et que le crâne de Hadjidimovo illustre un stade avancé de cette lignée.

MOTS CLÉS
Bulgarie,
Miocène supérieur,
Machairodontinae,
félin à canines en sabre.

INTRODUCTION

Hadjidimovo in the Mesta Valley of southwestern Bulgaria is one of the richest late Miocene localities of the Old World, with more than 20 000 collected fossils that have been partly published (Geraads *et al.* 2001, 2003, 2005, 2006; Kostopoulos *et al.* 2001; Koufos *et al.* 2003; Geraads & Spassov 2009; Spassov & Geraads 2004; Spassov *et al.* 2006). It is clearly a Turolian fauna; Spassov (2002) surmised that it might be earlier than Kalimantsi, another major locality of southwestern Bulgaria, and is probably of early MN12 age, if not MN11. Recent publications (Hristova *et al.* 2002; Hristova 2012; Li & Spassov 2017 and Spassov *et al.* 2018) also arrived at a late MN11 or early MN12 age. One of the major finds from Hadjidimovo is a complete machairodont skull with left hemi-mandible HD-9196. It was briefly described in Bulgarian by the late Dimitar Kovachev, who conducted the excavations in these sites (Kovachev 2002), but we believe that this remarkable specimen deserves a more detailed study. It will be compared below to other representatives of this genus (*Machairodus* s.l.) and with large modern Felinae, commonly called 'large conical-toothed felids' (hereafter LCTF) although 'conical' does not properly reflect the actual variation of their canine shape. In the descriptions, the alveolar line represents the horizontal. The MN zones assignments are only indicative, and represent no more than time slices (MN9 and MN10 belong to the Vallesian; MN11, MN12, and MN13 belong to the Turolian).

MATERIAL AND METHODS

Modern and fossil material has been examined in the Muséum national d'Histoire naturelle, Paris (MNHN), Centre de Conservation et d'Études des Collections, Lyon (CCEC), Hessisches Landesmuseum, Darmstadt (HLMD), National Museum of Natural History, Sofia, Bulgaria (NMNH), Kovachev Museum, a branch of the NMNH, Assenovgrad, Bulgaria (NMNHA), Natural History Museum, London (NHMUK). The 3D-reconstruction of HD-9196 was made with a NextEngine® laser scanner.

SYSTEMATIC PALAEONTOLOGY

Family FELIDAE Gray, 1821

Genus *Machairodus* Kaup, 1833

TYPE SPECIES. — *Felis aphanista* Kaup, 1832 is usually regarded as the type species of *Machairodus* Kaup, 1833, but this is incorrect. Kaup based his description of *Machairodus* on an upper canine from Eppelsheim in Darmstadt, but his title "*Machairodus*, Kaup" is followed by the sub-title "Ours [French for 'bear'], Cuv; Cultridens, Jobert et Croiset [sic]", and in his description (Kaup 1833: 25) he stated "je pense qu'il serait convenable […] d'employer le nom de *cultridens* pour le genre auquel appartiennent les canines trouvées dans la Toscane et dans le grand-duché de Hesse-Darmstadt." According to Art. 12.2.5 of the ICZN, these indications could be regarded as a designation of *Ursus cultridens* Cuvier, 1824 as the type species of *Machairodus*, even if the Eppelsheim canine turns out to be of the same species as the holotype of *Felis aphanista*, and no matter what Kaup and other authors wrote afterwards (*contra* Morlo & Semenov 2004). This would make *Machairodus* a junior synonym of *Megantereon* Croizet & Jobert, 1828, if the type species of the latter genus, *Me. megantereon* Croizet & Jobert, 1828, is indeed a synonym of *Me. cultridens* (Cuvier, 1824), as generally believed. Things are not so 'simple', however. As pointed out to us by L. Werdelin, the use of *cultridens* by Kaup is not unambiguous, as several taxa were included by him under this name, which might invalidate the new genus name. Another problem is that Cuvier's statement: "c'est ce qui me détermine à changer le nom d'*etruscus,* que j'avais donné à cet ours en celui de *cultridens*." creates a nice example of objective synonym. For the sake of stability, we will use *Machairodus* in its usual meaning.

Machairodus giganteus (Wagner, 1848)

HOLOTYPE (by monotypy). — Proximal ulna from Pikermi, Greece (Wagner 1848: pl. 10, fig. 6).

DESCRIPTION

The skull HD-9196 is virtually complete (Fig. 1; Appendix 1), as it lacks only the palatal roof and most of the right canine. It is almost undistorted, except for a strong crushing of the naso-frontal area, along the sagittal plane; this crushing also slightly affected the braincase, which shows longitudinal breaks along the squamoso-parietal suture, on either side of the skull. The associated left mandibular ramus lacks only the crowns of the incisors and canine.

Skull

The skull is deep and narrow, but the distortion prevents a reliable estimate of the skull outline in lateral view. All that can be said is that the sagittal crest was slightly inclined ventro-caudally; even accounting for some distortion, it was at most horizontal, not rising caudally.

Premaxillae

The premaxillae project strongly in front of the canines; they narrow upwards but remain broader than in *Panthera* Oken, 1816. The naso-maxillary sutures are caudally convergent in their rostral part, but probably (cracks obscures their precise course) almost parallel in their caudal part.

Face

Crushing obscures the naso-frontal suture. There is no evidence that it was transverse, as in most machairodonts, although it may not have been as V-shaped as in *Panthera*. Overall, the muzzle is not large, with the anterior border of the orbit located just anterior to the paracone of P4, and the ante-orbital foramen just in front of this tooth. This moderate size of the muzzle is probably related to the rather small size of the canine. The palatal roof is missing, but its posterior broadening is much weaker than in *Panthera*, as the toothrows diverged much less posteriorly.

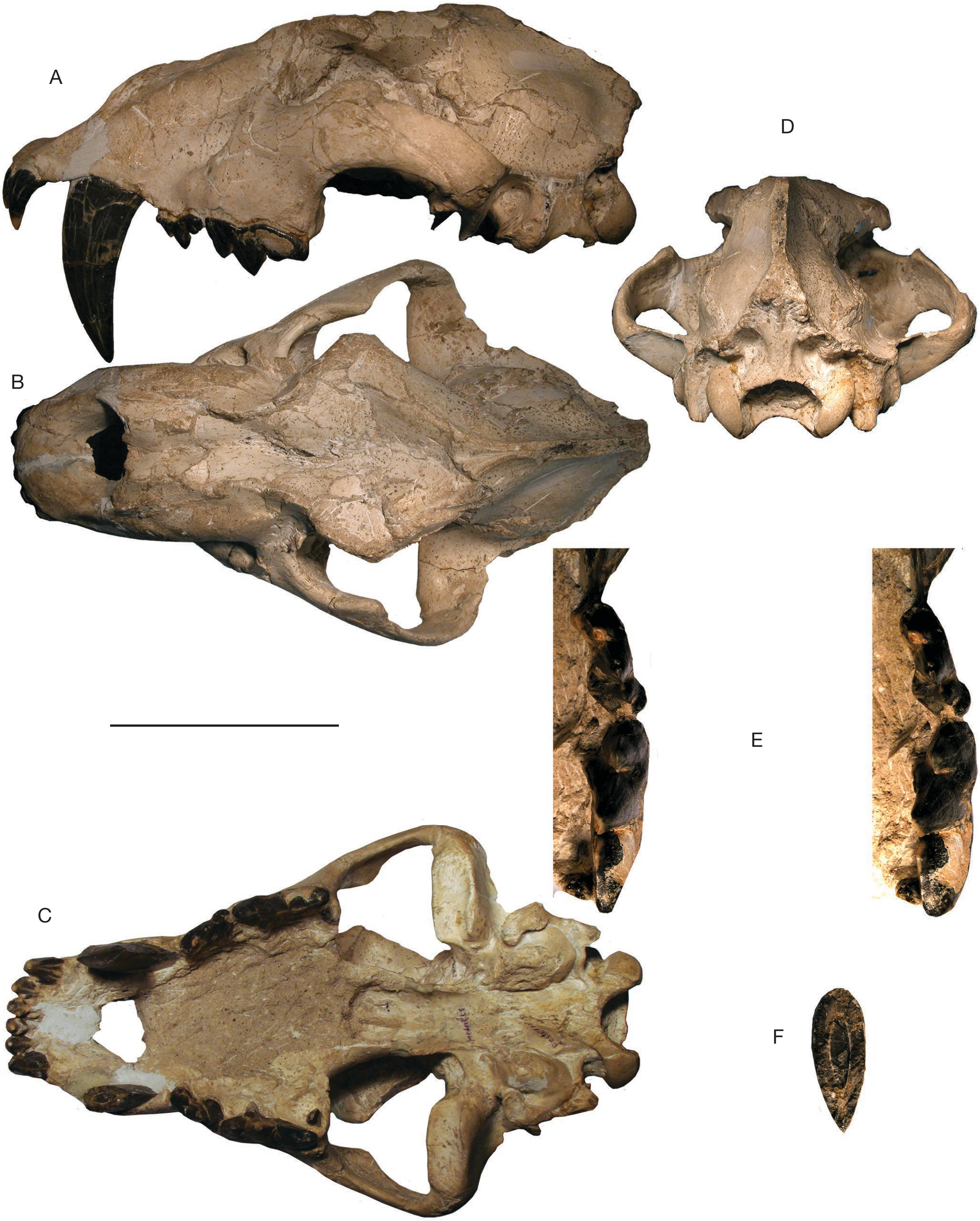

FIG. 1. — *Machairodus giganteus* (Wagner, 1848), HD-9196: **A**, lateral view; **B**, dorsal view; **C**, ventral view; **D**, caudal view; **E**, stereo view of upper teeth; **F**, section of the broken right canine. Scale bar: A-C, 10 cm; D, E, 5 cm.

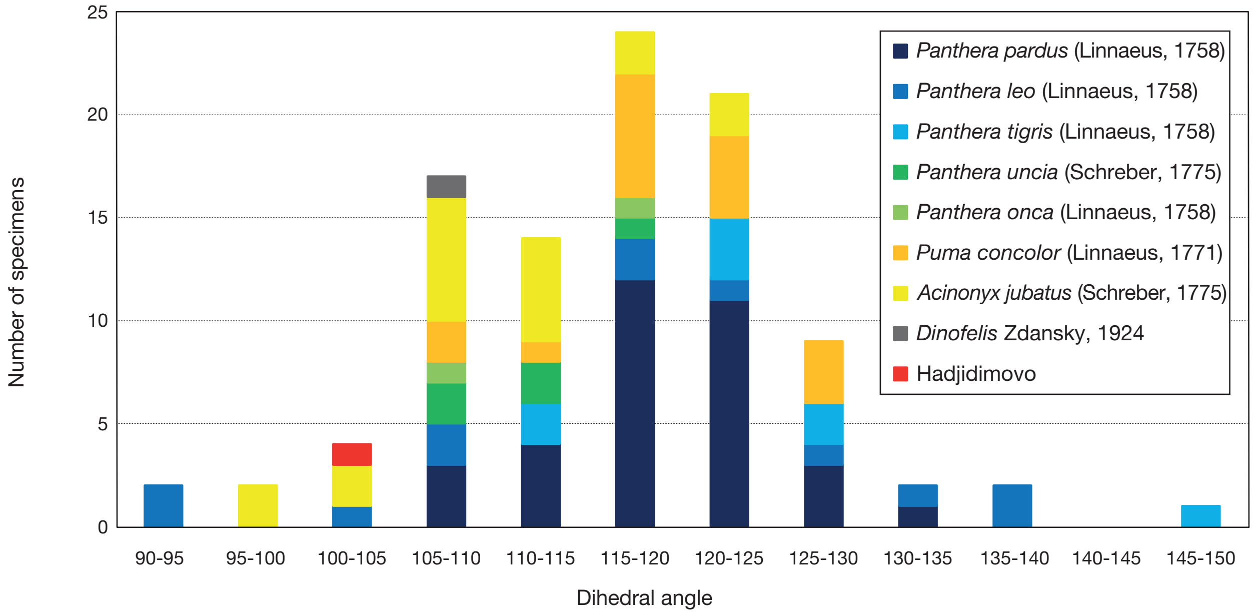

FIG. 2. — Orientation of the orbits in HD-9196 and LCTF. The values (in degrees) are those of the dihedral angle between the planes of the left and right orbits, defined by plotting the lowermost, uppermost, and anteriormost points of each orbit in space (this slightly differs from twice the convergence angle of Casares-Hidalgo *et al.* 2019, who used the most posterior point of orbit instead of the lowermost one). Although the accuracy is only moderate because these points are not very precisely defined, the general picture clearly shows less frontally oriented orbits in *Machairodus* Kaup, 1833 than in most LCTF. *Dinofelis* Zdansky, 1924 is an estimate for a cast of *D. cristata* (Falconer & Cautley, 1836), NHMUK M32148.

TABLE 1. — Tooth measurements of HD-9196, in mm.

	Upper teeth			**Lower teeth**			
	C>	**P3**	**P4**	**c<**	**p3**	**p4**	**m1**
Length	31.5	26.8	44.3	14.8	21.4	28.2	31.3
Width	12.6	13	15.9	8.8	10.1	12.2	13.2

As in other machairodonts, the orbits are small, and they face distinctly less forward than in LCTF (Fig. 2), an observation also made by Casares-Hidalgo *et al.* (2019) on *Homotherium serum* (Cope, 1893) and *Smilodon* Lund, 1842. Several parameters (the first of which is probably absolute size) are certainly involved in this orbital orientation, but we may observe that the orbits are less frontally oriented in cheetahs than in tigers, suggesting a possible connection with habitat (although Casares-Hidalgo *et al.* 2019 rejected it). In contrast to LCTF, the post-orbital processes are thick and laterally expanded, the skull being much broader at this level than across the muzzle. The skull narrows strongly but gradually behind this level, with a strong constriction anterior to the braincase. The ventral postorbital processes are rather large but rounded and not very prominent. The zygomatic arches are less expanded laterally and shorter antero-posteriorly than in Panthera, but with a similar antero-posterior curve. The area of insertion of the masseter muscle is not distinct, suggesting that this muscle was not strong. The glenoid fossa is located much more anteriorly than in Panthera, but its shape and concavity are very similar, with salient postglenoid processes mostly developed medially and a ridge-like anterior rim that is, however, of uniform height, unlike the laterally much taller crest of *Panthera*. It additionally differs from *Panthera* in that the root of the zygomatic arch is slightly stretched ventrally, so that the fossa is slightly more ventrally located (it is, e.g., more ventral than the base of the pterygoids, but this is also because the pterygoid blades are less expanded). Still, the glenoid fossae remain at about the same vertical level as the base of the occipital condyles, far above the alveolar line.

Cranial base

The basioccipital is similar to that of LCTF and the relief (anterior rugosities for longus capitis, posterior depressions for the rectus capitis anticus) is only slightly better marked.

The cranial base, like the skull as a whole, is more lengthened than in LCTF. The auditory bulla reaches farther anteriorly, and connects the base of the zygomatic root through a thick bridge forming the ventral wall of the external auditory meatus. Because of this, the foramen lacerum anterior is restricted in size, at the antero-medial end of the tympanic bulla. The condylar foramen opens in a fossa confluent with the foramen lacerum posterior, but well behind it.

The auditory bulla is almost invisible in lateral view, because it is wholly covered by a thick flange of bone, including the mastoid process anteriorly and the jugular process posteriorly: these two processes are located much farther apart than in LCTF. The mastoid process is very large; it forms a triangular protuberance, expanded anteriorly, laterally, and ventrally beneath the auditory bulla. The jugular process is shorter and more posteriorly directed than in LCTF. There is no remnant of the alisphenoid canal.

Fig. 3. — *Machairodus giganteus* (Wagner, 1848) HD-9196, mandible and lower teeth: **A**, lateral view of p3-m1; **B**, medial view of the same; **C**, occlusal view of the same (stereo); **D**, lateral view of the mandible. Scale bars: A-C, 5 cm; D, 10 cm.

Occipital

The occipital differs considerably from that of LCTF. The foramen magnum is broad, and the condyles are located far apart. Dorso-medially to each of them, the occipital is hollowed out by large, deep fossae, probably for nuchal muscles. At this level, the occipital is not wider than over the condyles, and it further narrows strongly dorsally, largely because the lambdoid crest, instead of expanding laterally, is stretched caudally, forming a roof over the occipital. As a whole, the occipital is triangular, rather than bell-shaped as in LCTF, but this may be partly due to the young ontogenic age of the specimen.

Upper teeth

The upper incisors are arranged in a gentle arch, well forward of the canines; they are large and high-crowned, I3 being distinctly larger than the others. They all have a mesial and a distal keel, best expressed in I3, which is almost caniniform. At least both keels of I3 and the lateral keel of I2 are serrated.

Compared to other teeth, the canines are rather small (Table 1); because this tooth is sexually dimorphic in this group (e.g., Antón *et al.* 2004), this probably means that HD-9196 is a female. The compression is also moderate. Both keels are serrated, with a distinct curvature in lateral view, but the tooth is straight in front view. There is no wear facet for the lower canine, and the other teeth are at most slightly worn.

There is almost no diastema between the canine and P3, whose anterior root probably contacts the canine within the bone. The main cusp of P3 is less than half of the tooth length, because there are a small mesio-lingual cingulum, a large anterior accessory cusp, almost in line with the main cusp, a smaller posterior one, and a strong posterior cingulum. The tooth is narrow, in spite of a lingual expansion at about two thirds of its length, quite long (it is the longest recorded machairodont P3), but shorter than in many LCTF.

The P4 is also among the longest recorded in *Machairodus*. The preparastyle is small, and in line with the other cusps. The parastyle and paracone bear strong anterior and posterior serrated keels. A ridge, inflated at its base, descends antero-lingually from the apex of the paracone, and ends in a lingual root, but there is no distinct protocone. The paracone is much taller than long, and also much taller than P3, in contrast to LCTF, where they are of comparable height. The metastyle is much longer than the paracone. Slight wear affects the posterior half of the paracone and the metastyle. On the whole, all cusps together form a long, narrow, almost straight shearing blade. The M1 is about as reduced as in modern LCTF, but is wholly lingual to P4, so that it is not visible in lateral view.

Mandible

The mandible (Fig. 3) is long and slender, with a corpus that is almost straight and bucco-lingually thin. Its anterior border is more vertical than in *P. uncia* (Schreber, 1775) or *Neofelis* Gray, 1867 (the modern taxa that have the most vertical chins). There is an incipient mental flange below the canine; its base reaches slightly farther ventrally than the symphysis, but not more than the angular process. There is no conspicuous scar for the digastric muscle. A very large mental foramen is located close to the ventral border of the corpus, below the anterior root of p3. The masseteric fossa and the condyle do not differ significantly from those of *Panthera*, but the coronoid process is distinctly lower and shorter antero-posteriorly, i.e., more reduced than in all modern felids, in which it is highly variable.

Lower incisors
The missing lower incisors were certainly rather large, and wholly visible in lateral view, in front of the broken canine. The latter was small, and much shorter than p3. There is no p2, and the diastema is rather short. The lower premolars are similar to each other in their extremely tall, slender main cusp that is less lanceolate ('fleur-de-lys') than in LCTF with tall premolars, like in *Acinonyx* Brookes, 1828; in p4, this main cuspid is inclined backwards. The anterior and posterior accessory cuspids are also tall, especially in p4, and subequal in length. The posterior cingulum is poorly expressed in p3, thicker in p4, but still rather thin. Both p3 and p4 are serrated; if serration was present on m1 before wear, it would have been restricted to the cutting edges of the paraconid and protoconid. These cuspids are subequal in length at the base, but the cutting edge of the paraconid is short, because the mesial edge of this cuspid is inclined backwards, parallel to the main axis of the cuspids of p4. A barely distinct basal bulge is all that remains of the metaconid/talonid complex.

SYSTEMATICS AND EVOLUTION OF *MACHAIRODUS*

There is no need to repeat here the evolution of ideas regarding the systematics of the genus *Machairodus* s.l. (see e.g., Beaumont 1975, 1987, 1988; Madurell-Malapeira *et al.* 2014; Spassov *et al.* 2018). In short, the extreme opinions are those of Christiansen (2013) who regards the two main species of the genus, *M. aphanistus* (Kaup, 1832) and *M. giganteus*, as belonging to distinct genera (*Machairodus* Kaup, 1833 and *Amphimachairodus* Kretzoi, 1929, respectively) and those who regard the two species as just the early and late stages of a single evolutionary lineage. This latter view can be made less simple by adding intermediate stages (such as *M. copei* Pavlow, 1914, or *Neomachairodus* Sotnikova & Noskova, 2004, but this subgenus name has no type species and is therefore unavailable). The difference between the two basic opinions is critical because, in the cladogram published by Christiansen (and in the one obtained, on unweighted characters, by Werdelin & Flink [2018]), *M. aphanistus* occupies a basal position, below *A. giganteus* (Wagner, 1848) and *Homotherium* Fabrini, 1890, but also below *Metailurus* Lund, 1842, *Dinofelis* Zdansky, 1924, and *Megantereon*, implying that there is no close relationship between the two main species of *Machairodus* s.l.

In addition, there are a few Old World fossils that may represent divergent branches:

Machairodus irtyschensis Orlov, 1936 is based upon a mandible from Pavlodar (MN13). We thank M. Sotnikova for confirming the tooth crenulation, mentioned by Orlov (1936) but not visible on his figures. The main characters of the mandible are the sloping mesial border of m1, and perhaps sloping front border of the symphysis. These characters are unlike *M. giganteus* of similar age, and might support species distinction, but it is more parsimonious to regard it as a mere local variant.

Machairodus africanus Arambourg, 1979 was first described by Arambourg (1979) on the basis of a relatively complete but edentulous skull, from the 'Villafranchian' of Aïn Brimba in Tunisia, which also yielded an upper P4 and a metapodial. The skull was studied in more detail by Petter & Howell (1987), who confirmed its genus attribution, but rejected a descent from *M. giganteus*. Instead, Werdelin & Lewis (2013) assigned it to *Homotherium*. Geraads (2004) suggested that the P4 might belong to *Dinofelis*, but this tooth was identified as *Megantereon* by Palmqvist *et al.* (2007). Unfortunately, the skull is presently unavailable in the MNHN, but the shape of the palate, very broad across the P4s following an abrupt broadening at the level of the obliquely inserted P3s, the equally broad choanae, as well as the very long mastoid process, whose tip is located very far from the (missing) jugular process, are unlike *Machairodus* and *Homotherium*, but match *Megantereon*. The absence of definitely associated teeth precludes a secure identification of this skull, but we assign it to this genus, suggesting that Palmqvist *et al.* (2007) were probably right, and that all machairodont material from Aïn Brimba belongs to *Megantereon africanus* (Arambourg, 1979), insofar as this is not a junior synonym of one of the species names already available for this genus.

Machairodus laskarevi Lungu, 1978 from Kalfa, Moldova (MN10; Lungu 1978) is usually regarded as close to *M. aphanistus* but is mostly known by an incomplete mandible. The missing lower incisors were fancifully reconstructed as *Panthera*-like, and this probably contributed to support the idea that early *Machairodus* have small lower incisors. Actually, the only evidence supporting the assignment of *M. laskarevi* to *Machairodus* is the mention of fine serrations on the canines and m1, but a revision of this material would be welcome. The lower premolars (Lungu 1978: fig. 26) have distinctly weaker accessory cuspids than those of *M. aphanistus* from Batallones, Spain (MN10; Antón *et al.* 2004: fig. 8). The purportedly extremely narrow symphyseal area is also unlike the latter (Monescillo *et al.* 2014: fig. 3D) and we believe that *M. laskarevi* should be left aside in a discussion of the genus.

Machairodus horribilis Schlosser, 1903, from the latest Miocene of China, has recently been revised by Qiu *et al.* (2008) and Deng *et al.* (2016). It has a primitive cranial shape (see below) in addition to a p3 very different from p4, in contrast to *M. giganteus*, and these authors were probably right in regarding it as a distinct species.

Lokotunjailurus Werdelin, 2003 from Lothagam (Werdelin 2003) and Toros-Menalla (Bonis *et al.* 2010), is certainly close to the *Machairodus*-*Homotherium* group but, since it is probably a divergent branch, we prefer to leave it out of the discussion; its dental metrics are close to those of early *Homotherium*.

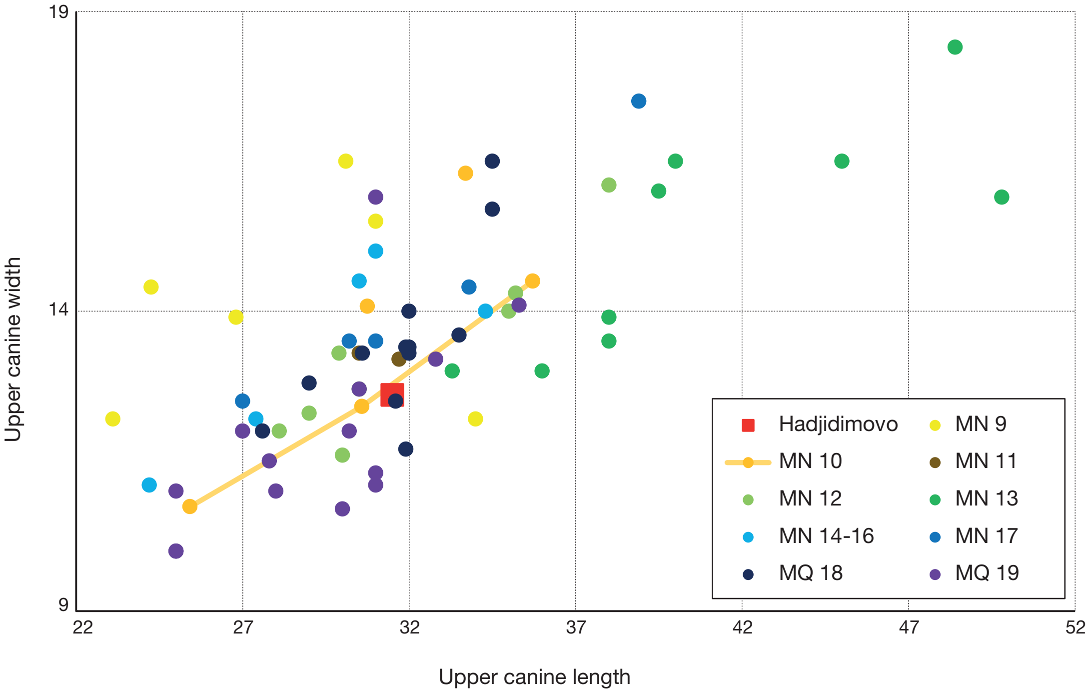

FIG. 4. — Scatterplot of upper canine length vs width in *Machairodus* Kaup, 1833 and *Homotherium* Fabrini, 1890 (blue and purple dots), in mm. In all scatterplots, the line joins the minimum, mean, and maximum values of Batallones-1 (Antón *et al.* 2004). Additional data from: Ballésio 1963; Beaumont 1975, 1988; Bonis 1976, 1994; Chang 1957; Collings 1972; Ficcarelli 1979; Geraads *et al.* 2004; Ginsburg *et al.* 1981; Hendey 1974; Kurtén 1978; Madurell-Malapeira *et al.* 2014; Melentis 1967; Monescillo *et al.* 2014; Morlo & Semenov 2004; Pei 1934; Qiu *et al.* 2004, 2008; Roussiakis & Theodorou 2003; Sardella & Iurino 2012; Scharapov 1996; Schmidt-Kittler 1976; Senyürek 1957; Sotnikova 1992; Spassov *et al.* 2018; Teilhard 1939; Vekua 1972; Zdansky 1924, and personal measurements.

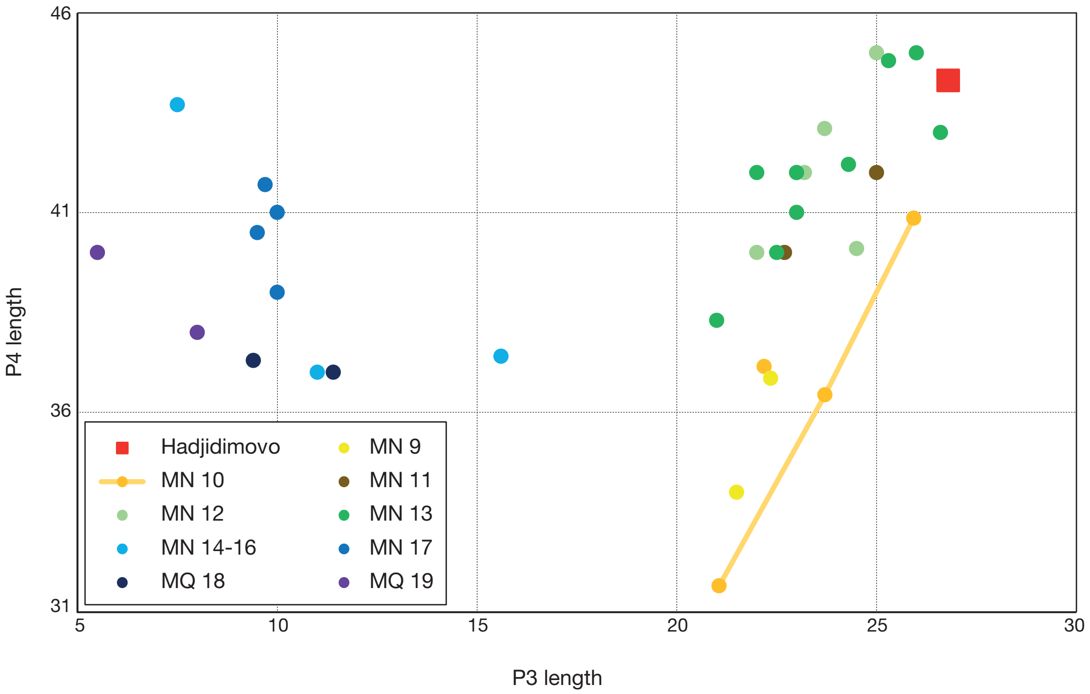

FIG. 5. — Scatterplot of P3 length vs P4 length in *Machairodus* Kaup, 1833 and *Homotherium* Fabrini, 1890. Data as for Figure 4, plus Pavlow 1914; Riabinin 1929.

Returning to the *aphanistus-giganteus* relationships, we believe that Christiansen's conclusion results (in addition to a disputable choice of variables and character states) from the choice of species as OTUs. Unless the specimens illustrating the species are just the holotypes (which, in the present case, are very incomplete), or unless specimens are OTUs (which brings a lot of noise in the matrix), one has to aggregate individual fossils under a species name, and this is a highly subjective process While species identification is rather straightforward for specimens at both ends of the *aphanistus-giganteus* morphocline, there are many intermediate forms that do not possess the whole set of extreme features

The main difference in cranial shape between *M. aphanistus* and *M. giganteus* is the elevation of the cerebral skull above the level of the tooth-row. At Batallones (Antón *et al.* 2004; Monescillo *et al.* 2014), as in LCTF, the upper cranial profile is convex, the occipital is oblique, the auditory region is located not far above the alveolar level, and the occipital condyles are not very far above this level (Antón *et al.* 2004: fig. 4C-D). Instead, in derived *M. giganteus* (including *M. palanderi* Zdansky, 1924 from Baode, MN13, which is the type species of '*Amphimachairodus*') they are far above this level (Chang 1957: pl. 2, fig. 1; Antón *et al.* 2004: fig. 5; Geraads *et al.* 2004: fig. 1A; Zdansky 1924: pl. 25), the cranial profile is straighter, and the occipital more vertical. The Hadjidimovo skull clearly falls in this second category, but undistorted skulls are so rare that the tempo of these changes is unknown.

By contrast, the face remains relatively unaffected. The orbit remains more or less in the same position relative to the tooth-row. Only in the latest Miocene skull from Kalmakpai (MN13; Sotnikova 1992) is it perhaps more posterior, as in *Homotherium*. The infra-orbital foramen is located above P3 at Batallones-1 (Antón *et al.* 2004; Monescillo *et al.* 2014), thus slightly more anteriorly than in most other *Machairodus*, but it is more posterior at Batallones-3 (Monescillo *et al.* 2014: fig. 3), and apparently very posterior at Grebeniki (MN11?; Pavlow 1914) so the forward shift of P3-P4 is not a very clear trend.

Other cranial characters are too rarely observable to be of much use, or follow no consistent pattern. Such is the case with the position of the caudal border of the nasal bones, the presence of the alisphenoid canal (definitely present only at Kemiklitepe D, MN11?: Bonis 1994, and vestigial at Kemiklitepe A-B, MN12; Geraads *et al.* 2004), the position of the condylar foramen, fused with the *foramen lacerum posterior* at Batallones (Antón *et al.* 2004), but also in some *Homotherium* (insofar as the definition of fused vs. separate is consistent across the various authors). According to Christiansen (2013: char. 34), the snout is elevated in '*Amphimachairodus*' *giganteus* but this is not true of *M. palanderi* (Zdansky 1924: pl. 26, fig. 4), and there is no evidence that the snout is elevated at Hadjidimovo and Kalmakpai (Sotnikova 1992). The diastema is never very long in early forms, but it can also be quite short in late forms (Kemiklitepe A: Geraads *et al.* 2004; Pikermi, MN12: NHMUK M8968). The mandibular flange is virtually absent at Batallones, but it is incipient at Eppelsheim, type-locality of *M. aphanistus* (MN9: NHMUK M49967) and probably not stronger at Kemiklitepe A (Geraads *et al.* 2004). Thus, although the general trend towards development of this flange is not in question, it does not clearly distinguish the two species.

Tooth characters can be observed in many more specimens. The transverse compression of the upper canine is weak in early Vallesian forms (except in *M. pseudailuroides* from Esme-Akçaköy [MN9], in which it is very strong [34 × 12.2; Schmidt-Kittler 1976] but this may be a distinct species) but at Batallones it is already similar to that of Turolian forms (Fig. 4). Thus, the main change in compression is between the early and late Vallesian (i.e., within *M. aphanistus*). Absolute size does not change much, except for an increase in latest Miocene forms.

There is no clear trend towards the loss of P2. It is variably present at Batallones, and often absent in *M. giganteus*, but present at Baode, Kalmakpai, and Novaja Emetovka (MN12; Morlo & Semenov 2004). Only *Homotherium* consistently lacks this tooth.

According to Christiansen (2013: char. 14), P3 is smaller in *M. giganteus*. This is indeed a clear difference (Fig. 5), and perhaps the only one that, according to the available sample, would allow a clear-cut distinction between the Vallesian *M. aphanistus* and the Turolian *M. giganteus*. However, Figure 5 shows that what occurred is not a shortening of P3, but a lengthening of P4. In spite of small size of the sample, Figure 6 strongly suggests that this lengthening of P4 is not just a result of larger size, as the condylo-basal length shows no increase, and Figure 7 confirms that there is no change in the size of P3. By contrast, an absolute shortening of P3 clearly occurred in *Homotherium* (blue dots).

Although wear frequently obscures its real size, the reduction of the protocone of P4 is also a very clear trend that is reflected in the narrowing of the tooth. Figure 8 shows that this is a very gradual process that cannot easily be split into discrete steps, as was done by Christiansen (2013: char. 7), because of large variations in any time-period (Morlo & Semenov [2004] observed that the protocone is still large at Novaja Emetovka, and it is also large in NHMUK M8975 from Pikermi). The position of the protocone is fairly constant, except in the Halmyropotamos skull (MN12; Melentis 1967; Roussiakis, pers. com.) where it is located on the lingual side of the paracone, thus more posteriorly than in other specimens.

The preparastyle of P4 is generally stronger in *M. giganteus* but, again, its development is a gradual process. The preparastyle is already present at Batallones (Antón *et al.* 2004), but still weak at Küçükyozgat, Turkey (*M.* '*romeri*' Senyürek, 1957), a locality that has yielded a Middle Turolian fauna (Sickenberg 1975).

The lower incisors of *M. giganteus* have been reported (Beaumont 1975) as larger and more procumbent, but their post-mortem loss and/or the distortion of the incisor arcade in many specimens make this hard to evaluate. Beaumont (1975) deduced their small size at Eppelsheim by observing that the distance between the canine and the sagittal plane is smaller than the diameter of this tooth, but this is partly due to the large size of this canine, and the size of the

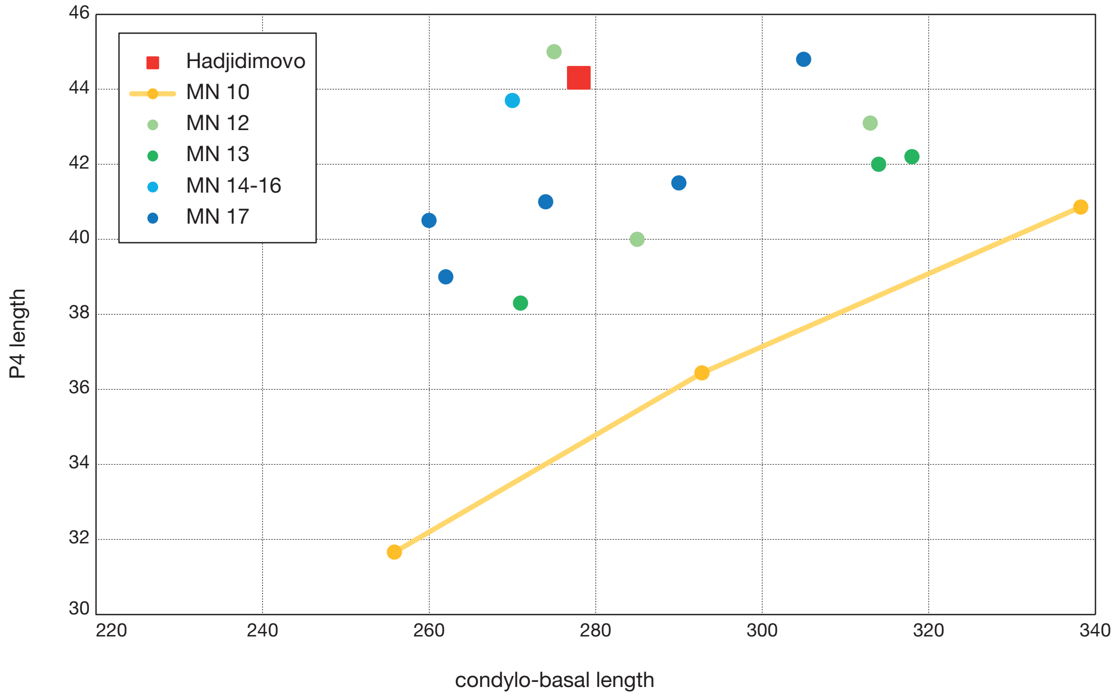

FIG. 6. — Scatterplot of P4 length vs. condylo-basal length in *Machairodus* Kaup, 1833 and *Homotherium* Fabrini, 1890. Because Antón *et al.* (2004) provided only values for basal length, condylo-basal lengths for Batallones are taken as 1.08 × basal length, a factor deduced from the proportions observed in other *Machairodus* and *Homotherium*. Data as for Figures 4 and 5.

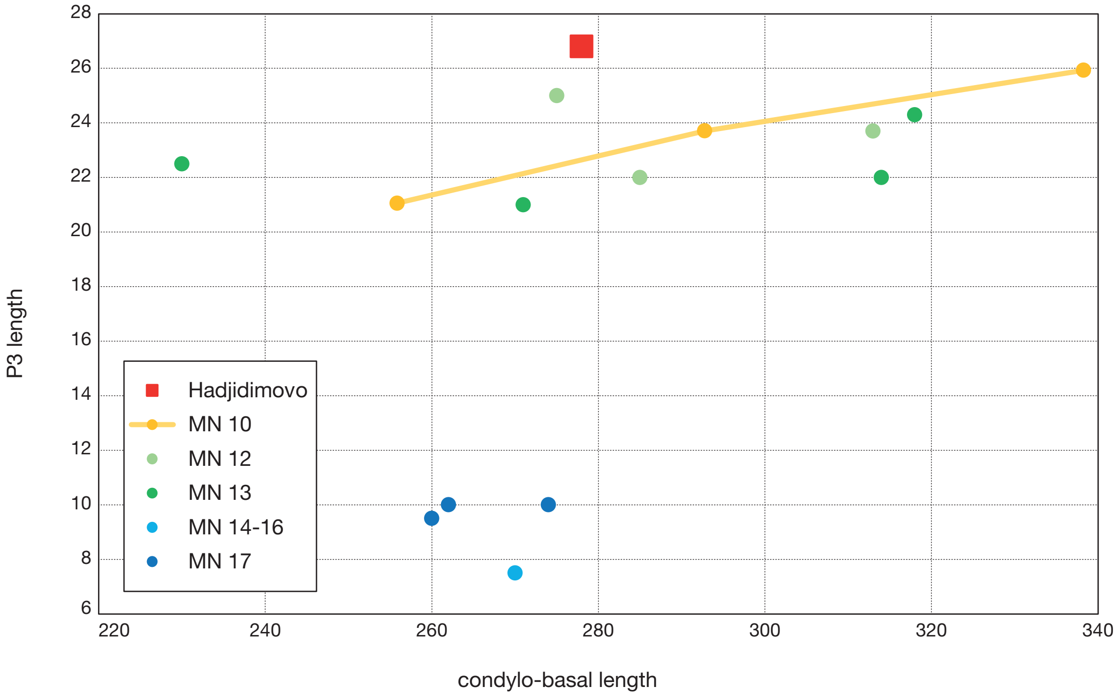

FIG. 7. — Scatterplot of P3 length vs condylo-basal length in *Machairodus* Kaup, 1833 and *Homotherium* Fabrini, 1890. Data as for Figures 4 and 5.

incisors themselves can easily be underestimated from what remains of their alveoli. The incisors were certainly not very small at Batallones (Monescillo *et al.* 2014: fig. 3D). The relative positions of the incisors and canine probably depend on the ontogenic age, as the only specimen with incisors located forward of the canines is a young adult from Pikermi with unworn teeth and a shallow corpus (Wagner 1860: pl. 5, fig. 1; cast MNHN.F.PIK3387). In short, it is likely that the incisors of *M. giganteus* were larger than those of *M. aphanistus*, but this remains to be further substantiated.

Beaumont (1975) also noted that the lower canine is small in *M. giganteus*, and this was accepted by Christiansen

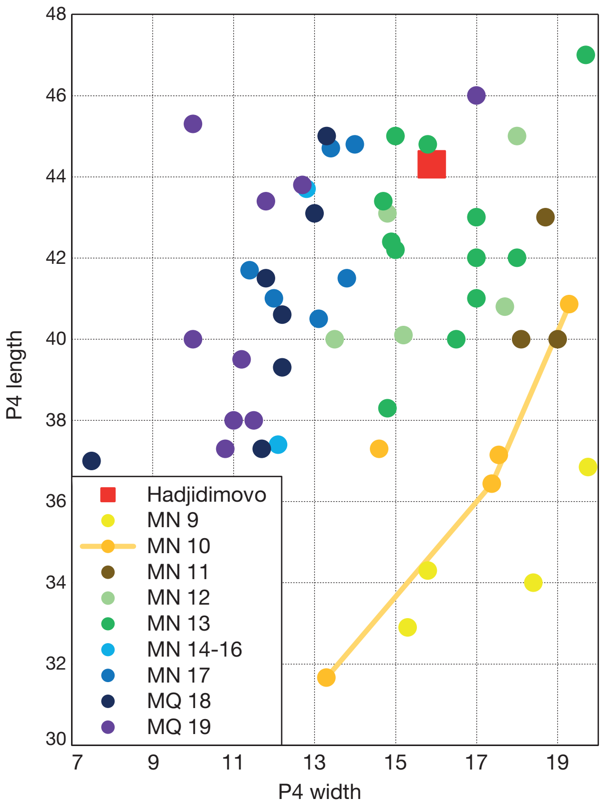

FIG. 8. — Scatterplot of P4 length vs P4 width in *Machairodus* Kaup, 1833 and *Homotherium* Fabrini, 1890. Data as for Figures 4 and 5, plus: Alcalà 1994; Bonis 1984; Peigné 2016; Pons-Moyá 1987; Sotnikova 1989; Turner 1987.

(2013: char. 4), who regarded this small canine as one of the main distinguishing features of his Eumachairodontia, which do not include *M. aphanistus*. Figure 9 shows that, although it is generally true than earlier forms have larger canines, and that the trend towards reduction of this tooth is clear, if two groups are to be distinguished, they match neither the *aphanistus/giganteus* distinction as identified by authors, nor the chronology, as some of the largest lower canines are from Baode (type specimen of *M. 'tingi'*) and Samos (MN12; Beaumont 1975).

The metric trends in the lower cheek-teeth parallel those of the upper ones. There is a relative (but no absolute) shortening of p3 (Fig. 10), and an increase of p4 and m1 lengths (Fig. 11). Again, only in *Homotherium* is there an absolute shortening of the premolars. The main cuspids of the HD-9196 premolars are taller than those of the type-specimen of *M. aphanistus* (Fig. 12), but the main difference is the small size of the posterior cingulum at Hadjidimovo. However, most specimens of *M. giganteus* have a strong posterior cingulum, while it is reduced in the Vallesian site of Höwenegg (Beaumont 1986: fig. 2); thus, intraspecific variation in both the Vallesian and Turolian overlaps the whole variation.

There is no change in the proportions of m1; the reduction of the talonid/metaconid complex is a clear trend (see Spassov & Koufos 2002: fig. 7), but several Turolian m1s (Mahmutgazi: Schmidt-Kittler 1976; Novaja Emetovka: Morlo & Semenov 2004; Pikermi: NHMUK M8968) still bear it, while it may be fully absent at Can Llobateres, MN9 (Madurell-Malapeira *et al.* 2014: fig. 3A-B).

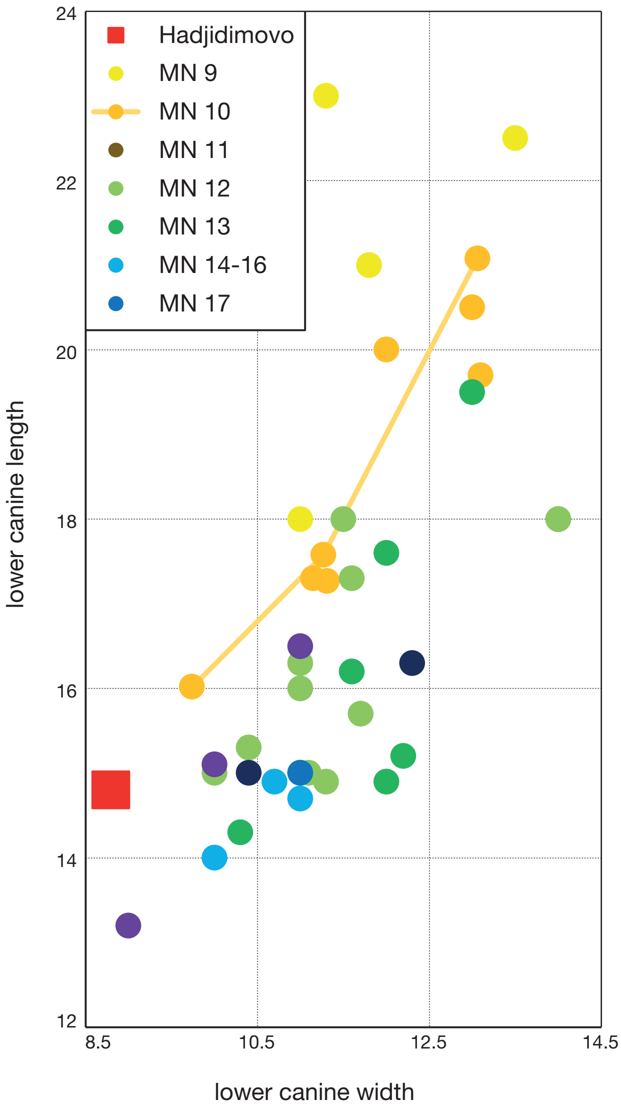

FIG. 9. — Scatterplot of lower canine length vs lower canine width in *Machairodus* Kaup, 1833 and *Homotherium* Fabrini, 1890. The values for Hadjidimovo are taken from the root, and may be slightly underestimated. Data as for Figures 4 to 8, plus Hemmer 2001; Lungu 1978; Morales & Soria 1979; Sotnikova & Titov 2009.

Lastly, it is likely that serration was better developed on post-canine teeth of later specimens, but this is hard to assert positively, as it is rapidly lost with wear, perhaps because it was less necessary for adult individuals. It is already present on the p4 of the type of *M. aphanistus*.

DISCUSSION AND CONCLUSION

None of the characters of *M. aphanistus*, as best illustrated by the Batallones specimens (Antón *et al.* 2004; Monescillo *et al.* 2014), can be regarded as apomorphic relative to their condition in *M. giganteus*, and nothing precludes an ancestor-descendant relationship. Thus, assigning the latter species to a distinct genus or sub-genus is useless. One might even argue that, being members of a single anagenetic lineage, all these fossils could be assigned to the same species, but the differences between the early and late stages far exceed what is commonly accepted for intra-specific variation. However, as first clearly stated by Morlo & Semenov (2004), the changes in this lineage were neither regular nor synchronous, blurring the limit between the two species and prompting authors to refer intermediate forms to *M.* cf. *aphanistus* (e.g., Beaumont 1986, 1988; Beaumont & Crusafont-Pairó 1982; Morlo 1997), *M.* cf. *giganteus* (e.g., Scharapov 1996), or to new species (Pavlow 1914; Senyürek 1957; Sotnikova 1992).

The cheek-teeth of the Hadjidimovo skull are among the largest recorded for *Machairodus*. Other features, such as the very small M1, tall cuspids of the lower premolars, complete absence of metaconid/talonid complex on m1, and perhaps the small lower canines, are in agreement with a derived stage of this lineage, equivalent to that reached by the Pikermi or Halmyropotamos samples, or even by later ones. This contrasts with the recent view (Spassov *et al.* 2018) that identified the Hadjidimovo specimen as *M. giganteus copei* and assigned it, if not to a subgenus (‘*Neomachairodus*’ sensu Sotnikova & Noskova 2004), then at least to a distinct pre-Pikermi stage in the evolution of *M. giganteus*, in agreement with their recent biochronological opinion (Hristova 2012; Li & Spassov 2018; Spassov *et al.* 2018) that regarded the site as of late MN11 age. Further studies on taxa that may have biochronological value are needed to reconcile these conclusions.

Although *Machairodus* and other saber-tooth felids have been widely described and discussed for two centuries, their behavior remains unclear. It is now taken for granted (e.g., Antón 2013; Werdelin *et al.* 2018) that *Machairodus* and other saber-tooth felids were active hunters and killers, perhaps (as first suggested by Bohlin 1940) because one cannot imagine that their formidable sabers were not active weapons. However, positive evidence for active hunting is still meager, as these taxa clearly have no modern equivalent. Sexual dimorphism in canine size suggests that sabers also had a significant role in display. The abundance of saber tooth felids in traps and pits (Rancho La Brea, Batallones, among others) reflects avoidance of high energy expense for food procurement, and both the long favored shear-bite hypothesis and the new class I lever model (Brown 2014) could apply to carcasses as well as to living prey (in contrast to the stabbing model). Did the orbits, which were smaller and less forward-facing than in large *Panthera,* make *Machairodus* a relatively poor performer in visual hunting ? Even though what happened at these accumulation sites is probably not representative of the normal behavior of these animals, it does not really support the terrifying image that they usually convey. Antón (2013) described in detail the scenario of a *Smilodon* immobilizing and killing a bison by cutting its throat, but the difficulties that modern lions face when trying to take hold of a large prey animal (that they were able to previously weaken by bites, in contrast to saber tooth cats) suggest that the task may have been less easy than ideal-

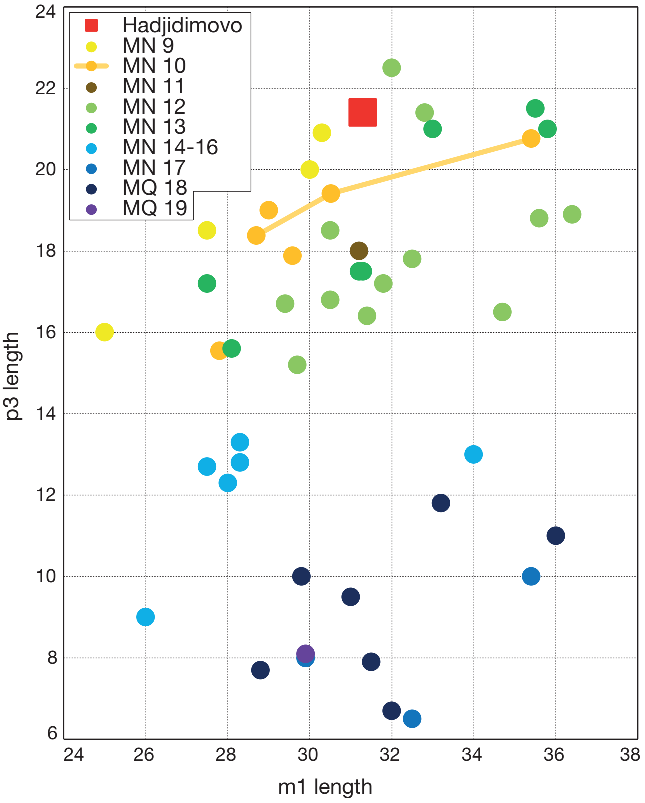

FIG. 10. — Scatterplot of p3 length vs m1 length. Data as for Figures 4 to 9, plus Orlov 1936; Peigné *et al.* 2005; Rook *et al.* 1991; Sotnikova *et al.* 2002; Sardella & Werdelin 2007.

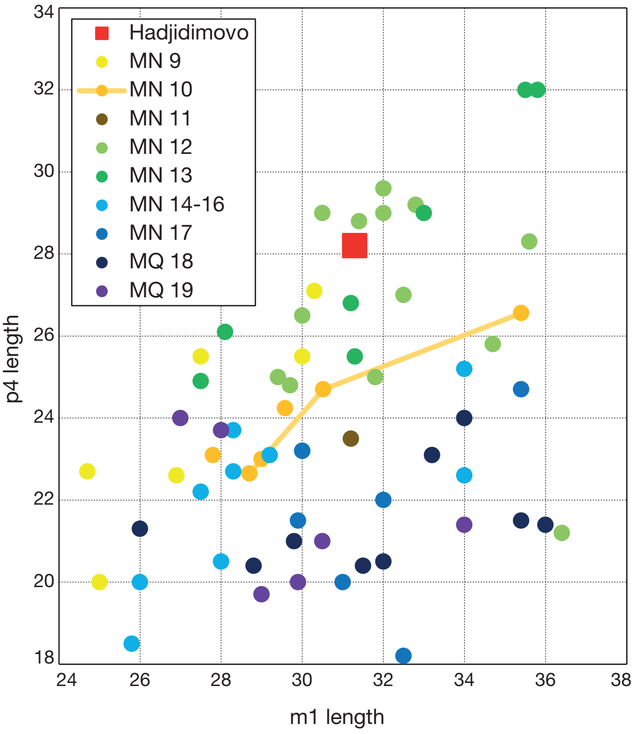

FIG. 11. — Scatterplot of p4 length vs m1 length. Data as for Figures 4 to 9, plus: Werdelin & Lewis 2013; Monguillon-Douillet 2000.

Fig. 12. — Type specimen of *M. aphanistus* (Kaup, 1832), HLMD Din-1132, in: **A**, labial; **B**, lingual; and **C**, occlusal stereo views. Scale bar: 5 cm. See also Kaup 1832: pl. 2, figs 3-4; Beaumont 1975: pl. 1, fig. 1.

ized by Antón. For instance, Bohlin (1940) noticed that the predator was unable to see the exact place where the critical bite was delivered. Andersson *et al.* (2011) showed instead that sabertooths were unable to inflict serious wounds to animals significantly larger than them, and suggested that they hunted medium size animals. This hypothesis is satisfactory in several aspects, as such a prey choice would have restricted the risk of canine breakage, limited competition and risky fights at killing spots, and perhaps allowed them to carry away their prey, so that we no longer need the ad-hoc assumption that they were able to quickly swallow large amounts of meat. The behavior of sabertooths is still imperfectly understood, but recent progress in the knowledge of their functional anatomy (Andersson *et al.* (2011; Antón 2013; Brown 2014; Werdelin *et al.* 2018, and refs therein) is shifting the reconstruction of their lifestyle from pure speculation to testable hypotheses.

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APPENDIX 1. — Supplementary data: 3D reconstruction of the *Machairodus giganteus* cranium from Hadjidimovo, HD-9196. The reconstruction in available in PLY version (http://sciencepress.mnhn.fr/sites/default/files/documents/en/geodiversitas2020v42a9_s1_machairodus_source.ply_.zip; *c.* 15 MB) and PDF (http://sciencepress.mnhn.fr/sites/default/files/documents/en/geodiversitas2020v42a9_s1_machairodus_textured.pdf; *c.* 25 MB).