

Musteloid carnivores from the upper Miocene of South-Western Bulgaria, and the phylogeny of the Mephitidae

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ABSTRACT

The upper Miocene sites of Hadjidimovo and Kalimantsi in southwestern Bulgaria have yielded fossils of three musteloids: the ailurid *Simocyon* Wagner, 1858, the mustelid *Promeles* Zittel, 1890, and several skulls of *Promephitis* Gaudry, 1861, an Eurasian member of the Mephitidae. Extant mephitids are represented by three New World and one South-Asian genera. *Palaeomephitis* Jäger, 1839, *Miomephitis* Dehm, 1950, and *Proputorius* Filhol, 1890, from the Middle Miocene of Europe, as well as several American Clarendonian to Hemphillian (late middle to late Miocene) genera have also been ascribed to the Mephitidae. We show that the mephitid status of *Palaeomephitis*, *Miomephitis*, and *Proputorius* is doubtful, and that the late Miocene *Promephitis* is at a lower grade of encephalization than modern Mephitidae and could be the sister taxon of Pleistocene and modern forms, which can be called Mephitinae. Within this subfamily, the American Pleistocene and modern taxa form the sister group of the Asian *Mydaus* Cuvier, 1821, which displays numerous autapomorphies. A major, previously unnoticed characteristic of the Mephitinae and *Promephitis* is that their P4 lingual cusp is an hypocone, unlike that of the Clarendonian American forms, in which it is a protocone. The latter taxa should therefore be excluded from the Mephitidae, although they are probably closely related.

KEY WORDS

Mammalia,
Carnivora,
Mephitidae,
upper Miocene,
Bulgaria.

RÉSUMÉ

Carnivores mustéloïdes du Miocène supérieur du Sud-Ouest de la Bulgarie, et phylogénie des Mephitidae. Les sites du Miocène supérieur de Hadjidimovo et Kalimantsi en Bulgarie du sud-ouest ont livré des fossiles de trois mustéloïdes : l'Ailuridé *Simocyon* Wagner, 1858, un crâne et sa mandibule de *Promeles* Zittel, 1890, et plusieurs crânes de *Promephitis* Gaudry, 1861, un membre eurasiatique des Mephitidae, famille représentée aujourd'hui par trois genres américains et un genre asiatique, mais à laquelle ont aussi été rapportés *Palaeomephitis* Jäger, 1839, *Miomephitis* Dehm, 1950, et *Proputorius* Filhol, 1890, du Miocène moyen d'Europe, et plusieurs genres du Clarendonien et de l'Hemphillien (fin du Miocène moyen au Miocène supérieur) américains. Nous montrons que les appartenances de *Palaeomephitis*, *Miomephitis* et *Proputorius* aux Mephitidae sont douteuses, et que *Promephitis* du Miocène supérieur n'a pas atteint le degré d'encéphalisation des Mephitidae modernes et pourrait être le groupe-frère des formes pléistocènes et actuelles, qu'on peut appeler Mephitinae. À l'intérieur de cette sous-famille, les formes américaines pléistocènes et modernes sont le groupe-frère du genre asiatique *Mydaus* Cuvier, 1821, qui présente de nombreuses autapomorphies. Nous montrons que les Mephitinae et *Promephitis* sont caractérisés par la nature de la cuspidé linguale de leur P4, qui est un hypocône, à la différence des formes du Clarendonien américain. Ces dernières doivent par conséquent être exclues des Mephitidae, bien qu'elles leur soient probablement étroitement apparentées.

MOTS CLÉS

Mammalia,
Carnivora,
Mephitidae,
Miocène supérieur,
Bulgarie.

INTRODUCTION

Upper Miocene fossiliferous continental deposits are common in Eastern Mediterranean countries, and Bulgaria is no exception. The sites of Kalimantsi and Hadjidimovo in the valleys of the Struma and Mesta Rivers, which flow southwards in the south-western corner of the country (map in Geraads *et al.* 2001) have yielded more than 30 000 mammalian fossils. Most of them have been studied, allowing placement of the main Kalimantsi assemblage at about the same biostratigraphic level as Pikermi in Greece, or slightly below it, in zone MN 12 (middle Turolian), Hadjidimovo being probably slightly earlier, perhaps in zone MN 11 (Early Turolian; Spassov 2002; Spassov *et al.* 2006; Geraads *et al.* 2011; Hristova *et al.* 2013, and references therein). Some of the carnivores remain unpublished, and we describe and discuss below those that can be ascribed to the Mephitidae, Mustelidae and Ailuridae, i.e., all members of the Musteloidea, as these sites yielded no Procyonidae.

MATERIAL AND METHODS

The fossils from Kalimantsi and Hadjidimovo described below are part of the rich collections built up under the leadership of the late D. Kovachev, and deposited in the Kovachev Museum of Paleontology (a branch of the National Museum of Natural History, Sofia), Assenovgrad, Bulgaria. We have compared them to modern and fossil material kept in the institutions listed below. Skull HD-9505 was CT-scanned at the AST-RX platform of the MNHN, with a voxel size of 43.7 µm, and reconstructed with Mimics®, allowing visualization of tooth morphology and some internal cranial structures.

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History;
CCEC	Centre de Conservation et d'Étude des Collections, Lyon, France;
HD	Hadjidimovo;
K	Kalimantsi;
LPGUT	Laboratory of Geology and Paleontology, University of Thessaloniki, Greece;
MCGL	Musée Cantonal de Géologie, Lausanne, Switzerland;
MNHN	Muséum national d'Histoire naturelle, Paris;
NBC	Naturalis Biodiversity Center, Leiden, Netherlands;
NHMUK	Natural History Museum, London;
NHMW	Naturhistorisches Museum Wien, Austria;
NMNA	Kovachev Museum of Paleontology (branch of the National Museum of Natural History, Sofia), Assenovgrad, Bulgaria.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Sub-Order CANIFORMIA Kretzoi, 1943
Infra-Order ARCTOIDEA Flower, 1869
Superfamily MUSTELOIDEA Fischer, 1817

Family MEPHITIDAE Bonaparte, 1845

DESCRIPTION

Members of the Mephitidae, consisting today of the American skunks (*Mephitis* Geoffroy Saint-Hilaire & Cuvier, 1795, *Spilogale* Gray, 1865, and *Conepatus* Gray, 1837) and south-Asian stink badgers (*Mydaus* Cuvier, 1821), were previously included in the Mustelidae but are now united in a family of their own, which is not more closely related to the Mustelidae than to some other Musteloidea (Dragoo & Honeycutt 1997; Finarelli 2008; Eizirik *et al.* 2010; Nyakatura & Bininda-Emonds 2012; Catalano *et al.* 2015). Their best-known osteologic feature is the lateral expansion of the epitympanic recess into the

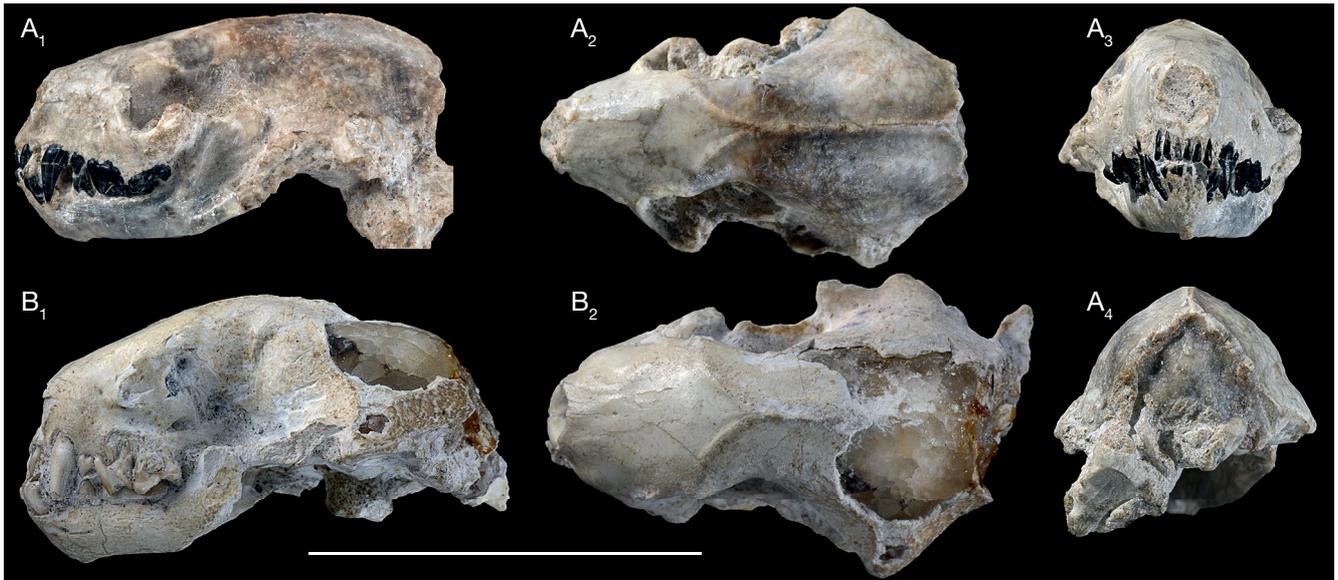


FIG. 1. — *Promephitis* Gaudry, 1861 from Hadjidimovo: **A**, *Promephitis majori* Pilgrim, 1933 (HD-9505) in lateral (**A**₁), dorsal (**A**₂), rostral (**A**₃), and occipital (**A**₄) views; **B**, *Promephitis lartetii* Gaudry, 1861, HD-9508 in lateral (**B**₁) and dorsal (**B**₂) views. Scale bar: 5 cm.

petrosal and squamosal, forming a large sinus that inflates the ventral part of the lateral side of the braincase, if not its ventral side. In some Mustelidae, such as *Taxidea* Waterhouse, 1839 and *Melogale* Geoffroy Saint-Hilaire, 1831, there is also a large sinus in this area, but in the former genus it communicates with the bulla through a wide, caudal opening, whereas in the latter it can be considered as an expansion of the suprameatal fossa (what Schmidt-Kittler 1981: fig. 12, called the epitympanic recess in “*Helictis*” is in fact the tensor tympani fossa; the expansion of what he called the “Fossa suprameatale” corresponds to the epitympanic recess). In these latter genera the epitympanic recess, although relatively deep, has no connection with the mastoid sinus, and the latter is, therefore, not homologous with the mephitid one, although probably playing the same role. The Mephitidae may also be characterized by the extreme shortening of the premolar row. A major feature of the Mephitidae, seemingly previously unnoticed, is that the major cusp of the lingual talon of P4, when present, is a hypocone, because it interlocks within the trigonid of m1, and not a protocone as reported by most authors (Pilgrim 1933; Şenyürek 1954; Petter 1971; Baskin 1998; Koufos 2006; Wang & Carranza-Castañeda 2008). Bryant *et al.* (1993) recognized the presence of a hypocone in *Mydaus*, but incorrectly denied its presence in *Mephitis*. Other diagnostic features, although not exclusive of this family (e.g., Baskin 1998; Finarelli 2008) are the palatine foramina open far rostrally; the choanae are separated by a bony septum; there is no suprameatal fossa, and no osseous tentorium; M1 has a strong buccal cingulum and an expanded hypocone; on m1 the paraconid is long, the metaconid robust, the talonid large and basined, with its buccal and lingual cristids separated by notches from the trigonid; m1 has accessory roots. By far the best known and most widespread fossil form is *Promephitis* Gaudry, 1861, to which genus the Bulgarian fossils belong.

Genus *Promephitis* Gaudry, 1861

TYPE SPECIES. — *Promephitis lartetii* Gaudry, 1861 by monotypy.

EMENDED DIAGNOSIS. — A mephitid ranging in size from that of *Spilogale* to that of *Mephitis*. Skull and face short and broad; muzzle inflated; zygomatic arch robust; angle of the mandible unexpanded; mastoid sinus moderately inflated; cerebral features primitive (frontal sinus absent, sylvian sulcus not distinct, supra-sylvian short, lateral sulcus almost straight, cruciate sulcus and post-cruciate complex virtually absent); premolar series extremely shortened; P2 extremely reduced; P3 even smaller than in *Conepatus*; P4 hypocone long, tall, and distally located; buccal cingulum of M1 very strong (in part from Wang & Qiu 2004).

One skull from Bulgaria, HD-9505, was CT-scanned; it is thus much better known, and we will start with the description of the species to which this specimen belongs.

Promephitis majori Pilgrim, 1933

HOLOTYPE. — Well-preserved cranium AMNH 20585, from Quarry 1 in Samos, Upper Miocene, probably close to 7 Ma (Koufos *et al.* 2009).

REFERRED MATERIAL FROM BULGARIA. — HD-9505, cranium with mandible.

DIAGNOSIS. — A species slightly smaller than the type species, *P. lartetii*. Snout less inflated, occipital relatively higher.

DESCRIPTION

HD-9505 is an almost complete, well-preserved specimen that includes the cranium and attached mandible (Fig. 1A). Being virtually undistorted, it was chosen for CT-scanning, but poor contrast between bone and sediment and imperfect internal preservation made observation of fine structures very limited. The description below includes both its externally visible features and those only visible in the 3D reconstruction.

TABLE 1. — Cranial measurements of *Promephitis* Gaudry, 1861 (in mm). Reference: 1, Koufos 2006.

	condylo-basal length	width over mastoids	width across orbits	width over post-orbital processes	post orbital width	length C-M1
<i>P. majori</i> Pilgrim, 1933						
HD-9505	53.8	33.7	15.5	16.2	12.9	16.9
AMNH 20585 holotype	53.6	33	16.6	17.3	14.7	17.1
<i>P. lartetii</i> Gaudry, 1861						
K-9504	–	c. 39.7	19.9	21.6	16.7	–
HD-9506	59.4	38.2	18.2	20	16	18.5
HD-9508	c. 58	39.5	19.5	20.8	15.4	17.5
NHMMW A4798 ¹	c. 59	–	–	20.6	–	–
<i>P. maeotica</i> Alexejew, 1915	67.5	44	22	24	16.6	21.4

The skull is small (measurements: Table 1), about as large as that of *Spilogale putorius* (L.), and much more similar, in its short, broad face to American mephitids than to the south-Asian *Mydaus*. The facial sutures are not discernible. The nasal opening is slightly higher than broad; the anterior border of the orbit is located above the metacone of P4 but the face is short because the teeth are crowded rostrally. The snout narrows rostrally and is inflated, as in American mephitids, with no concave part, except shallow depressions between the canine and nasal aperture, and at the infra-orbital foramen, which is single and small. On the palate, the incisive foramina are large, and the choanae reach the level of the middle of M1; they are separated by a bony septum. The orbit is small, and limited posteriorly by a blunt but conspicuous post-orbital process of the frontal; the zygomatic arch is broken off. The temporal lines converge slightly behind the post-orbital constriction, where the skull is narrower than across the orbits, to form a long, low sagittal crest that diverges, at the top of the occipital, into almost straight lambdoid crests that border a high, triangular occipital. The paroccipital processes are of moderate size, and antero-posteriorly compressed. A condyloid canal is present; the condylar (hypoglossal) foramen is located close to the occipital condyle. The jugular foramen is large. The large post-glenoid foramen is located above the anterior part of the long external auditory duct. There is no supra-meatal fossa. The bulla is poorly inflated. In ventral view, postero-laterally to it, the ventral floor of the mastoid sinus forms a smooth, concave area between the paroccipital and mastoid processes. The mastoid processes do not protrude significantly, but the skull is much broader at this level than across the paroccipital processes. Above them, the lateral walls of the braincase are laterally displaced by the expansion of the underlying mastoid sinus. In the endocranium, a distinctive feature is the very deep subarcuate fossa, housing a long paraflocculus (Fig. 2A).

Because of cracks in the walls of the braincase, the reconstructed parts of the endocranium lack precision, but the main features are discernible. The mastoid sinus is mostly lateral with respect to the brain and labyrinth and extends far laterally; it is roughly pyramidal, with an apex above the mastoid. The frontal sinus is restricted to minute canals.

The brain shape, as reflected by the endocranial reconstruction (Fig. 2A), is remarkably primitive. The olfactory bulbs are not very large and not quite distinct from the rest of the brain. All sulci are shallow; the rhinal sulcus is located high; the sylvian sulcus is not discernible; the supra-sylvian sulcus is moderately arched, and short; the lateral sulcus is barely arched; there is no cruciate sulcus.

The CT-scan allowed examination of the well-preserved teeth (Fig. 3A-C). The upper incisors are small, with I3 slightly larger than the central ones. The canine bears small but distinct cusps at the base of the mesiolingual and distal keels. On the left side only, there is a minute P2, displaced lingually by the closeness of C and P3. P3 is a simple tooth, broadest distally, with two fused roots. P4 is a short, triangular tooth. There is a minute parastyle; the paracone is much longer and taller than the metacone, and the blade is not notched. A crest descends from the distobuccal angle of the tooth, along its distal margin, towards the main lingual cusp, but is interrupted before reaching it. This cusp, which assumes the shape of a mesiobuccally to distolingually compressed cone along the distolingual margin of the tooth, is a hypocone, because it interlocks with the trigonid of m1. The protocone is indistinct as a cusp, but forms a small shelf instead. M1 is slightly longer than P4, but much broader than long. The paracone and metacone are subequal in size; an extremely strong buccal cingulum greatly increases the width of the tooth; its mesial half forms a high, strong ridge around the paracone, and almost forms a cusp near the middle of the tooth. The protocone is crescentic, and separated from the buccal blade by a narrow valley, but not too much weight should be given to this morphology, because there is much variation in the shape of the postprotocrista in modern forms; the hypocone consists of a long crescent along the distolingual edge of the tooth. Dental measurements are given in Table 2.

The mandibular symphysis has a moderately inclined ventral border. The masseteric fossa is limited ventrally by a sharp crest that descends antero-ventrally from the condyle; ventrally to this ridge, the angle of the mandible is reduced, so that the ventral border of the mandible clearly ascends from below m1 to the angular process, which is located close to the condyle.

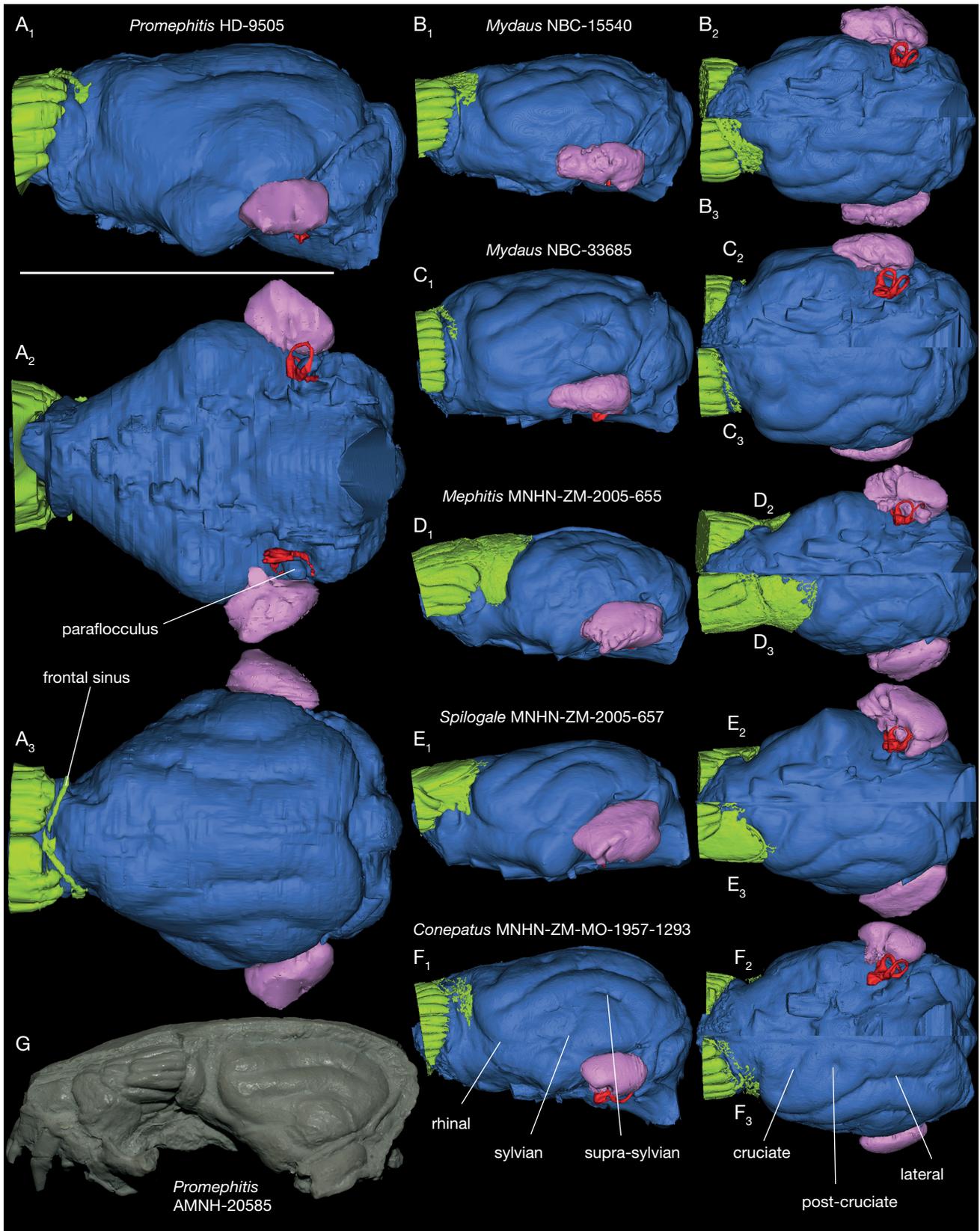


FIG. 2. — Reconstruction of the endocranial structures in the Mephitidae, showing the brain, frontal sinus, mastoid sinus, and semi-circular canals: **A**, *Promephitis majori* Pilgrim, 1933 (HD-9505) in lateral (**A₁**), ventral (**A₂**), and dorsal (**A₃**) views; **B**, *Mydaus javanensis* (NBC-15540) in lateral (**B₁**), ventral (**B₂**), and dorsal (**B₃**) views; **C**, *Mydaus javanensis* (NBC-35685) in lateral (**C₁**), ventral (**C₂**), and dorsal (**C₃**) views; **D**, *Mephitis mephitis* (MNHN-ZM-2005-655) in lateral (**D₁**), ventral (**D₂**), and dorsal (**D₃**) views; **E**, *Spilogale putorius* (MNHN-ZM-2005-657) in lateral (**E₁**), ventral (**E₂**), and dorsal (**E₃**) views; **F**, *Conepatus chinga* (MNHN-ZM-MO-1957-1293) in lateral (**F₁**), ventral (**F₂**), and dorsal (**F₃**) views; **G**, cast of AMNH-20585, holotype of *P. majori*. Colors: **blue**, brain endocast; **green**, frontal and nasal sinuses; **pink**, mastoid sinus; **red**, semicircular canals. Scale bar: A, 5 cm; other figures, not to scale.

TABLE 2. — Tooth measurements of *Promephitis* (in mm). Abbreviations: **L**, length; **W**, width; **Wmax**, oblique maximum width. References: 1, Koufos 2006, mean left and right; 2, Pilgrim 1933; 3, measured on cast; 4, Şenyürek 1954; 5, Alexejew 1915; 6, this measurement at least is clearly incorrect; from the photos provided by M. Sotnikova, M1 is almost exactly as long as P4; 7, measurements provided by J. O. Ebbestad; 8, Bonis 2005; 9, Schlosser 1924.

Upper teeth	C		P3		P4		M1			
	L	W	L	W	L	W	L	W	Wmax	
<i>P. lartetii</i> Gaudry, 1861										
MNHN.F.PIK3019 (holotype)	–	–	–	–	6 ?	c. 4.2	–	–	8.1	
HD-9507	–	–	–	–	6	4.7	5.9	6.5	8.1	
HD-9508	3.6	–	c. 2.5	–	6.3	–	6.8	–	–	
PER-1278 ¹	4.45	3.45	3.8	2.2	6.8	5.6	c. 6.4	c. 8.0	–	
NHMMW A4798 ¹	4	3.45	–	–	6	4.4	5.55	7.9	–	
<i>P. majori</i> Pilgrim, 1933										
AMNH-20585 holotype ²	3.5	2.3	2	1.6	5.6	4.1	5.6	6.5	7.23	
HD-9505	3.1	1.9	2	1.4	5.5	4.2	5.4	7.5	7.9	
<i>P. hootoni</i> type ⁴										
	4	3.1	2.8	1.9	6.1	5.1	5.7	7.6	–	
<i>P. maeotica</i> type ⁵										
	4.8	3.3	2.5	2	7.1	5.3	5.76	9.1	–	
<i>P. alexejewi</i> type ⁷										
					7.16	–	6.23	–	–	
Lower teeth	c		p3		p4		m1		m2	
	L	W	L	W	L	W	L	W	L	W
<i>P. lartetii</i>										
MNHN.F.PIK3019 (holotype)										
	3.9	–	2.6	–	–	–	8.8 ?	–	–	–
HD-9505	3.1	2.1	2.3	–	3.2	2.1	8.5	3.6	2.4	2.8
HD-9508	3.7	–	2.5	–	3.5	–	c. 9.3	–	–	–
PER-1278 ¹	4.5	3.7	3.2	2	3.55	3.4	8.6	4.4	3.5	3.4
NHMMW A4798 ¹	3.5	3	2.55	1.75	3.5	2.5	8.45	3.8	–	–
Akkaşdağ ⁸	4.2	2.9	2.6	2	3.9	2.9	8.5	3.9	–	–
<i>P. majori</i> holotype ²										
	3.5	1.8	2	1.4	3	2	7.9	3.5	2.4	2.4
<i>P. hootoni</i> holotype ⁴										
	4	3	2.5	1.8	3.7	2.8	8.8	4.3	–	–
<i>P. maeotica</i> holotype ⁵										
	–	–	–	–	–	–	10.2	4.7	–	–
<i>P. alexejewi</i> holotype ⁹										
	–	–	–	–	–	–	10.6	4.8	–	–

The lower incisors are vertically inserted, and mesiodistally narrow, with i3 slightly larger than i1 and i2. The canine has a strong ridge around its lingual half. There are only two premolars, but on neither side is the area between p3 and the canine well preserved, so that the presence of a p2 cannot definitely be ruled out. The p3 and p4 have two roots and are tall and slender, with a steep mesial edge, a distinct cingulum mesially and a broad distal part, bordered by a robust cingulum on p4.

On m1, the trigonid is slightly longer than the talonid. The protoconid is by far the tallest cuspid; it is unconnected to the metaconid, but a cristid descends towards the hypoconid, from which it is separated by a notch. In connection with the long, oblique hypocone of P4, the metaconid is distinctly more posterior than the protoconid, and the paraconid is long and longitudinally oriented, so that the three cuspids form an angle distinctly larger than 90°. The talonid is deeply basined, the central depression occupying most of the area, and the ridge-like cuspids being marginally located. The hypoconid is taller than the entoconid; in front of the latter is a second lingual cuspid, separated from the metaconid by a notch, deeper in the right m1. The CT-scan shows that the left m1 has a single accessory buccal root while the right one also has an additional lingual one; we observed the same variability in CT-scanned *Mydaus* skulls, with NBC-33685 having a single, accessory lingual root and NBC-14540 having both lingual and buccal accessory roots. The m2 is shorter than broad, and also consists of a central basin circled by ridge-like elements.

Promephitis lartetii Gaudry, 1861

Promephitis hootoni Şenyürek, 1954: 281, figs 1-14.

HOLOTYPE. — Much distorted skull and attached mandible from Pikermi, Greece (MNHN.F.PIK3019).

REFERRED MATERIAL FROM BULGARIA. — There are three skulls of *Promephitis lartetii* from Hadjidimovo, and one from Kalimantsi. The latter, K-9504, is very incomplete as it includes only the dorsal part of the braincase and frontal area; HD-9506 is a relatively complete cranium but is somewhat crushed dorsoventrally and the dentition is in poor condition; HD-9507 is much distorted and lacks most of the snout and dentition, except the right P4-M1; HD-9508 is an undistorted skull with attached mandible, but it lacks most of the parietals and occipital.

DIAGNOSIS. — A species of *Promephitis* slightly larger than *P. majori*; snout more inflated, broader over the canines; occipital lower.

DESCRIPTION

HD-9508 (Fig. 1B) is very similar to HD-9505, assigned above to *P. majori*, and we will mostly note the differences. It is slightly larger; the difference does not exceed what one would expect within a single species, but the other specimens are dimensionally close to HD-9508 rather than intermediate between it and HD-9505, suggesting bi-modal size distribution (Tables 1; 2). The face of HD-9508 is distinctly broader in the frontal region and the snout is more inflated;

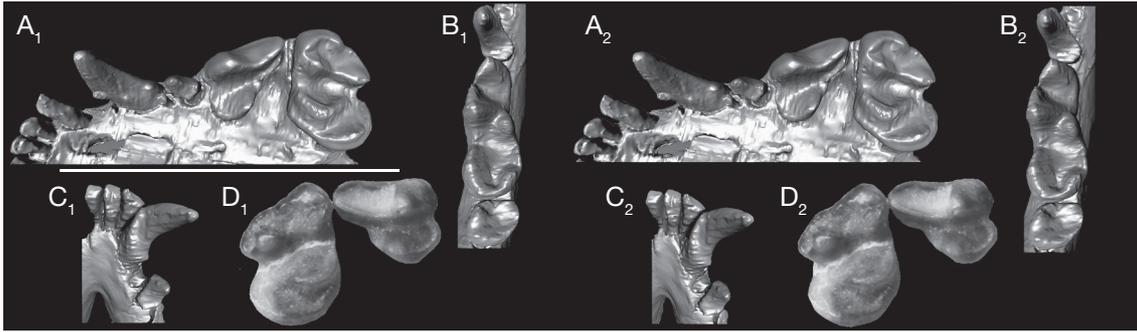


FIG. 3. — Dental remains of Bulgarian Mephitidae: **A-C**, *Promephitis majori* Pilgrim, 1933 (HD-9505); **A**, 3D model of left I1–M1 in occlusal view (stereo pair **A₁–A₂**); **B**, 3D model of left p4–m2 in occlusal view (stereo pair **B₁–B₂**); **C**, 3D model of right i1–p3 in occlusal view (stereo pair **C₁–C₂**); **D**, *Promephitis lartetii* Gaudry, 1861 (HD-9507), right P4–M1 (stereo pair **D₁–D₂**). Scale bar: 2 cm.

the post-orbital processes are slightly better developed, but remain weak. The occipital is relatively lower. A minute P2 is present on the right side at least. The buccal cingulum of M1 is less prominent than in HD-9505. A minute p2, displaced lingually, is visible between the canine and p3. The p3 and p4 are similarly tall and slender, with mesial and distal accessory cusps.

Skull HD-9506 is similar in size to HD-9508 and has the same broad snout, but no details are observable. HD-9507 has well-preserved P4 and M1 (Fig. 3D); on P4 there is a distinct ridge descending from the hypocone around the mesio-lingual part of the tooth, which is more expanded than in HD-9505, although without forming a distinct protocone. The buccal cingulum of M1 is moderate. The skull fragment K-9504 also agrees in size and snout width with HD-9508; its sagittal crest was certainly shorter, if not absent, but whether this is due to individual variation or to the age difference between the sites is unknown.

COMPARISONS

We compared the Bulgarian material with most modern species of Mephitidae and to fossil material from Pikermi (MNHN) and Perivolaki (LPGUT) in Greece. In addition, G. Koufos made available photos and cast of skulls from Samos, whose original specimens are stored in the AMNH and NHMW, and M. Sotnikova provided photos of material from Novo Elisavetovka, Ukraine.

All skulls of *Promephitis* from Hadjidimovo and Kalimantsi are very similar, and the presence of two species is not obvious at first sight. However, of the two best preserved skulls, HD-9508 is distinctly larger than HD-9505, and some of the few dental measurements are also larger. The main difference is in the greater inflation of the fronto-maxillary area, especially in the rostral part; the width of the maxilla over canine roots, in front of the infra-orbital foramina, is 18.9 mm in HD-9508, in contrast to only 13.6 mm in HD-9505. Given the documented co-occurrence of two different species of *Promephitis* in the late Miocene of China (Wang & Qiu 2004), and of modern species of both *Mustela* and *Martes* in Europe (Geptner *et al.* 1967; Wolsan 1999a; Šálek *et al.* 2013), we have no hesitation in referring these two skulls to different

species, but it is not so easy to clarify the systematics of European and Eastern Mediterranean forms of the genus.

Few characters are observable on the type specimen of the type species, *P. lartetii* from Pikermi, because of its extreme crushing, and poor preservation of the teeth. The few cranial measurements provided by Gaudry of the specimen that he figured (Gaudry 1862: pl. 6), repeated by several authors since then, are either grossly incorrect or unreliable. Neither the few dental measurements that can be taken nor the morphology differ from those of the two Hadjidimovo species. Pilgrim (1931: 53) diagnosed *P. lartetii* in having a “metacoinid of m1 somewhat in front of the protoconid”, but this is clearly incorrect. However, the mandible of the holotype is distinctly longer from condyle to most rostral point of the dentary (44.5 mm, slightly overestimated by crushing) than that of HD-9505 (36 mm), and closer to that of HD-9508 (42.5 mm), so that there is no reason to distinguish HD-9508 from *P. lartetii*, implying that HD-9505 must belong to another, smaller species.

The holotype and only specimen of *Promephitis gaudryi* Schlosser, 1902, an m1 from the Vallesian (?) of Melchingen, Germany, obviously does not belong to this genus, as noted by Pilgrim (1933) and later authors, because of its small talonid, low trigonid cusps, and lack of accessory roots. There is no reason to include it in the Mephitidae; Pilgrim (1933) assigned it to *Trocharion* Major, 1903.

The next species to be described was *P. maeotica* Alexejew, 1915 from the Turolian of Novo Elisavetovka in Ukraine. The skull is clearly distinct from those of the Bulgarian and Pikermi forms in its larger size, gently converging temporal lines, and especially in its narrow P4 with a shallow buccal depression, short hypocone located centrally instead of more distally, small but distinct protocone that bulges mesially, and extremely twisted M1. *P. maeotica* is clearly distinct from the Balkan forms. Zdansky (1937) described some remains from Baode, China, as *P. cf. maeotica*, with which they agree in size, but Wang & Qiu (2004) referred them to another species, *P. hootoni* Şenyürek, 1954 (see below).

Promephitis alexejewi Schlosser, 1924 was erected for scrappy remains from Ertemte, China. Wang & Qiu (2004), on the basis of Schlosser’s measurements, assumed that this species

had a long P4 compared to M1 but the difference is less than stated by Schlosser (Table 2), and the two teeth might well be from two different individuals. Besides large size, probably due to the young geological age of the localities (the species was also reported from the uppermost Miocene of Venta del Moro in Spain by Montoya *et al.* 2011), *P. alexejewi* lacks distinctive features.

Promephitis malustenensis Simionescu, 1930 (this name was chosen by Wang & Qiu [2004], in preference to *P. rumanus*, erected by Simionescu for the same type specimen), is based upon a mandible from Mălușteni, Romania, which has far too long a premolar row to belong to this genus, but the poor illustration (Simionescu 1930: fig. 13) forbids identification.

Pilgrim (1933) erected a new species from Samos, *P. majori*. Cranial, dental and mandibular features do not differ from the few ones that can be observed in *P. lartetii*. The brain, observable on a cast of the holotype AMNH 20585 (Fig. 2G), is very similar to that of HD-9505. Dental features are also virtually identical to those of *P. lartetii*. In contrast to Pilgrim's claims, there is no evidence that: 1) M1 is shorter than P4 in *P. lartetii*; 2) a parastyle was present in the P4 of *P. majori*, as the missing mesial part of P4 may just be the paracone; and 3) a P1 and/or a P2 was present in *P. lartetii*. The clearest difference is of size: the teeth are slightly smaller in *P. majori* (Table 2), and so is the length of the mandible (35 mm according to Pilgrim [1933], vs 44.5 mm in the type of *P. lartetii*). In addition, *P. majori* differs from specimens assigned to *P. lartetii* (other than the distorted type) in its relatively high occipital, a feature also present in HD-9505. Thus, *P. majori* differs from *P. lartetii* in the same way as HD-9505 differs from HD-9508, and we refer HD-9505 to *P. majori* and HD-9508 to *P. lartetii*.

Şenyürek (1954) erected *P. hootoni* for a partial skull and associated mandible from the Turolian of Küçükyozgat (Western Turkey); listed differences from previously named species are either subtle or non-existent, being based on Gaudry's (1862) incorrect drawings and measurements (presence vs absence of postorbital process and of p2, shape of the ventral mandibular corpus). In size and inflation of the snout, the type of *P. hootoni* matches *P. lartetii* and HD-9508, so that there is no reason to separate it from this species, as also suggested by Koufos (2006). Bonis (2005) described as *P. hootoni* a mandible from Akkaşdağı (Turkey); assuming that the scale (Bonis 2005: fig. 14) is correct, this mandible is indeed likely to represent *P. lartetii*.

Promephitis pristinidens Petter, 1963, from the Vallesian of Spain, is based on a maxilla fragment in which P4 has a distinct parastyle and a weak lingual talon with no distinct cusp, while M1 has a poorly inflated hypocone and weak buccal cingulum. These are primitive features, but no derived character links this form with later *Promephitis*, and we consider the generic assignment unsupported, although it could be an early member of this group.

Promephitis brevirostris Meladze, 1967 from Bazaleti in Georgia is so poorly known that it is better to restrict the name to the type series, and regard it as a nomen dubium.

The loss of one pair of incisors may have occurred post-mortem.

Among other significant remains of *Promephitis* in the Eastern Mediterranean, there is a skull from Samos NHMW A4798, discussed by Koufos (2006), who concluded that it suggests the presence of a larger species at Samos, in addition to the smaller *P. majori*. We agree with him; although the occipital is dorsoventrally compressed, in its broad, inflated snout and overall size, A4798 matches HD-9507 and HD-9508 and we assign it to *P. lartetii*.

The material from Perivolaki in Greece is crushed and distorted, but the mandible length of LPGUT-PER-1278 (42.2 mm) is close to those of HD-9508 and of the type of *P. lartetii*, a species to which Koufos (2006) ascribed it. We agree with his identification, even though P3, p3, and p4 are larger than usual in this species.

We conclude that, in the Turolian of Western Eurasia, *Promephitis* includes three species, in decreasing size order *P. maeotica* from Novo Elisavetovka, *P. lartetii* from Pikerimi, Samos, Perivolaki, Küçükyozgat, Akkaşdağı, Hadjidimovo and Kalimantsi, and *P. majori* from Samos and Hadjidimovo. Thus, in these two latter sites (although the precise origin of the Samos fossils is unknown), both species co-exist, the smaller form being rarer.

From the Pliocene of China, He & Huang (1991) described *P. maxima*; it is much larger than Upper Miocene forms but there is reason to doubt the generic attribution, although the illustrations are too imperfect for detailed comparisons.

Wang & Qiu (2004) described rich collections from the Upper Miocene of China, and named two species *P. parvus* and *P. qinensis*, in addition to what they called *P. hootoni* which is, in our opinion, identical with *P. lartetii* (the teeth are very similar to those of HD-9507, and differ from other Chinese species, in their much expanded P4 talon, strong buccal cingulum around the paracone of M1, and deep distal notch on this tooth; their size is similar to those of *P. lartetii*, and the muzzle is broad in both forms). We have not seen this material, but the coexistence of two species of different sizes, as in some Eastern European sites, is worth noting.

CONTENTS OF THE FAMILY MEPHITIDAE

The removal of the Mephitidae from the Mustelidae is now generally accepted. The inclusion of the South-Asian *Mydaus* (including *Suillotaxus* Lawrence, 1939) in the Mephitidae, first suggested by Pocock (1921) and more recently by Petter (1971) and Radinsky (1973), has been confirmed by recent molecular analyses (e.g., Flynn *et al.* 2005; Nyakatura & Bininda-Emonds 2012; Sato *et al.* 2012). All recent analyses (Bryant *et al.* 1993; Finarelli 2008; Wang & Carranza-Castañeda 2008; Eizirik *et al.* 2010) recognize that the three extant genera of New World mephitids, together with the closely related Pleistocene genera *Osmotherium* Cope, 1896 and *Brachyprotoma* Brown, 1908 but to the exclusion of Eurasian *Mydaus*, *Promephitis* and *Palaeomephitis*, form a monophyletic group, the Mephitini. Relationships of other purported Mephitidae with this core group are discussed below.

Miocene Eurasian Forms

Palaeomephitis steinheimensis Jäger, 1839 is based upon the posterior half of a Middle Miocene juvenile skull from Steinheim described by Helbing (1936) as *Trocharion albanense*, and further discussed by Wolsan (1999b). Helbing (1936) noted that it differs from *Conepatus* and *Promephitis majori* in that the condylar foramen is distinct from the posterior lacerate foramen, but this is incorrect, as they are also separated in *Conepatus* and in HD-9505, while Pilgrim (1933) made no positive observation on the type of *P. majori*. Wang *et al.* (2005) accepted *P. steinheimensis* as a member of the Mephitidae. However, this family attribution solely rests on the assumption that the enlarged mastoid sinus is homologous with the mephitid one, i.e., that it is an expanded epitympanic recess, but the large opening to which Wolsan (1999b) gave this name faces ventrally instead of medially as in the Mephitidae, showing that this area is imperfectly preserved. Given that this partial cranium is probably (Wolsan 1999b) of the same taxon as the highly derived teeth called *Trochotherium cyamoides* Fraas, 1870, and that it further differs from the Mephitidae in the presence of a supra-meatal fossa and large caudal entotympanic, we believe that the mephitid affinities of *Palaeomephitis* remain doubtful. What is known of the still earlier *Miomephitis* Dehm, 1950 also lacks clear mephitid characters and is best left aside. *Proputorius* Filhol, 1890, is known only by dental and mandibular remains that display no exclusive mephitid features. In the best known species, *P. sansaniensis* Filhol, 1890, from the Middle Miocene of Sansan, the P4 has a very small and mesially located protocone (Peigné 2012: figs 88, 89), unlike that of modern Mephitidae; the seven isolated m1s have no accessory roots. Pending cranial evidence, we do not include this genus in the Mephitidae. The m1 of the Vallesian type species of the poorly known *Mesomephitis* Petter, 1967, *M. medius* (Petter, 1963) from Can Llobateres, Spain, differs from that of the Mephitidae in its low lingual talonid margin and lack of accessory roots, and inclusion in this family is poorly supported. We conclude that *Promephitis* is the only definite fossil Old World member of the Mephitidae.

American forms

Wang & Carranza-Castañeda (2008) included in one clade, together with what we have called Mephitini above but to the exclusion of *Mydaus* and *Promephitis*, the Miocene to Pliocene *Martinogale* Hall, 1930 and *Buisnictis* Hibbard, 1950. They defined this clade by: 1) the presence of a parastyle on P4; 2) a hypoconid taller than the entoconid on m1; and 3) a cingulum not surrounding the protocone on M1. However, characters (1) and (2) are also present in Bulgarian *Promephitis*, and character (3) is quite variable, as we have observed many Mephitini in which the cingulum surrounds the protocone of M1.

In fact, a previously unnoticed character clearly separates modern and Plio-Pleistocene forms from earlier North American ones: in the latter, the P4 lingual cusp is clearly a protocone, because it is located mesially or very mesially (Hibbard 1950:

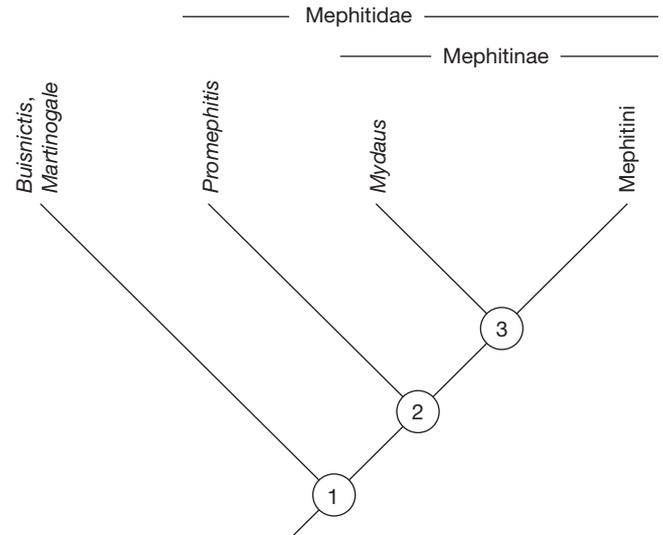


FIG. 4. — Most likely relationships of the mephitids. Main apomorphies are: **Node 1**, expansion of the epitympanic recess into a mastoid sinus, extra-roots on m1; **Node 2** (Mephitidae), rhinal sulcus higher, P2 smaller, P4 protocone much reduced, P4 hypocone large; **Promephitis**, face short, broad, and inflated, anterior premolar series much shortened, strong basal cingulum on canines, P4 hypocone long and tall, M1 very large, with strong buccal cingulum; **Node 3** (Mephitinae), shallow fossa subarcuata, slender zygomatic arch, angular region of the mandible somewhat expanded, masseteric fossa shallow, distinct sylvian sulcus, long supra-sylvian sulcus (less so in *Mephitis*), arched lateral sulcus, cruciate and post-cruciate sulci present; **Mydaus**, long and narrow skull and face, long premolar row, choanae far behind M1, indistinct tensor tympani fossa, incisors in broad arch, lower ones procumbent and spatulate, M1 buccal cingulum absent, femur trochanter low, shallow intertrochanteric fossa; **Mephitini**, no protocone on P4, angular region of the mandible more expanded, loss of epitrochlear foramen on the humerus.

fig. 21, in *Buisnictis meadensis*; Stevens & Stevens 2003: fig. 9.8, in *Buisnictis chisoensis* Stevens & Stevens, 2003; Wang *et al.* 2005: fig. 5, in *Martinogale faulli* Wang, Whistler & Takeuchi, 2005; Wang *et al.* 2014: fig. 5A, in *Buisnictis metabatos* Wang, Carranza-Castañeda & Aranda-Gómez, 2014); the P4 of *M. alveodens* remains unknown, since the tooth described under this name by Baskin (1998: 159) belongs to *M. faulli* (J. A. Baskin pers. comm.). This sharply contrasts with the condition in modern and Pleistocene American Mephitini, also found in *Mydaus* and *Promephitis*, in which the lingual cusp interlocks with the trigonid of m1 and is therefore a hypocone. We regard this difference in homology of the lingual cusp of P4 as fundamental, and sufficient to exclude *Martinogale* and *Buisnictis* from the clade containing *Promephitis* and modern Mephitidae. It echoes to the suggestion of Baskin (1998), followed by Stevens & Stevens (2003), that the American “mephitids” were the result of two migration waves, one in the Clarendonian giving rise to *Martinogale* and *Buisnictis*, and a second one in the early Blancan giving rise to modern and closely related genera. If the inflated mastoid sinus of *Martinogale* and *Buisnictis* is homologous of the one found in modern Mephitidae, these genera could be the sister group of this family, but they are not part of the clade in which the P4 lingual cusp is a hypocone. As a consequence, we will restrict the following discussion to these latter forms.

TABLE 3. — Tooth measurements (in mm) of *Promeles* spp. Abbreviations: **L**, length; **W**, width. References: 1, Weithofer 1888 ; 2, Koufos 2006; 3, Kaya *et al.* 2005; 4, Schmidt-Kittler 1995.

Upper teeth	C		P3		P4		M1	
	L	W	L	W	L	W	L	W
<i>P. palaeattica</i> (Weithofer, 1888)								
type 1	–	–	6	3.3	9	3.7	6.5	10
K-9502	–	–	–	–	9.7	5.4	8.5	c.11
M 9028	–	–	–	–	10.4	6.5	9.8	12.9
M 9029	–	–	–	–	9.6	6	7.8	11.4
PER-1280 2	5.2	4.2	5.3	3.2	8.3	5.7	9.7	–
MCGL S272	–	–	–	–	10.3	6.6	–	–
<i>P. smyrnensis</i> Kaya, Geraads & Tuna, 2005	5.2	–	5.7	3.1	10.2	6.3	6.8	9.9
IKE-33 3	–	–	–	–	–	–	–	–
<i>P. macedonicus</i> Schmidt-Kittler, 1995 MA 406 4	–	–	–	–	8.2	6.8	6.6	9.3
Lower teeth	p3		p4		m1		m2	
	L	W	L	W	L	W	L	W
<i>P. palaeattica</i>								
K-9503	5.3	3	5.9	3	13.5	5	–	–
type 1	4.8	2.6	6.3	3	11.8	5	4.5	4.2
M 9028	–	–	7	3.8	15	7	–	–
M 9029	–	–	6.4	3.6	12.8	6	–	–
M 9030	–	–	–	–	13.5	6.4	–	–
PER-1280 2	5	3	6.3	3.2	12.3	5.4	4.6	4.4
<i>P. macedonicus</i> MA 409 4	–	–	–	–	10.7	4.7	–	–

PHYLOGENY OF THE MEPHITIDAE

Parsimony analysis

The main distinctive characters of *Promephitis*, of modern genera, and of the purported American Clarendonian mephitids are listed in Appendix 1. A parsimony analysis conducted with TNT (Goloboff *et al.* 2008), using any of the latter as outgroup, yields a single shortest tree shown in Appendix 2, of which Figure 4 would be a simplified version. *Promephitis* appears as the sister group of a clade, including all modern forms, defined by several characters reflecting increased brain complexity and a stronger superficial masseter muscle. This might look surprising given the overall skull similarity between *Promephitis* and modern American forms, but the cladogram suggests that reluctance to admit *Mydaus* within the Mephitinae is based upon features that are in fact autapomorphic. It could be argued that the derived brain characters that unite *Mydaus* with the American Mephitini are merely the consequence of the well-known increased complexity of carnivore brains over time, and could have in fact occurred in parallel, as also suggested by the very unlikely reversal that is inferred for *Mephitis*. Still, this cladogram is in agreement with chronology, and it is also informative in highlighting the numerous autapomorphies of *Promephitis* and *Mydaus*, but we certainly do not take it at face value.

Pleistocene and modern American forms (Mephitini) share small incisive foramina, a larger P4 parastyle, complete loss of P4 protocone, and a shelf-like hypocone more mesially located than in Eurasian forms, a mandible with expanded angular area, and loss of the entepicondylar foramen in the humerus. Their monophyly matches geography, and thus is strongly supported. Some further characters used by Finarelli (2008) to define the American clade; but, in contrast to his figure 3, their mastoid process is not weaker than in *Promephitis*, the

metacone-metaconule crest is not better indicated on M1, and the m1 is not more basined, so that the only remaining additional synapomorphy of the Mephitini would be the reduction of the buccal cingulum of M1. However, this cingulum is so strong in *Promephitis* that it is more probably its condition that is derived.

A Eurasian Clade?

Wang & Carranza-Castañeda (2008) recognized the fossil and recent American and Eurasian Mephitidae as sister-groups. Of the characters that they used to define the Eurasian clade, the reduction of P2 and the lengthening of M1 are also found in most American forms, and the exclusion of the maxillae from the border of the incisive foramina is hard to document because these bones are fused with the premaxillae (even the CT-scans failed to visualize their limits). Wang *et al.* (2005) also considered as a derived feature of Eurasian forms the lack of a notch between entoconid and metaconid in m1, but this notch is present in *Mydaus* and *Promephitis*. The only important feature shared by *Mydaus* and *Promephitis* is the shape of the hypocone of P4.

The Position of Promephitis

Compared to other Mephitidae, *Promephitis* has both more primitive and more derived characters. Among the latter are some features of the dentition, such as the marked basal cingulum on canines, the reduction of the anterior premolar series, and the very large M1 with a prominent buccal cingulum; *Promephitis* brought these trends further than other mephitids. However, it also retains primitive traits that are lost in *Mydaus* and American Mephitini. The brain remains at a very primitive stage of folding. The zygomatic arch is of normal size, which is probably related to a deep masseteric

fossa in the mandible, which lacks the ventral flat extension of the Mephitinae; in the latter, the very slender zygomatic arch, shallow fossa and ventrally expanded angular region are probably related to the greater importance of the superficial masseter, which might, as in *Procyon* (Gorniak 1986), originate on an aponeurosis and not on the arch itself. Lastly, the subarcuate fossa is deep; the polarity of this character is debatable, but the resemblance of *Promephitis* with *Mustela* is striking.

THE POSITION OF *MYDAUS*

Finarelli (2008) excluded *Mydaus* from a clade consisting of *Promephitis* and the Mephitini, defined by: 1) more anterior choanae; 2) lack of a condyloid canal; 3) M1 hypocone formed by swelling of the cingular ridge; 4) parastyle stronger than metastyle on M1; and 5) M1 parastyle oriented mesio buccally. In fact, the very caudal choanae of *Mydaus* are obviously derived, a condyloid canal is present in *Promephitis*, and there is no reason to differentiate the origin of the M1 hypocones in all these taxa, so that the only remaining difference is the absence of styles in the M1 of *Mydaus*. It is more likely, however, that the latter feature is derived, like many other characters: long skull and face creating a long mandibular diastema, very posterior choanae, ventrally inflated mastoid wall, indistinct tensor tympani fossa, complex post-cruciate sulcus in the brain, loss of parastyle on P4, procumbent ventral incisors, shape of m1 trigonid with a mesially located protoconid and short paraconid, and a proximal femur with a weak trochanter and flat caudal side with almost no trochanteric fossa. *Mydaus* lacks the characters, listed above, that define the Mephitini.

CONCLUSION

The monophyly of modern and Pleistocene American forms is strongly supported, and they can be called Mephitini. The identity of their sister taxon is more debatable. Overall skull shape suggests *Promephitis*, but this similarity does not hold if the skull shape of *Mydaus* is autapomorphic, as are many of its characters. We believe instead that the more derived brain morphology, slender zygomatic arch and related changes in masticatory musculature, and shallow subarcuate fossa, unite *Mydaus* with the Mephitini, as Mephitinae (Fig. 4). Regarding *Promephitis* as the sister-group of the Mephitini implies convergent brain evolution between the latter and *Mydaus*. Because of the retention of a large protocone and absence of hypocone, we exclude *Buisnictis* and *Martinogale* from the Mephitidae; they might, however, represent the sister-group of this family.

Family MUSTELIDAE Fischer, 1817

Genus *Promeles* Zittel, 1890

TYPE SPECIES. — *Mustela palaeattica* Weithofer, 1888 by original designation.

DIAGNOSIS. — Skull profile regularly curved, frontals rather broad, sagittal crest usually present but weak, choanae located very posteriorly. I3 much larger than I1-I2, canine conical, upper premolars



FIG. 5. — **A**, *Promeles palaeattica* (Weithofer, 1888), right upper tooth row of skull K-9502 from Kalimantsi; **B**, *Simocyron* sp., unnumbered right M1 from Hadjidimovo. Scale bar: 4 cm.

much increasing in size from P1 to P4, the latter with a parastyle and a strong protocone. M1 with a robust buccal cingulum along the paracone, a metacone close to the paracone, and a long, crescent-shaped protocone that ends distally in a prominent metaconule. Trigonid of m1 long, paraconid long and directed forwards, talonid about as long as the trigonid, central basin entirely surrounded by a ridge consisting of numerous cusps and cusplets.

Promeles palaeattica (Weithofer, 1888)

HOLOTYPE. — Unnumbered cranium and associated mandible, in the Institut für Paläontologie, University of Wien, Austria (Weithofer 1888: pl. 10, figs 1-11).

DIAGNOSIS. — As for genus.

REFERRED MATERIAL FROM BULGARIA. — K-9502, an incomplete cranium; K-9503, incomplete mandible.

DESCRIPTION

K-9502 (Fig. 5A) and K-9503 are probably of the same individual but, like many specimens from Kalimantsi, they are imperfectly preserved. In general shape and size, the skull does not differ from other specimens of *P. palaeattica*. The only visible cranial characters are that the front border of the orbit is above P4, and that its anterior rim overhangs the infra-orbital foramen. The incisors are inserted in a shallow arch, with I3 distinctly larger than the subequal I1 and I2. The canines are broken off; their basal outline is a poorly compressed oval. A noticeable feature is the absence of P1 on both sides, P2 coming almost in contact with the canine. The right P3 is triangular in buccal view, with minute mesial and distal cingular accessory cusps; the left cheek-teeth are missing. The P4 is short, with a thin blade; its protocone reaches farther mesially than the paracone. The very large M1 is incomplete buccally; lingually, the cingulum is widely expanded, increasing both the width and length of the tooth.

On the mandible, i2 and i3 are larger than i1; the canine is conical, separated by a very short diastema from p2; p4 has no clear distal accessory cuspid. On the incomplete m1, the protoconid is not much taller than the paraconid; the talonid is deeply basined, and bordered by a sharp rim of which the hypoconid is the tallest and most distinct cuspid. Dental measurements are provided in Table 3.

COMPARISONS

Besides the type locality, Pikermi, *Promeles palaeattica* has been reported from Samos, Maragha and Dorn-Dürkheim

(Kaya *et al.* 2005, and references therein), and Perivolaki (Koufos 2006). New species names have been erected for the specimens from Maramena in Greece (*Promeles macedonicus* Schmidt-Kittler, 1995) and Esendere in Turkey (*Promeles myrnenensis* Kaya, Geraads & Tuna, 2005) on the basis of some differences in the proportions of P4, the position of its protocone, the thickness of its blade, the size of the lingual expansion of M1, the shape of its buccal side, and the proportions of m1. Given the observed variations in the Pikermi population, it may well be that all these forms can be accommodated within *P. palaeattica*. For instance, the M1 of NHMUK M9028 is distinctly more expanded distally than that of M9029, both from Pikermi, and on M9028 the buccal cingulum is much stronger along the paracone than along the metacone, whereas it is of regular thickness on M9029. However, we refrain from synonymizing all these names because at least the specimens from Samos (MCGL S272) and Esendere seem to have less expanded M1s than at Pikermi. In any case, K-9502/K-9503 is more like the Pikermi fossils, and we ascribe it to *P. palaeattica* with confidence.

Family AILURIDAE Gray, 1843
Genus *Simocyon* Wagner, 1858

Simocyon primigenius (Roth & Wagner, 1854)

REMARKS

This species has recently been discussed by Spassov & Geraads (2011) who confirmed the identification by Bakalov & Nikolov (1962) of two incomplete mandibles from Kalimantsi. An isolated, unnumbered M1 from Hadjimidovo (Fig. 5B), badly worn and damaged, could be of the same species. It is broader mesially than distally. The central basin is open mesially, and a distinct crest descends lingually from the paracone, but the metacone and protocone are worn out. Its buccal length (16.5 mm) is close to the upper end of the range of *S. primigenius*, to which we tentatively refer it, pending revision of the early Turolian forms of Central Europe.

CONCLUSION

Three species of *Promephitis* (*P. lartetii*, *P. majori*, and *P. maotica*) can be distinguished in the late Miocene of Southeastern Europe and Turkey, with two species co-existing in some sites, as in China. *Promephitis* is an early offshoot of the Mephitidae; its sister-group (Mephitinae) includes all modern forms, with the American (and Plio-Pleistocene) species (Mephitini) being the sister-group of the Asian *Mydaus* that displays numerous autapomorphies. The subfamily Promephitinae and tribe Mydausini would therefore include a single genus each. The mephitid status of several Middle Miocene European genera is doubtful.

In addition to the well-known expansion of the epitympanic recess into the squamosal and lateral part of the petrosal, the Mephitidae can be defined by the reduction or loss of the

protocone and the presence of a large hypocone on P4; this character is definitely present in *Promephitis*, *Mydaus*, and in Pleistocene and modern American Mephitini, but not in Clarendonian forms, which should therefore be excluded from the Mephitidae.

The only Bulgarian late Miocene member of the Mustelidae is *Promeles*; we tentatively assign all late Miocene Balkano-Iranian forms to *P. palaeattica*; the genus may include more than one species, but their boundaries are unclear. A few remains represent the ailurid *Simocyon*.

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