The Middle Miocene musteloid *Trochotherium cyamoides* and the evolution of bunodont dentition in stem mephitids

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The enigmatic musteloid species *Trochotherium cyamoides* is a poorly understood carnivoran that has been found at several fossil sites in Europe dating exclusively to the latest Middle Miocene (MN 7/8). Newly described material of *T. cyamoides* from La Grive-Saint-Alban (France) and Kleineisenbach (Germany) lead to a comprehensive re-evaluation of the species and the designation of a lectotype and paralectotype from the Steinheim am Albuch type locality. The highly derived dentition of *Trochotherium* obscures its systematic position. Nevertheless, the morphology of the upper fourth premolar (P4) and the presence of accessory rootlets in the lower carnassial (m1) indicate an affinity with the family Mephitidae. In contrast, the bunodont morphology of the upper first molar (M1) and the m1 suggests that *T. cyamoides* represents a stem mephitid, closely related to the Early Miocene *Miomephitis* from Wintershof-West (Germany) and especially to the Late Miocene *Neoyunnanotherium* from Lufeng and Yuanmou (China). While previously interpreted as a semi-aquatic molluscivorous mammal, we find that its unique dental morphology among Carnivora is more similar to that of certain snail-eating marsupials and lizards, leading us to suggest that it fed primarily on terrestrial gastropods.

Key words: Mammalia, Mephitidae, *Miomephitis*, *Neoyunnanotherium*, durophagy, Miocene, Germany, France.

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Introduction

Trochotherium cyamoides Fraas, 1870, is an enigmatic medium-sized member of the superfamily Musteloidea with an extreme bunodont adaptation, found exclusively in the uppermost Middle Miocene (MN 7/8) of Europe. It was first described in the German locality of Steinheim am Albuch (MN 7/8; Fraas 1870; Helbing 1936; Heizmann 1973), and has subsequently been found in Opole-1 (Poland, MN 7/8; Wegner 1913), La Grive-Saint-Alban (France, MN 7/8; Viret 1935, 1951; Mein and Ginsburg 2002) and Anwil (Switzerland, MN 7/8; Engesser 1972) (Fig. 1). The systematic classification of *T. cyamoides* has also been a subject of debate. Wolsan (1999) proposed that *T. cyamoides* is a junior synonym of the primitive skunk *Palaeomephitis steinheimensis* Jäger, 1839. These two species are of similar size and have been found in the same type locality (Steinheim am Albuch). *Palaeomephitis steinheimensis* possesses an expanded epitympanic recess that may represent a predecessor of the enlarged mastoid sinus seen in later mephitids (Wolsan 1999; Wang et al. 2005), and its bulla has a more inflated entotympanic than in modern members of this

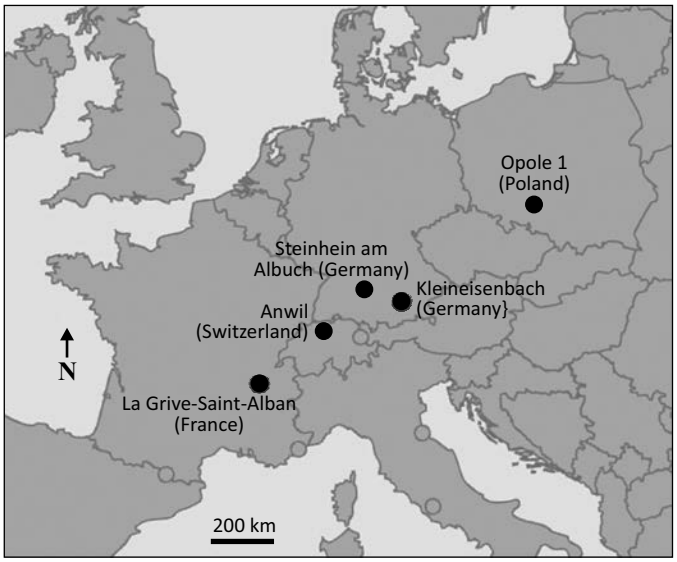

Fig. 1. Fossil sites where *Trochotherium cyamoides* Fraas, 1870, has been described from. Map created using the MapChart website.

family. However, as the synonymy with *T. cyamoides* was based on a fragmentary skull of *P. steinheimensis* without dentition (Wolsan 1999), other authors still consider *T. cyamoides* a valid taxon (Robles et al. 2010; Deshmukh and Valenciano 2022). Regarding its family and subfamily rank, some authors have interpreted *T. cyamoides* as a mustelid, either as part of the subfamilies Melinae Bonaparte, 1838 (Wegner 1913; Viret 1935; Helbing 1936; Heizmann 1973) or Leptarctinae Gazin, 1936 (sensu Qiu and Schmidt-Kittler 1982; see also Ginsburg 1999; Bonis 2005), or as a stem Mustelidae (Schmidt-Kittler 1981; Qiu and Schmidt-Kittler 1982). However, others consider it to be a member of the Mephitidae (Dehm 1950; Wolsan 1999; Robles et al. 2010) or a stem Mephitidae (Deshmukh and Valenciano 2022).

The bunodont dentition of *T. cyamoides* has been interpreted by numerous authors as ideal for a durophagous diet (Fraas 1870; Viret 1935; Helbing 1936; Heizmann 1973; Ginsburg 1999; Deshmukh and Valenciano 2022). Other Miocene musteloids with similar dental adaptations are the Early Miocene *Miomephitis pilgrimi* Dehm, 1950 (Wintershof-West, Germany, MN 3) and the Late Miocene *Neoyunnanotherium lufengense* (Qi, 2014) (China, c. MN 12–13). Deshmukh and Valenciano (2022) suggested recently that these three genera could have comprised an extinct lineage of bunodont stem mephitids.

This study aims to document new fossil material of *T. cyamoides* from France and Germany, reexamine the previously described La Grive-Saint-Alban specimens, and assess the systematic position and dietary ecology of this highly specialized carnivoran.

Institutional abbreviations.—FMNH, Field Museum of Natural History, Chicago, USA; GPIT, Palaeontological Collections of the University of Tübingen, Germany; IPS, collections of the ICP (Institut Català de Paleontologia Miquel Crusafont), formerly known as Institut de Paleontologia de Sabadell, Cerdanyola del Vallès, Spain; LACMNH, Los Angeles County Natural History Museum, Los Angeles, USA; MdC, Musée des Confluences, Lyon, France; NHMW, Naturhistorisches Museum Wien, Austria; NRM, Naturhistoriska Riksmuseet, Stockholm, Sweden; ONM, Palaeontological collections of the Museum of the Office National des Mines, Tunis, Tunisia; QM, Palaeontological collections of the Queensland Museum, Brisbane, Australia; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany; SNSB-BSPG, Bavarian State Collection for Paleontology and Geology, Munich, Germany; UC, University of California, Berkeley, USA; UCBL-FSL, Collections of the Université Claude-Bernard Lyon 1, France; USNM, Smithsonian National Museum of Natural History, Washington D.C., USA.

Other abbreviations: We follow standard convention in abbreviating tooth families as I, C, P, and M, with upper and lower case letters referring to upper and lower teeth, respectively.

Geological setting

La Grive-Saint-Alban constitutes a group of Upper Aragonian (Middle Miocene) karst deposits located in the village of Saint-Alban-de-Roche (Isère, France), about 30 km to the southeast of Lyon (Filhol 1883; Depéret 1892; Viret 1933, 1951, 1961; Mein and Ginsburg 2002). This site is formed by a series of quarries, named Lechartier, Milliat, and Peyre et Beau. Here, the Jurassic limestone hosts abundant karst caves filled with siderolithic clay containing a rich variety of tetrapod remains attributed to the MN 7/8 biozone (Filhol 1883; Depéret 1892; Viret 1933, 1951, 1961; Mein and Ginsburg 2002). The Milliat quarry provides the reference fauna for this biozone (de Bruijn et al. 1992; Mein and Ginsburg 2002). The Lechartier quarry has multiple levels numbered L1 to L8, but only L3, L5, L5′, L6, and L7 contain fossils (Mein and Ginsburg 2002; López-Antoñanzas and Mein 2011). Even though all the quarries are roughly of the same age (MN 7/8), the M (Milliat quarry) and L7 fissures belong to an earlier point in time (MN 7) than the L3 and L5 fissures (MN 8) (Mein and Ginsburg 2002; Pavia and Mourer-Chauviré 2011). The fauna found in this locality includes a wide diversity of mammals, including primates, insectivorans, bats, rodents, ungulates, and carnivorans, such as felids, barbourofelids, hyaenids, viverrids, ursids, amphicyonids, mustelids, mephitids, and ailurids (Mein and Ginsburg 2002).

The Kleineisenbach fossil site consists of a sand and marl pit, located about 12 km to the southeast of Freising, near Munich (Germany) (Fahlbusch 1975). It is part of the North Alpine foreland basin and can be correlated with the Swiss locality of Anwil (MN 7/8) (Engesser 1972; Prieto 2007, 2010). This vertebrate assemblage is dominated by small mammals, reptiles and amphibians (Black 1966; Fahlbusch 1975; de Bruijn et al. 1993; Prieto 2007, 2012; Klaus and Gross 2010).

Material and methods

The previously known fossils of *Trochotherium cyamoides* from La Grive-Saint-Alban (Viret 1935, 1951) come from the L7 level of the site (Mein and Ginsburg 2002). These fossils are two M1s and one m1. One of the M1s (MdC-LGR. 1300) is housed at the Musée des Confluences in Lyon (France). The other M1 (UCBL-FSL 540485, formerly Université 5020; Viret 1951) and the m1 (UCBL-FSL 540484, formerly Université 5019; Viret 1951) are part of the collections of the Université Claude-Bernard Lyon 1 (Lyon, France). The new mandibular remains and lower dentition of *T. cyamoides* described here (UCBL-FSL 540482, 540483, 540486, and 540488), come from the M level and are housed in the collections of the Université Claude-Bernard Lyon 1.

The new material of *T. cyamoides* from Kleineisenbach is a right hemimandible with an almost complete dentition (SNSB-BSPG-1972 XVI 317) housed at the Bavarian State Collection for Paleontology and Geology (Munich, Germany). The dental nomenclature used here broadly follows Ginsburg (1999) and Smith and Dodson (2003). We interpret the P4 lingual cusp of *T. cyamoides* and other mephitids as the protocone following Pilgrim (1933), Baskin (1998), Wang and Qiu (2004) and Wang and Carranza-Castañeda (2008); contrary to Geraads and Spassov (2016) and Araslanov and Lavrov (2024), who interpret it as the hypocone. Figure 2 shows the upper and lower first molars cusps, as well as the measurements of the M1.

The comparative material used includes fossils of *T. cyamoides* from Steinheim am Albuch (Fraas 1870, 1885; Helbing 1936; Heizmann 1973) housed at SMNS; *Trocharion albanense* Forsyth Major, 1903, from Devínska Nová Ves (Slovakia, MN 6; Sabol 2000) housed at NHMW; *Miomephitis pilgrimi* from Wintershof-West (Germany, MN 3; Dehm 1950) housed at SMNS and SNSB-BSPG; and *Palaeomeles pachecoi* Villalta Comella & Crusafont-Pairó, 1943, from Can Mata 1 (formerly Hostalets de Pierola) and Castell de Barberà (Spain, MN 9; Villalta Comella and Crusafont-Pairó 1943, 1944; Crusafont Pairó and Golpe Posse 1982) housed at IPS, and from Hammerschmiede (Germany, MN 7/8; Kargopoulos et al. 2022) housed at GPIT. We utilized a hemimandible cast of *T. cyamoides* from Anwil (Engesser 1972) housed at UCBL-FSL. Lastly, we studied *T. cyamoides* from Opole-1 (Wegner 1913), *Neoyunnanotherium lufengense* from Lufeng, Yunnan (Section D of the *Lufengpithecus* Locality, China, MN 12–13; Qi 2014), *Malleodectes mirabilis* Arena et al., 2011, from RRR Site (Riversleigh World Heritage Area, Queensland, Australia, upper Middle Miocene) (Arena et al. 2011; Archer et al. 2016); and *Terastiodontosaurus marcelosanchezi* Georgalis et al., 2024, from Chambi-1 (Djebel Chambi National Park, Tunisia, lower Middle Eocene) (Georgalis et al. 2024; Churchill et al. 2025) through their original publications. The extant comparative material includes *Mephitis mephitis* (Schreber, 1776) housed at FMNH; *Mydaus javanensis* (Desmarest, 1820) housed at FMNH; *Procyon cancrivorus* Cuvier, 1798, housed at NRM; and *Enhydra lutris* (Linnaeus, 1758) housed at USNM.

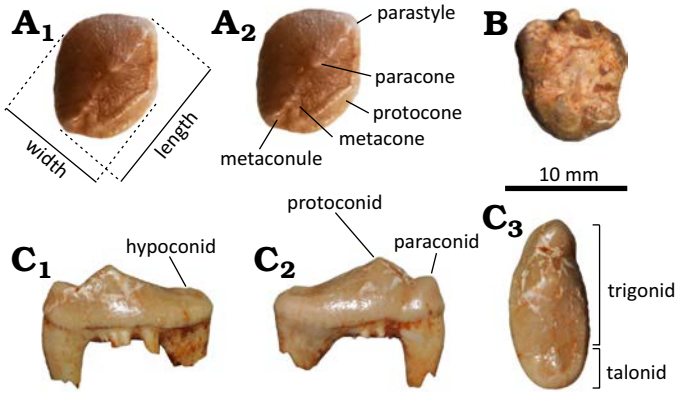

Fig. 2. Teeth nomenclature and measurements of the musteloid mammal *Trochotherium cyamoides* Fraas, 1870. **A**. Right M1 (MdC-LGR. 1300) in occlusal view. **B**. Right M1 (UCBL-FSL 540485) in basal view. **C**. Left m1 (UCBL-FSL 540488), in buccal (C_1), lingual (C_2), and occlusal (C_3) views.

Systematic palaeontology

Order Carnivora Bowdich, 1821

Superfamily Musteloidea Fischer, 1817

Family Mephitidae Bonaparte, 1845

Genus *Trochotherium* Fraas, 1870

Type species: Trochotherium cyamoides Fraas, 1870; Middle Miocene (Aragonian, MN 7/8), Steinheim am Albuch.

Trochotherium cyamoides Fraas, 1870

Figs. 3–5.

Type material: Lectotype: designated herein, SMNS-P-16193, partial right maxilla with C, P3, P4 and M1 from Steinheim am Albuch (Fig. 3A; figured by Fraas 1885: pl. 4: 4). Paralectotype: designated herein, SMNS-P-5283, right hemimandible with c, p3, p4 and m1 from Steinheim am Albuch (Fig. 3B; figured by Fraas 1885: pl. 4: 5a, b).

Type locality: Steinheim am Albuch, Germany.

Type horizon: Middle Miocene, Aragonian, MN 7/8 (Fraas 1870, 1885; Helbing 1936; Heizmann 1973).

Emended diagnosis.—Carnivoran intermediate in size between *Mephitis* and *Mydaus*. Premolars unicuspid. P1, P2 absent. P3 reduced. P4 short, with a reduced and rounded protocone placed next to the paracone. M1 enlarged and sub-rhomboidal, with a bunodont and hyperdeveloped paracone occupying the central area of the crown; two crests extend from the paracone: one reaches the metacone and metaconule in the distolingual corner, and the other extends towards the parastyle in the mesiobuccal corner; very reduced protocone in the mesiolingual area, connected to a small cingulum in the lingual platform; presence of several accessory rootlets. p1 absent. p2, p3 reduced. p4 short and wide. m1 bunodont and elongated, with a low paraconid smaller than the protoconid; the distobuccal wall of the

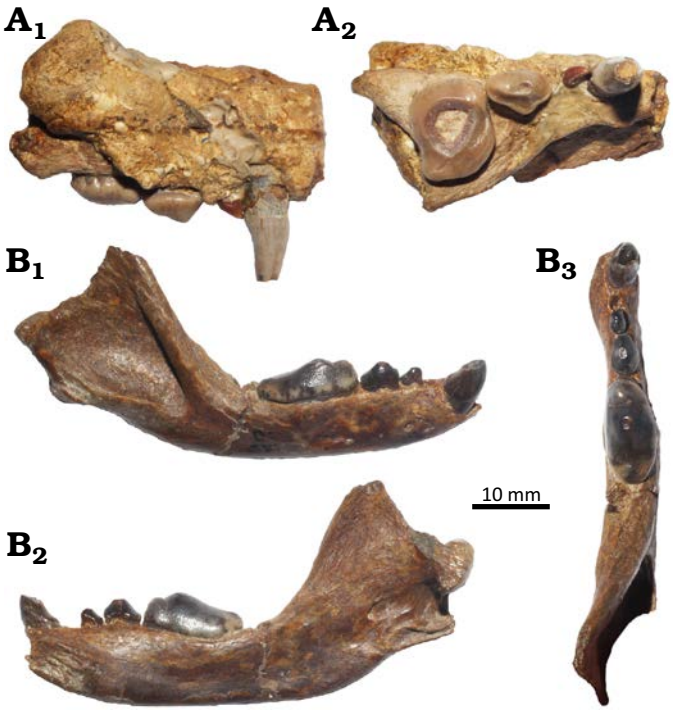

Fig. 3. Lectotype and paralectotype of the musteloid mammal *Trochotherium cyamoides* Fraas, 1870, from Middle Miocene, MN 7/8, Steinheim am Albuch, Germany. **A**. Lectotype, SMNS-P-16193, right maxilla in buccal (A_1) and occlusal (A_2) views. **B**. Paralectotype, SMNS-P-5283, right hemimandible in buccal (B_1), lingual (B_2), and occlusal (B_3) views.

protoconid is elongated and forms an almost concave slope that reaches the hypoconid; two main roots and multiple accessory rootlets placed in the buccal and lingual edges. m2 small and rounded, with a single root.

Material.—Seven specimens from La Grive-Saint-Alban, France, Middle Miocene, Aragonian, MN 7/8: MdC-LGR. 1300, right M1 from level L7 (Fig. 4A; Viret 1935, 1951); UCBL-FSL 540485, right M1 from level L7 (Fig. 4B; Viret 1935, 1951); UCBL-FSL 540484, left m1 from level L7 (Fig. 4C; Viret 1935, 1951); UCBL-FSL 540482, right m1 from level M (Fig. 4D); UCBL-FSL 540483, right m1 from level M (Fig. 4E); UCBL-FSL 540486, left m1 in association with a fragment of the masseteric fossa from level M (Fig. 4F, G); UCBL-FSL 540488, left m1 in association with the canine, part of the mandibular corpus, and the coronoid and articular processes from level M (Fig. 4H–K). One specimen from Kleineisenbach, Germany, Middle Miocene, MN 7/8: SNSB-BSPG-1972 XVI 317, fragmentary right hemimandible with c, p3, p4, m1 and alveolus of m2 (Fig. 4L).

Description.—*Previously known material from La Grive-Saint-Alban, level L7*: MdC-LGR. 1300 (Fig. 4A) is a right M1, sub-rhomboidal in shape and slightly wider than long, and it has a large paracone. Two thin crests depart from the paracone, connecting either to a small parastyle in the mesiobuccal corner of the tooth or to a small metacone in the distolingual corner. The metacone is placed next to a small metaconule.

UCBL-FSL 540485 (Fig. 4B) is a right M1 larger than MdC-LGR. 1300. Its occlusal facet is extremely worn and shows a mesiodistal fracture close to the buccal edge. The paracone is worn, with only its base remaining. The mesiolingual area of the tooth is fractured. The parastyle and metaconule are still present, but the metacone is absent. Both M1s have many small, accessory rootlets bordering the tooth. In the case of UCBL-FSL 540485, these accessory rootlets are broken at their base.

UCBL-FSL 540484 (Fig. 4C) is a left m1 with only three cuspids: paraconid, protoconid and hypoconid. The paraconid has a dome-like shape. The protoconid is situated in the middle of the buccolingual axis of the tooth and is much larger than the paraconid. Its distal wall is slightly concave and reaches the hypoconid, which is quite low. The m1 has large mesial and distal roots, as well as many additional rootlets in the buccal and lingual edges of the tooth; these rootlets are broken at their base.

New material from La Grive-Saint-Alban, level M: The four m1s vary in size (12.15–15.38 mm in length, 6.21–7.04 mm in width; Table 1). UCBL-FSL 540482 (Fig. 4D) shows a high degree of wear in the protoconid, while UCBL-FSL 540483 (Fig. 4E), and UCBL-FSL 540488 (Fig. 4I) are less worn. UCBL-FSL 540486 (Fig. 4F) possesses a tall, unworn hypoconid; this tooth is quite wide, possessing a lesser length/width ratio (1.97) than the other m1s (Table 1). The m1s have two large main roots (which are broken in UCBL-FSL 540483), as well as many additional rootlets. Almost all these additional rootlets are broken at their base, except for

Table 1. Measurements (in mm) of the teeth of *Trochotherium cyamoides* Fraas, 1870, from La Grive-Saint-Alban (MdC-LGR. 1300 through UCBL-FSL 540488) and Kleineisenbach (SNSB-BSPG-1972 XVI 317). L, length; W, width.

Specimen numbers	M1		c		p3		p4		m1		
	L	W	L	W	L	W	L	W	L	W	L / W
MdC-LGR. 1300	7.70	10.80									
UCBL-FSL 540485	10.22	11.62									
UCBL-FSL 540482									15.38	7.04	2.20
UCBL-FSL 540483									13.35	6.28	2.13
UCBL-FSL 540484									15.34	6.80	2.25
UCBL-FSL 540486									12.15	6.21	1.97
UCBL-FSL 540488			4.91	3.75					14.08	6.70	2.10
SNSB-BSPG-1972 XVI 317			4.43	3.51	2.96	1.81	4.38	2.65	13.70	6.01	2.28

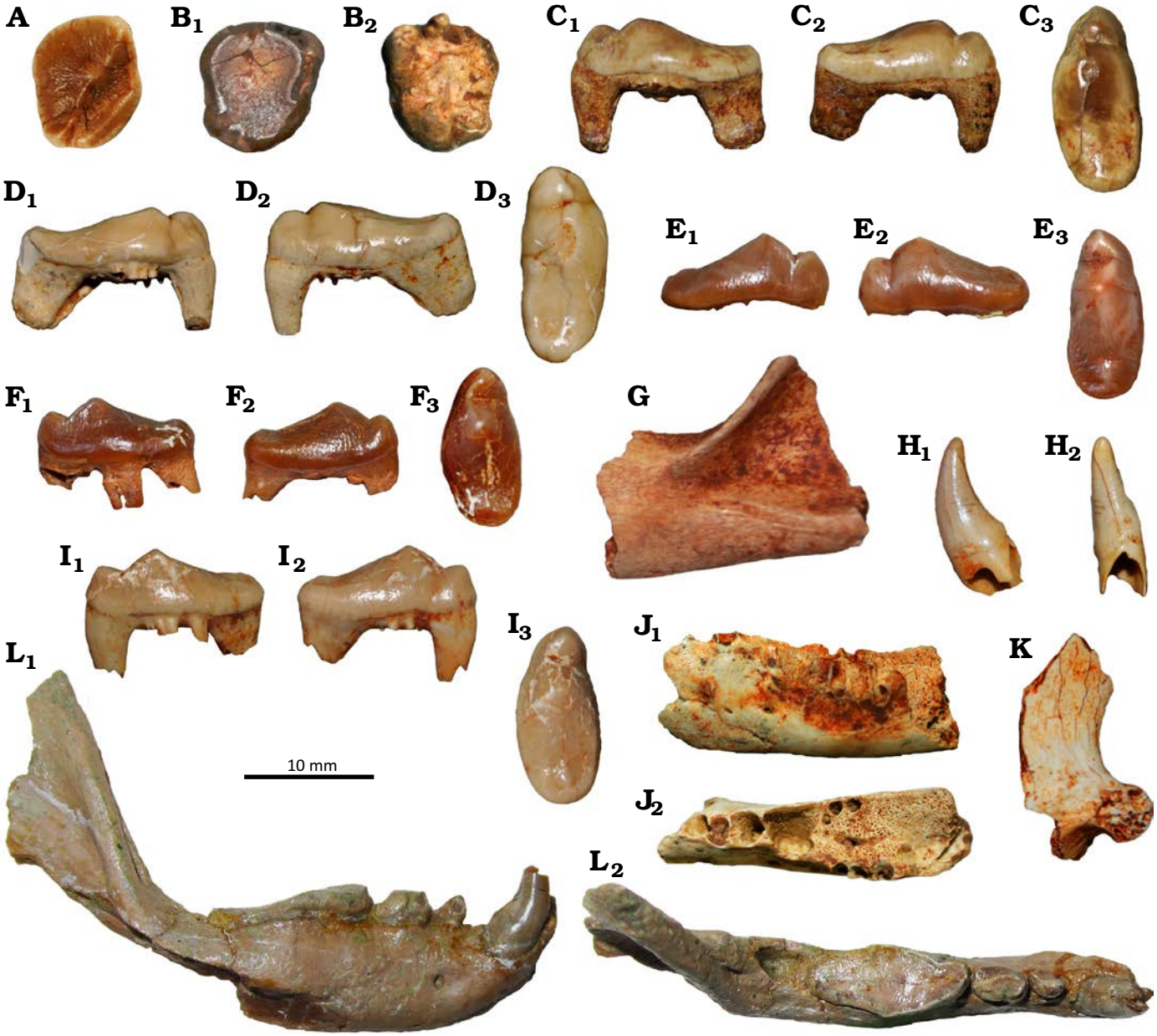

Fig. 4. Musteloid mammal *Trochotherium cyamoides* Fraas, 1870, from from the Middle Miocene (MN 7/8) of La Grive-Saint-Alban, France (A–K) and Kleineisenbach, Germany (L). A–C, classical material from level L7 of La Grive-Saint-Alban (Viret, 1935, 1951); D–K, new material from level M of La Grive-Saint-Alban. **A**. MdC-LGR. 1300, right M1 in occlusal view. **B**. UCBL-FSL 540485, right M1 in occlusal (B_1) and basal (B_2) views. **C**. UCBL-FSL 540484, left m1 in buccal (C_1), lingual (C_2), and occlusal (C_3) views. **D**. UCBL-FSL 540482, right m1 in buccal (D_1), lingual (D_2), and occlusal (D_3) views. **E**. UCBL-FSL 540483, right m1 in buccal (E_1), lingual (E_2), and occlusal (E_3) views. **F**. UCBL-FSL 540486, left m1 in buccal (F_1), lingual (F_2), and occlusal (F_3) views. **G**. Left masseteric fossa associated with the UCBL-FSL 540486 m1 in buccal view. **H**. UCBL-FSL 540488, canine associated with left m1 in buccal (H_1) and distal (H_2) views. **I**. UCBL-FSL 540488, left m1 in buccal (I_1), lingual (I_2), and occlusal (I_3) views. **J**. Fragment of the mandibular corpus associated with the UCBL-FSL 540488 m1 in buccal (J_1) and occlusal (J_2) views. **K**. Coronoid and articular processes associated with the UCBL-FSL 540488 m1 in buccal view. **L**. SNSB-BSPG-1972 XVI 317, right hemimandible with the canine, p3, p4, and m1 in buccal (L_1) and occlusal (L_2) views.

the buccal ones of UCBL-FSL 540486, which appear to be fused at their bases.

The specimen UCBL-FSL 540486 consists of the m1 and an associated mandibular fragment that includes the masseteric fossa (Fig. 4F, G). The specimen UCBL-FSL 540488 includes part of the mandibular ramus with the coronoid and articular processes, a canine with a missing root, and the m1 (Fig. 4H–K). The mandibular ramus is low. It shows alveoli for the distal root of the p3, the mesial and distal roots of the p4, and the mesial root and six accessory rootlets (three buccal and three lingual, close to the mesial root) of the m1. The alveolus for the distal root is not visible because there appears to be porous bone growth covering it. Both the coronoid and articular processes are broken.

New material from Kleineisenbach: The mandibular ramus is broken at its ventrocaudal border, and there is a men-

tal foramen under the p3. The ascending ramus only preserves its cranial area, which is mediolaterally engrossed, suggesting a wide area for the insertion of the temporal muscle. The canine is robust and broken at the tip. There is a single small alveolus for the p2. The p3 possesses only a main cuspid, and it lacks part of the enamel on its buccal wall. Similar to the p3, the p4 possesses only one worn cuspid. The m1 is more worn than the p4, as its cuspids have disappeared, resulting in a flat occlusal surface. There is an alveolus for a single-rooted m2.

Stratigraphic and geographic range.—Middle Miocene (Aragonian, MN 7/8) from Steinheim am Albuch (Germany) (Fraas 1870, 1885; Helbing 1936; Heizmann 1973), Opole-1 (Poland) (Wegner 1913), La Grive-Saint-Alban (France) (Viret 1935, 1951; Mein and Ginsburg 2002), Anwil (Switzerland) (Engesser 1972), and Kleineisenbach (Germany) (Fahlbusch 1975).

Discussion

Taxonomy and systematics.—The novel m1s of *Trochotherium cyamoides* from La Grive-Saint-Alban (level M) herein described (Fig. 4D–K) are very similar to the previously known m1 (UCBL-FSL 540484) of this species from the L7 level of the same locality (Viret 1935) (Fig. 4C). The specimens from both levels, which belong to the early MN 7/8 zone (Mein and Ginsburg 2002), share the diagnostic traits of the species, such as an overall bunodont morphology, a low paraconid, a protoconid with an elongated and concave distal wall, presence of several accessory rootlets, and lack of metaconid and entoconid. The mandible from Kleineisenbach (Fig. 4L) exhibits significant wear on the m1, resulting in the complete absence of its cuspids. However, the occlusal outline of the lower carnassial and the morphology of the p3 and p4 are identical to those of *T. cyamoides* from Steinheim am Albuch (Fraas 1885; Helbing 1936) (Fig. 5K).

The known dentition of *T. cyamoides* (Fraas 1870, 1885; Wegner 1913; Viret 1935, 1951; Helbing 1936; Engesser 1972; Heizmann 1973; Mein and Ginsburg 2002) exhibits a certain degree of morphological variation. The specimens from Steinheim am Albuch possess the the P4 protocone close to the midpoint of the mesiodistal axis of the tooth, while Engesser (1972) described and illustrated a P4 from Anwil with the protocone in a more mesial position. The shortest recorded M1 of *T. cyamoides* comes from La Grive-Saint-Alban (MdC-LGR. 1300; 7.70 mm in length) (Fig. 6), and it has a less pronounced metaconule than in the individuals from Steinheim am Albuch (Fig. 5B–I). Some of the M1s from Steinheim am Albuch also have a more pronounced curvature in the midpoint of their distal wall (Fig. 5B, E, F, H), while in MdC-LGR. 1300 this distal wall is straighter (Fig. 4A). Regarding the lower dentition, the m1s from La Grive-Saint-Alban show less variation in width than those from Steinheim am Albuch, but both populations have a similar variation in length (Fig. 6E). The talonid width also shows variation in La Grive-Saint-Alban and Steinheim am Albuch, with some specimens having a narrower talonid (Figs. 4E, F, 5J, K, L) than others (Figs. 4C, D, I, 5M, N). The m1 from Kleineisenbach (Fig. 4L) as well as the single known m1 from Anwil (Fig. 5O), are completely worn, so comparing their cuspid morphology is not possible. Regarding their size, the specimen from Kleineisenbach is close to the center of the size range for this taxon, while the one from Anwil is shorter (Fig. 6). The specimen from Opole-1 (Fig. 5P) lacks the m1, but it shows the large number of accessory rootlets diagnostic of this species. Accordingly, the overlapping temporal ranges of *T. cyamoides* populations and the magnitude of variation documented in the Steinheim am Albuch and La Grive-Saint-Alban samples suggest that interpopulation and intralocality differences primarily reflect phenotypic plasticity. Within Musteloidea, the mustelids, procyonids and ailurids exhibit sexual dimorphism in their canine size, with the males possessing larger canines than the females (Gittleman and Van Valkenburgh 1997; Abramov and Puzachenko 2005; Korablev et al. 2013; Fulwood and Wallace 2015). Some extant mephitids, such as several species of the genus *Conepatus*, also display dental differences between males and females (Dragoo 2009), e.g., in the distance between the lower incisors and the length of the upper canines of *Conepatus amazonicus* (Machado et al. 2024). However, there are not enough known canines of *T. cyamoides* to determine if it also displayed sexual dimorphism.

The distinct and highly bunodont dentition of *T. cyamoides* has made it difficult to discern its systematic position. Based on cranial and postcranial traits present in the fossils from Steinheim am Albuch, Viret (1935), Helbing (1936), and Heizmann (1973) recognized it as a Melinae, the Mustelidae subfamily that includes the Eurasian badgers. However, we do not consider *T. cyamoides* a member of this subfamily, as it differs from the current diagnosis of Melinae (see Wolsan and Sotnikova 2013) in many aspects: the bunodont dentition, the absence of P4 hypocone, the sub-rhomboidal shape of the M1, the short m1 talonid, and the absence of m1 metaconid, entoconid and hypoconulid. Other authors have classified it as a Leptarctinae mustelid according to its bunodont dentition (e.g., Ginsburg 1999; Bonis 2005). This is an extinct subfamily of bunodont mustelids from the Miocene of North America and Eurasia (e.g., Baskin 1998; Wang et al. 2004; Robles et al. 2010), with *Trocharion albanense* being the only European species (Qiu and Schmidt-Kittler 1982; Sabol 2000; Robles et al. 2010; Kargopoulos et al. 2022; Tseng 2025). It occurs alongside *T. cyamoides* in La Grive-Saint-Alban (Viret 1935, 1951) and Steinheim am Albuch (Helbing 1936). The coexistence of these two carnivorans has sometimes resulted in the misidentification of fossils of one taxon as belonging to the other. This was the case with the postcranial material from Steinheim am Albuch originally assigned to *T. cyamoides* (Helbing 1936), later transferred to *Trocharion albanense* by Qiu and Schmidt-Kittler (1982). Engesser (1972) de-

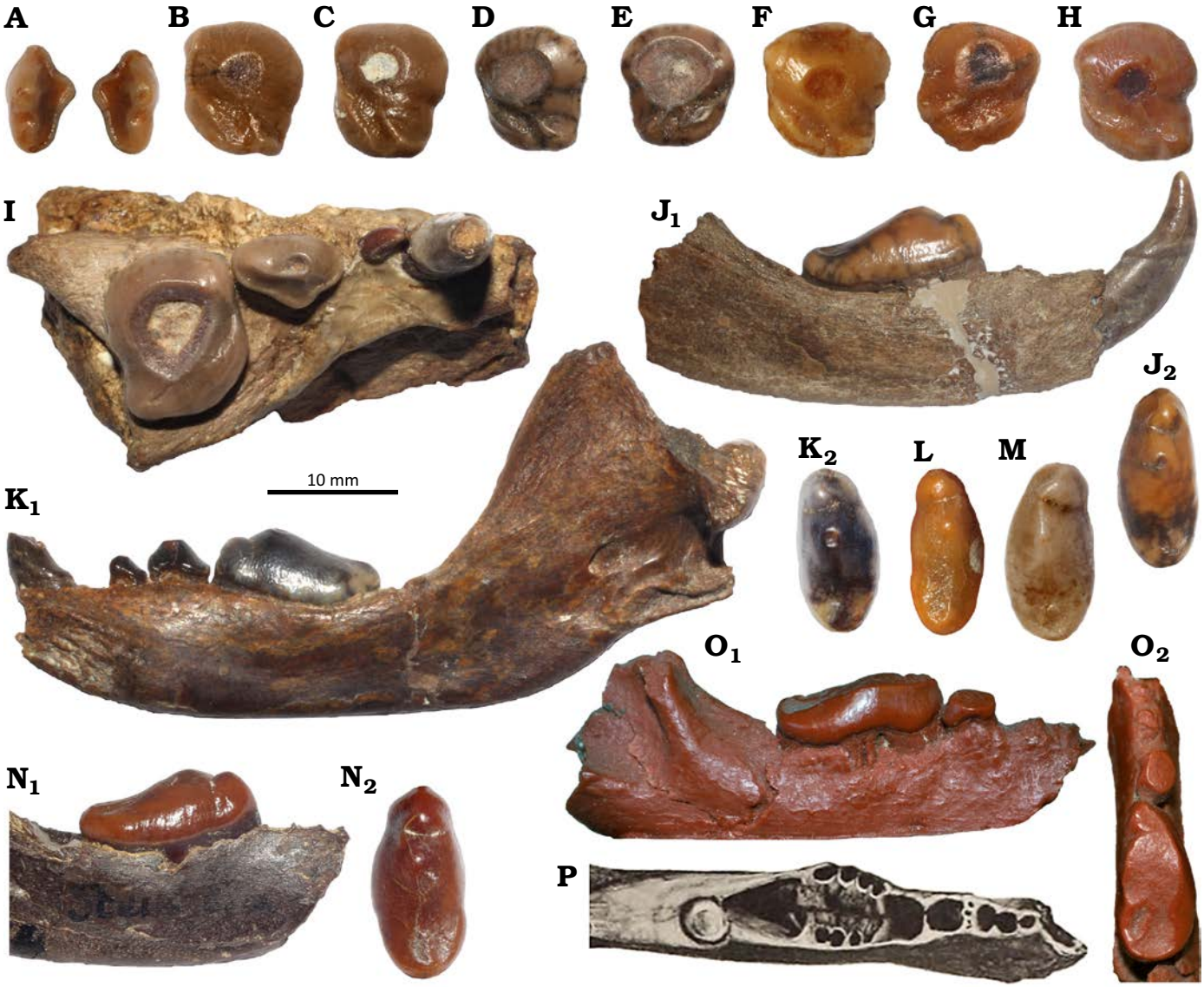

Fig. 5. Musteloid mammal *Trochotherium cyamoides* Fraas, 1870, from the Middle Miocene (MN 7/8) of Steinheim am Albuch, Germany (A-N), Anwil, Switzerland (O), and Opole-1, Poland (P). **A**. SMNS-P-5283b and SMNS-P-5283c, left and right P4s in occlusal view. **B**. SMNS-P-5042b, left M1 in occlusal view. **C**. SMNS-P-16187, left M1 in occlusal view. **D**. SMNS-P-5042c, left M1 in occlusal view. **E**. SMNS-P-5042d, right M1 in occlusal view. **F**. SMNS-P-5042a, right M1 in occlusal view. **G**. SMNS-P-8137, right M1 in occlusal view. **H**. SMNS-P-1921, left M1 in occlusal view. **I**. SMNS-P-16193, right maxilla with C, P3, P4 and M1 in occlusal view. **J**. SMNS-P-12223, left hemimandible with c and m1 in lingual view (J_1), and m1 in occlusal view (J_2). **K**. SMNS-P-5283, right hemimandible with c, p3, p4, and m1 in lingual view (K_1), and m1 in occlusal view (K_2). **L**. SMNS-P-16185, right m1 in occlusal view. **M**. SMNS-P-4391, left m1 in occlusal view. **N**. SMNS-P-16184, left hemimandible with m1 in lingual view (N_1), and m1 in occlusal view (N_2). **O**. Cast of UCBL-FSL Al. 166, right hemimandible with p4 and m1 in buccal (O_1) and occlusal (O_2) views. **P**. Image of a left hemimandible (unknown catalogue number; modified from Wegner 1913).

scribed a complete ulna of *T. cyamoides* from Anwil which is very similar to the previously known ulna from Steinheim am Albuch (Helbing 1936). However, we consider that this ulna should be reclassified as *Trocharion albanense*, following the review of the material from Steinheim am Albuch (Qiu and Schmidt-Kittler 1982). Therefore, with all the postcranial fossils originally attributed to *T. cyamoides* now reclassified as *Trocharion albanense*, the postcranial morphology of *T. cyamoides* remains unknown, and the interpretations about its aquatic lifestyle (Helbing 1936; Ginsburg 1999) have no solid basis. Schmidt-Kittler (1981) and Qiu and Schmidt-Kittler (1982) considered *T. cyamoides* to be a stem mustelid instead of a crown member of this family, based on the procyonid-like structure of the middle ear region of a partial skull from Steinheim am Albuch, originally also misidentified as *Trocharion albanense* by Helbing (1936). Dental and mandibular morphology clearly distinguish *T. cyamoides* from *Trocharion albanense*, indicating that the two taxa are not closely related. The former has proportionally larger molars and more slender premolars (Fig. 6), whereas the latter is characterized by a molariform P4 with a shelf-like protocone, a subquadrate, crest-bearing

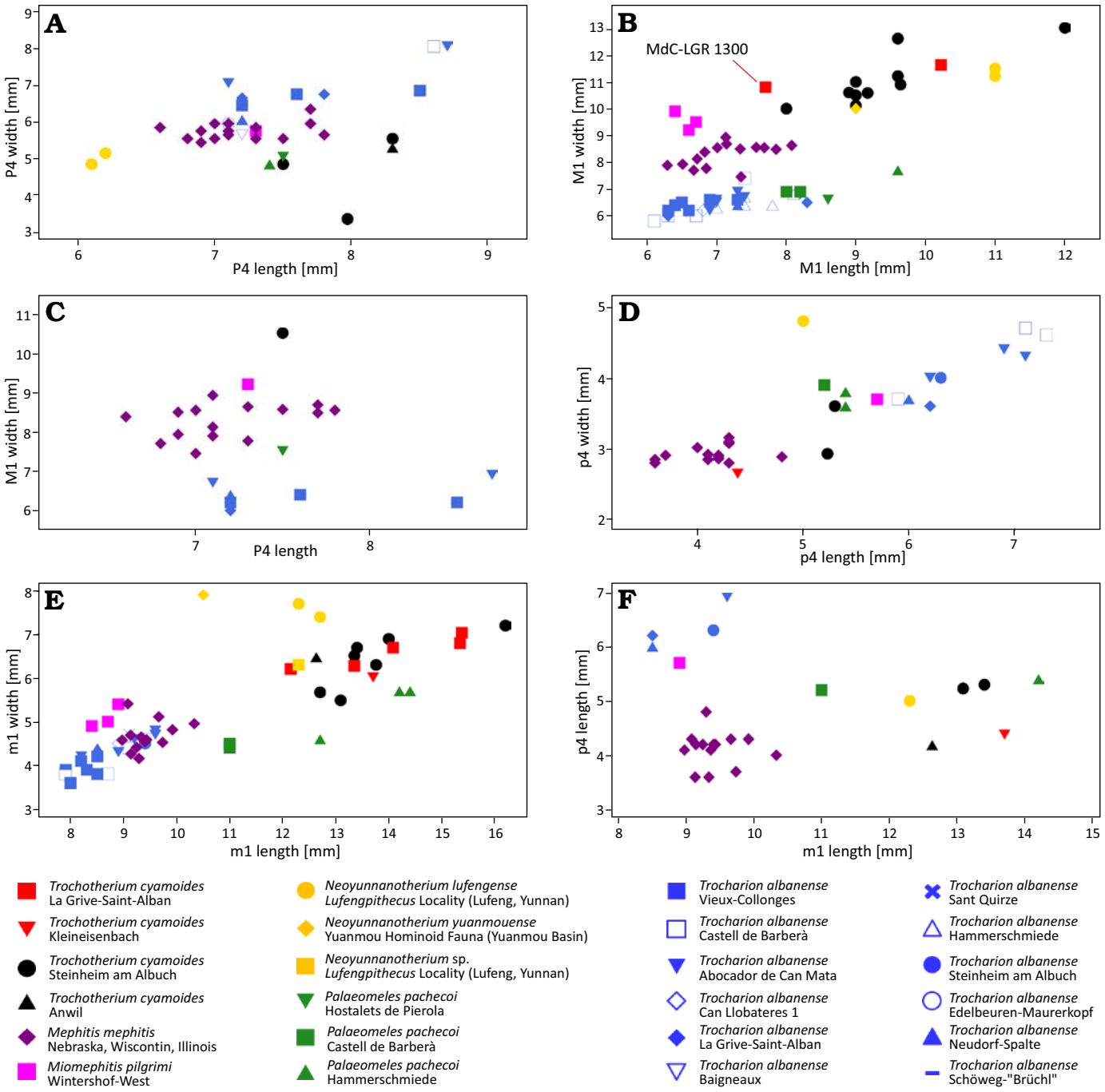

Fig. 6. Bivariate plots of the dentition of *Trochotherium cyamoides* Fraas, 1870 compared with the extant striped skunk (*Mephitis mephitis*), the Miocene Mephitidae *Miomephitis pilgrimi*, *Neoyunnanotherium* spp., *Palaeomeles pachecoi*, and the Leptarctinae *Trocharion albanense*. **A**. P4 length and width. **B**. M1 length and width. **C**. P4 length and M1 width. **D**. p4 length and width. **E**. m1 length and width. **F**. m1 length and p4 length. Values in mm. Sources: this work and Fraas (1870), Forsyth Major (1903), Wegner (1913), Pilgrim (1932), Helbing (1936), Villalta Comella and Crusafont-Pairó (1943), Viret (1946, 1951), Dehm (1950), Zapfe (1950), Mein (1958), Engesser (1972), Heizmann (1973), Crusafont Pairó and Golpe Posse (1982), Zong (1997), Robles et al. (2010), Qi (2014), Kargopoulos et al. (2022), and Prieto et al. (2022).

M1, a complete m1 trigonid, a shorter mandibular corpus, enlarged p3–p4, and the absence of accessory rootlets on both M1 and m1 (Fig. 7A, B).

Lastly, *T. cyamoides* has been interpreted as closely related to Mephitidae (e.g., Dehm 1950; Wolsan 1999; Robles et al. 2010; Deshmukh and Valenciano 2022), interpretation herein followed. This family currently includes the American skunks and the Southeast Asian stink badgers, and has traditionally been considered a subfamily of Mustelidae close to Melinae (e.g., Muizon 1982; Bryant et al. 1993; Baskin 1998; Ginsburg 1999; Wolsan 1999). However, there is strong molecular evidence that supports Mephitidae and Mustelidae as distinct families within Musteloidea (e.g., Dragoo and Honeycutt 1997; Sato et al. 2004, 2009; Flynn et al. 2005;

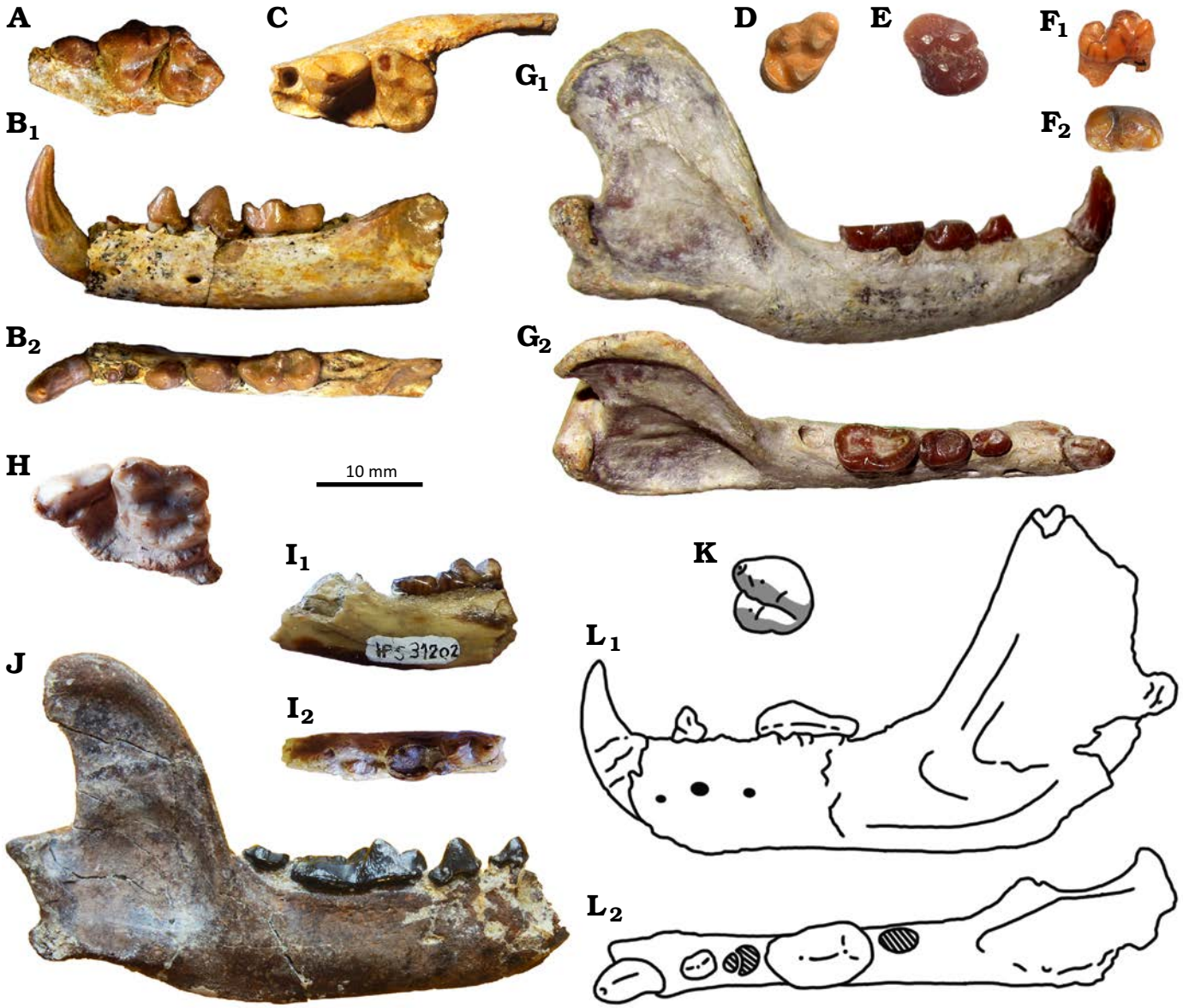

Fig. 7. Bunodont musteloids from the Miocene of Europe and China. **A**, **B**. *Trocharion albanense* Forsyth Major, 1903, from Devínska Nová Ves (Slovakia, MN6). **A**. NHMW 1976/1818, left maxilla with P3, P4 and M1 in occlusal view. **B**. NHMW 1976/1818, left hemimandible with p3, p4 and m1 in lingual (B_1) and occlusal (B_2) views. **C**–**G**. *Miomephitis pilgrimi* Dehm, 1950, from Wintershof-West (Germany, MN3). **C**. SNSB-BSPG-1938 V 21, left maxilla with P4 and M1 in occlusal view. **D**. SNSB-BSPG-1937 II 13397, right M1 in occlusal view. **E**. SNSB-BSPG-1937 II 13398, left M1 in occlusal view. **F**. SNSB-BSPG-1937 II 13326, left m1 in lingual (F_1) and occlusal (F_2) views. **G.** SNSB-BSPG-1937 II 13324, right hemimandible with c, p3, p4 and m1 in buccal (G_1) and occlusal (G_2) views. **H**–**J**. *Palaeomeles pachecoi* alta Comella & Crusafont-Pairó, 1943, from Can Mata 1 (Spain, MN 7/8) (H, I) and from Hammerschmiede (Germany, MN 7/8) (J). **H**. IPS697, left maxilla with P4 and M1 in occlusal view. **I**. IPS31202, left hemimandible with m1 in lingual (I_1) and occlusal (I_2) views. **J**. GPIT/MA/13711, right hemimandible with p3, p4, m1 and m2 in buccal view. **K**, **L**. *Neoyunnanotherium lufengense* from Lufeng, Yunnan (Section D of *Lufengpithecus* Locality, China, MN 12–13). **K**. V 1168-9, left M1 (modified from Qi 2014) in occlusal view. **L**. V 1168-11, left hemimandible with c, p3 and m1 (modified from Qi 2014) in buccal (L_1) and occlusal (L_2) views.

Fulton and Strobeck 2007; Koepfli et al. 2018; Law et al. 2018; Hassanin et al. 2021). Mephitidae is also unique in the expansion of the epitympanic process into the mastoid and squamosal areas, forming an elaborate epitympanic sinus connected to the similarly sized middle ear cavity by a small foramen (Schmidt-Kittler 1981; Bryant et al. 1993; Wolsan 1999; Wang and Qiu 2004; Wang et al. 2005; Geraads and Spassov 2016; Araslanov and Lavrov 2024). Some dental traits common in Mephitidae, but not exclusive to this family, are the absence of P1/p1, M2 and m3; the lack of a carnassial notch in the small P4; the transformation of the M1 cusps into shearing crests, as well as the presence of a strong buccal cingulum and an expanded hypocone in the M1; and the presence of at least one accessory rootlet in the m1, a robust metaconid and a long and basined talonid with an entoconid (Bryant et al. 1993; Baskin 1998; Wolsan 1999; Wang et al. 2005; Finarelli 2008; Geraads and Spassov 2016) (Fig. 8). *Trochotherium cyamoides* shares some traits with modern

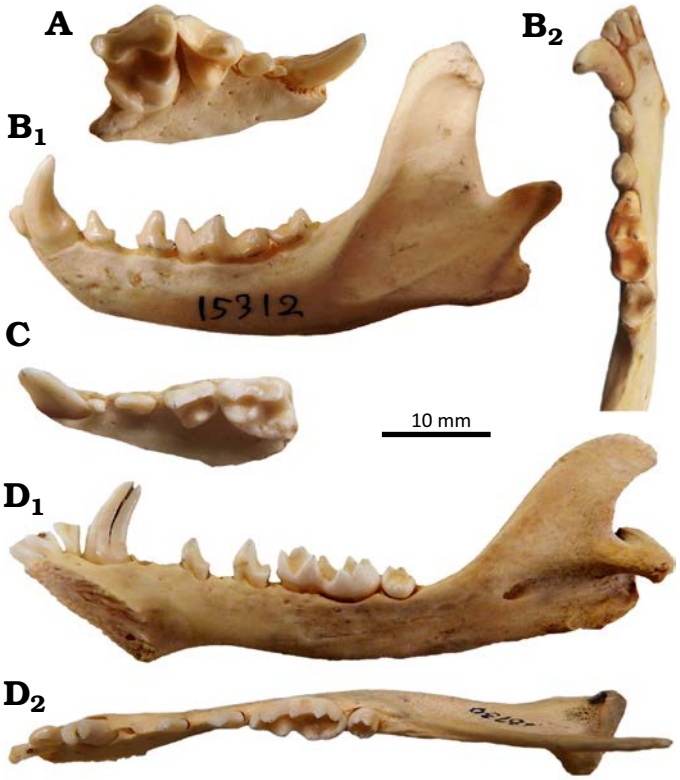

Fig. 8. Dentition of extant Mephitidae. **A**, **B**. *Mephitis mephitis* (Schreber, 1776). **A**. FMNH 90577, right maxilla with C, P2–4 and M1 in occlusal view. **B**. FMNH 15132, left hemimandible with i1-i3, c, p3–4, m1–m2 in buccal (B_1) and occlusal (B_2) views. **C**, **D**. *Mydaus javanensis* (Desmarest, 1820). **C**. FMNH 68730, left maxilla with C, P2–P4 and M1 in occlusal view. **D**. FMNH 68730, right hemimandible with i1-i3, p3–4, and m1–2 in lingual (D_1) and occlusal (D_2) views.

mephitids that support its relationship to this family (Dehm 1950; Wolsan 1999): absence of carnassial notch in the P4, with the protocone situated at the level of the paracone (Fig. 5A, I); larger M1 than P4 (Fig. 5I); lack of a posterior accessory cusp in p4 (Figs. 4L, 5K); presence of accessory rootlet(s) in m1 (Figs. 4J, 5P); and single-rooted m2 (Fig. 5P).

Mephitids were much more diverse in the Neogene (Fig. 9). The oldest known mephitid is *Miomephitis pilgrimi*, from the Early Miocene (MN 3) of Europe (Dehm 1950; Anderson 1989; Ginsburg 1999). The family later expanded to North America during the Late Miocene (Wang et al. 2005, 2014) and almost disappeared completely from Eurasia during the Late Pliocene (He and Huang 1991; Jiangzuo et al. 2023; Araslanov et al. 2026), with the exception of the extant *Mydaus* Cuvier, 1821, from Southeast Asia. Besides *Miomephitis*, several other genera of mephitids were present in Eurasia during the Miocene and Early Pliocene: *Proputorius* Filhol, 1890, (Middle to Late Miocene, MN 5–7/8) (e.g., Ginsburg 1961; Morales et al. 1999; Koufos 2008; Nagel et al. 2009; Peigné 2012; Kargopoulos et al. 2022), *Palaeomephitis* Jäger, 1839 (Middle Miocene, MN 7/8) (e.g., Wolsan 1999), *Palaeomeles* Villalta Comella & Crusafont-Pairó, 1943 (Middle to Late Miocene, MN 7/8–9) (e.g., Crusafont Pairó & Golpe Posse 1982; Kargopoulos et al. 2022), *Mesomephitis* Petter, 1967 (Late Miocene, MN 9) (e.g., Petter 1967; Morales et al. 1999; Robles 2014; Arranz et al. 2023), *Sabadellictis* Petter, 1963 (Late Miocene, MN 9) (Petter 1963), *Promephitis* Gaudry, 1861 (Late Miocene to Late Pliocene, MN 9–16) (e.g., He and Huang 1991; Wang and Qiu 2004; Montoya et al. 2011; Geraads and Spassov 2016; Jiangzuo et al. 2023; Araslanov and Lavrov 2024; Araslanov et al. 2026), and *Neoyunnanotherium* Deshmukh & Valenciano, 2022 (Late Miocene, c. MN 12–13) (Zong 1997; Qi 2014; Deshmukh and Valenciano 2022) (Fig. 9). Despite the shared similarities of *T. cyamoides* with Mephitidae described previously, its highly specialised bunodont dentition contrasts strongly with most members of this family, that have well-developed shearing crests on the M1 paracone-protocone and metacone (Figs. 7K, 8A). In addition, *T. cyamoides* shows a reduced m1 talonid and lacks the metaconid, entoconid, and hypoconulid, traits typi_cally present in other mephitids (Fig. 7I, J; Fig. 8B). Its M1s and m1s are also proportionally larger than in most other members of the group (Fig. 6). Based on these traits, *Trochotherium* is most closely allied with *Miomephitis* and especially *Neoyunnanotherium* (Dehm 1950; Heizmann 1973; Deshmukh and Valenciano 2022).

Miomephitis pilgrimi, known exclusively from the German locality of Wintershof-West, shares with modern mephitids the shortening of the premolar row, the subquadrangular M1, the prominent m1 metaconid and the single-rooted m2 (Dehm 1950), as well as similar P4 proportion to the extant *Mephitis mephitis* (Fig. 6). However, *M. pilgrimi* still possesses a series of primitive traits compared to later species of the family such as a less developed shelf-like platform distal to the P4 protocone (Fig. 7C), blunt and differentiated cusps instead of shearing crests in the M1 (Fig. 7C–E), a small metaconule in the M1 (Fig. 7C–E), a short m1 talonid (Fig. 7F, G) and lack of accessory rootlets. The rudimentary metaconule is absent in most extant mephitids (Wolsan 1999) but can be seen in certain primitive forms, such as *Palaeomeles pachecoi* (Vallès-Penedès basin, Spain, MN 7/8–9) (Fig. 7H), *Promephitis larteti* Gaudry, 1861 (Tuva, Taralyk-Cher Locality, Russia, MN 12–13), *Promephitis maeotica* Alexejew 1915 (Novoelizavetovka, Ukraine, MN 12) (Araslanov and Lavrov 2024), *T. cyamoides* (Fig. 4A), and in the extant *Mydaus javanensis* (Fig. 8C). *Miomephitis* and *Trochotherium* share a bunodont M1 with a lack of shearing crests and a shortened m1 talonid. However, *M. pilgrimi,* has a more primitive M1 characterized by a distinct paracone and metacone that do not occupy most of the occlusal area, and it differs as well in the presence of m1 metaconid and hypoconulid and the lack of accessory rootlets. In contrast, the most similar taxon to *Trochotherium* is the Late Miocene *Neoyunnanotherium*, which comprises two species: *Neoyunnanotherium lufengense* (Section D of the *Lufengpithecus* Locality, Lufeng, Yunnan, China) and the slightly smaller *Neoyunnanotherium yuanmouense* (Zong, 1997) (Yuanmou Hominid Fauna, Yuanmou Basin, China) (Zong 1997). Both genera display a highly derived bunodont condition, with hyperdeveloped M1s bearing a large and

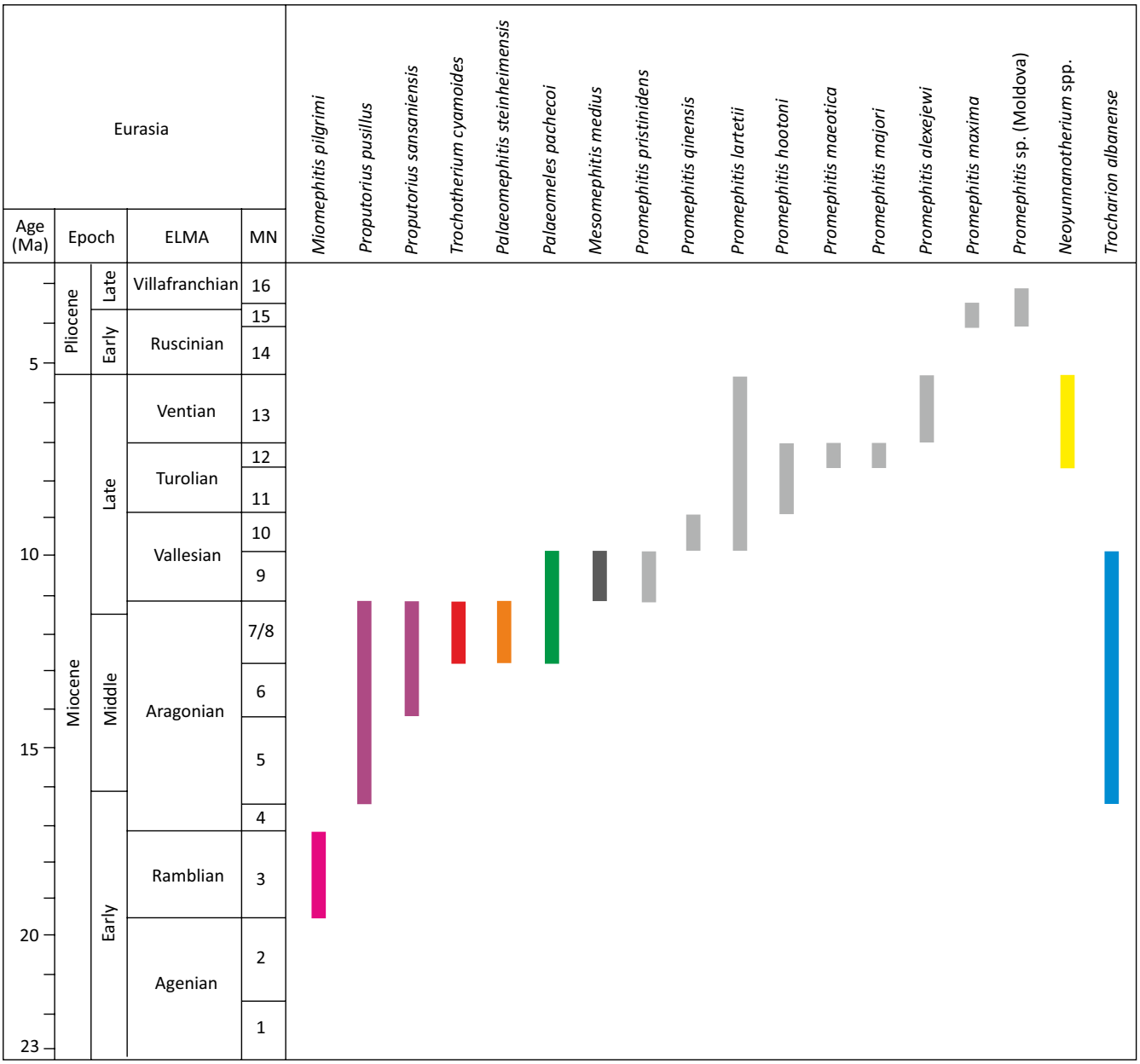

Fig. 9. Chronological ranges of selected crown and stem Mephitidae species from Eurasia, together with the leptarctine mustelid *Trocharion albanense*. Sources: Dehm (1950), Ginsburg (1961, 1999), Petter (1967), Crusafont Pairó and Golpe Posse (1982), He and Huang (1991), Zong (1997), Morales et al. (1999), Wolsan (1999), Mein and Ginsburg (2002), Wang and Qiu (2004), Koufos (2008), Nagel et al. (2009), Montoya et al. (2011), Peigné (2012), Qi (2014), Geraads and Spassov (2016), Kargopoulos et al. (2022), Jiangzuo et al. (2023), Araslanov and Lavrov (2024), and Araslanov et al. (2026).

centrally placed paracone (Fig. 7K), shortened p4s relative to *Trocharion* and *Miomephitis* (Fig. 6), a reduced m1 talonid with an elongated distal protoconid wall (Fig. 7L), and accessory rootlets on both M1 and m1 (Qi 2014; Deshmukh and Valenciano 2022). This Chinese carnivoran possesses traits that can be interpreted towards a more durophagous diet than *Trochotherium*, a more robust mandibular corpus, relatively shorter P4s and m1s and wider lower premolars (Figs. 6, 7L).

As outlined previously, the dental morphology of *T. cyamoides* and *Neoyunnanotherium* spp., and to a lesser extent *M. pilgrimi*, differs significantly from that of crown group mephitids (Fig. 8). In the case of *M. pilgrimi*, the combination of primitive and derived traits leads us to question whether it is a true member of the family Mephitidae or if it should instead be interpreted as a stem Mephitidae. Its morphology is considerably different from that of subsequently younger mephitids (such as *Proputorius*, Middle to Late Miocene, MN 5–7/8; see Peigné 2012, Kargopoulos et al. 2022 and references therein), which already exhibit the typical morphology of Mephitidae seen in other Eurasian members of this family from the Middle to Late Miocene (*Palaeomeles*, *Mesomephitis*, and *Promephitis*) (Fig. 9). Neogene mephitids in North America, such as *Martinogale* Hall, 1930 (late Clarendonian to late Hemphillian, c. Late

Miocene) and *Buisnictis* Hibbard, 1950 (early to middle Blancan, c. Middle to Late Pliocene), also exhibit clear Mephitidae dental characteristics (Wang et al. 2005, 2014). Molecular estimations suggest that Mephitidae first appeared in the early Oligocene c. 28 Ma (e.g., Sato et al. 2009, 2012; Law et al. 2018), meaning there would be a gap of almost 10 myr between their divergence from the other Musteloidea and the appearance of *M. pilgrimi* in the Early Miocene. Therefore, *M. pilgrimi* may not be the first crown group member of this family, and its combination of primitive and derived traits suggests that it belonged to a lineage of stem mephitids instead. In fact, certain authors consider the Late Miocene *Promephitis* to be the first crown Mephitidae genus (Geraads and Spassov 2016; Araslanov and Lavrov 2024). If *Miomephitis* represents a morphological precursor to *Trochotherium* and *Neoyunnanotherium*, as some authors have suggested (Dehm 1950; Heizmann 1973; Deshmukh and Valenciano 2022), then these two genera would also be placed outside of crown Mephitidae.

Insights into dietary adaptations.—Durophagy can be defined as the feeding mechanism of an animal that consumes hard-shelled prey, including mollusks and crustaceans (Vermeij 1977), but can also be used in reference to animals that feed on bones or hard plant material (e.g., Werdelin 1989; Figueirido et al. 2013). This type of diet requires a specific dental morphology, in which teeth are usually blunt and low-crowned. These dental traits are perfect for producing widespread fractures on hard skeletal elements, as well as dissipating the stress caused by strong occlusal forces (Lucas 2004; Constantino et al. 2011; Crofts 2015; Crofts et al. 2020). Multiple groups of extinct vertebrates with blunt teeth have been inferred as feeding on hard-shelled invertebrates, such as some Paleozoic placoderms and chondrichthyans (Vermeij 1977; Sallan and Coates 2010; Sallan et al. 2011; Salamon et al. 2014), Mesozoic marine reptiles (Vermeij 1977; Massare 1987; Gorzelak et al. 2012; Huang et al. 2020), terrestrial amphisbaenian lizards (Estes and Williams 1984; Martín et al. 2013; Georgalis et al. 2024) and mammals. Several examples of durophagous mammals have been described in Marsupialia (Maga and Beck 2017; Churchill et al. 2025), Eulipotyphla (Ziegler 1999; Furió et al. 2011; Crespo et al. 2018), Chiroptera (Dumont and Herrel 2003), Hominoidea (Berthaume et al. 2010; Constantino et al. 2011) and Carnivora, including hyaenids (Van Valkenburgh 1999; Palmqvist et al. 2011), canids (Werdelin 1989; Tseng and Wang 2011), ursids (Johnson et al. 1988; Figueirido et al. 2010, 2011), ailurids (Johnson et al. 1988), procyonids (Emmons 1990), pinnipeds (Amson and Muizon 2014; Loch et al. 2016), and mustelids (Riedman and Estes 1990; Morales and Pickford 2005; Grohé et al. 2013; Valenciano et al. 2016). Durophagous carnivorans tend to possess shorter, wider and more robust skulls and mandibles, enlarged areas for the insertion of masticatory muscles, and reinforced tooth enamel (Davis 1964; Binder and Van Valkenburgh 2000; Van Valkenburgh 2007; Chai et al. 2009; Figueirido et al. 2013 and references therein). However, there are some differences between durophagous carnivorans based on their diet. For instance, bamboo-feeders like the giant and red pandas possess a condylar process with a higher position relative to the tooth row than bone-cracking carnivores (Figueirido et al. 2013). The bamboo-feeders are adapted to withstand the fatigue that comes with long periods of chewing, while the carnivorans that feed upon bones (hyaenids and Borophaginae canids) exert maximal force during short-duration forceful bites (Figueirido et al. 2013). Extant musteloids who feed on hard-shelled aquatic invertebrates, as the sea otter (*Enhydra lutris*) and the crab-eating raccoon (*Procyon cancrivorus*), possess a series of dental traits perfect for cracking the shells of their prey: large P4s and M1s, with multiple blunt and rounded cusps; wide m1s with blunt cuspids; and very thick enamel (Riley 1985; Márquez and Fariña 2003; Constantino et al. 2011; Quintela et al. 2014; Ziscovici et al. 2014; Law et al. 2017; Selig 2023) (Fig. 10).

Multiple authors have interpreted *T. cyamoides* as a durophagous carnivoran (Fraas 1870; Viret 1935; Helbing 1936; Heizmann 1973; Ginsburg 1999; Deshmukh and Valenciano 2022), with a diet primarily based on aquatic shelled invertebrates. This interpretation is supported by its bunodont dentition, characterized by low, rounded cusps, thickened enamel, and a typical flat wear pattern in old specimens. Furthermore, the occlusal wear observed on several M1s and m1s of *T. cyamoides* suggest that the extremely enlarged and pointed M1 paracone (when unworn) occluded with the distal, elongated wall of the m1 protoconid, forming a crushing surface well suited for breaking invertebrate shells (Fig. 11A, B). This diet would be quite different from that of extant mephitids, who are omnivorous and utilize

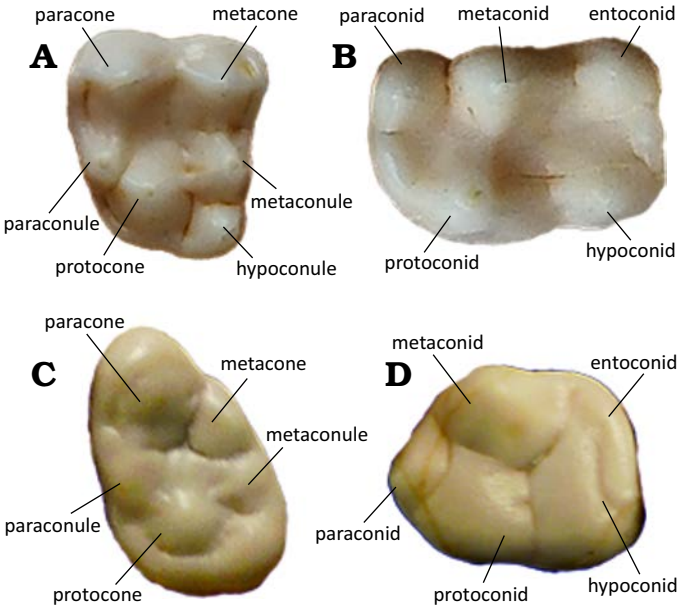

Fig. 10. Upper and lower first molars of extant durophagous musteloids in occlusal view. **A**, **B**. *Procyon cancrivorus* Cuvier, 1798, NRM-A587124. **A**. Left M1. **B**. Left m1. **C**, **D**. *Enhydra lutris* (Linnaeus, 1758), USNM 286400. **C**. Right M1 (mirrored). **D**. Left m1. Not to scale.

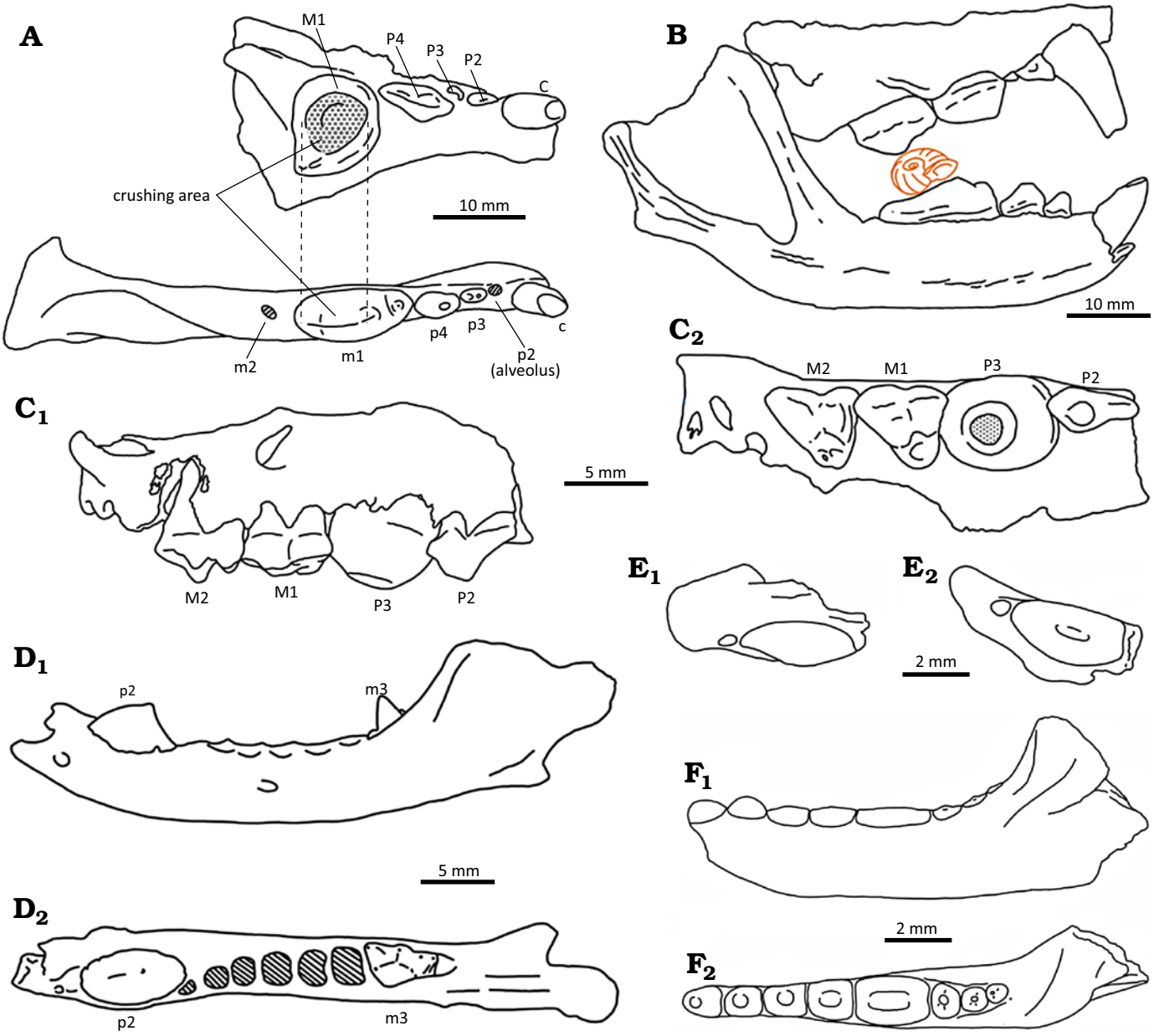

Fig. 11. Examples of small-sized durophagous tetrapods. **A**, **B**. Scheme of crushing mechanism in *Trochotherium cyamoides* Fraas, 1870. **A**. Crushing area formed between the M1 paracone and the m1 protoconid distal wall. **B**. Representation of *T. cyamoides* feeding on a *Gyraulus* snail (traced from Rasser 2014) from Steinheim am Albuch. **C**, **D**. *Malleodectes mirabilis* Arena et al., 2011 (modified from Churchill et al. 2025). **C**. QM F61725, left maxilla in buccal (C_1) and occlusal (C_2) views. **D**. QM F61727, left hemimandible in buccal (D_1) and occlusal (D_2) views. **E**, **F**. *Terastiodontosaurus marcelosanchezi* Georgalis et al., 2024 (modified from Georgalis et al. 2024). **E**. ONM CBI-1-667, right maxillary tooth in buccal (E_1) and occlusal (E_2) views. **F**. ONM CBI-1-646, left dentary in buccal (F_1) and occlusal (F_2) views.

the crest-like cusps in their M1s to slice their prey (Nowak 1999). However, when compared to the extant durophagous musteloids who feed on aquatic invertebrates such as the sea otter (*Enhydra lutris*) and the crab-eating raccoon (*Procyon cancrivorus*) (Fig. 10), *T. cyamoides* and *Neoyunnanotherium* spp. differ from them in possessing smaller P4s, an enlarged M1 paracone occupying most of the occlusal surface, and longer m1. Thus, the dental morphology of *T. cyamoides* and *Neoyunnanotherium* spp. is unique within the order Carnivora. Instead, it bears a closer resemblance to the upper premolars of certain Cenozoic tetrapods such as Malleodectidae marsupials (Arena et al. 2011; Archer et al. 2016; Churchill et al. 2025), Dimylidae insectivores (van den Hoek Ostende 1995; Furió et al. 2011; Crespo et al. 2018), and amphisbaenian lizards (Georgalis et al. 2024). The M1 of *T. cyamoides* resembles the P3 of the Middle Miocene Australian marsupial *Malleodectes mirabilis* Arena et al., 2011, which is hypertrophied, occlusally ovate and lacks distinct cusps or blades (Churchill et al. 2025) (Fig. 11C). The P3 of this marsupial is also similar to the maxillary teeth of snail-eating skink lizards (Arena et al. 2011). Meanwhile, the m1 of *T. cyamoides* appears to be similar to the p2 of this

marsupial (Fig. 11D) and to the elongated, unicuspid teeth present in the Eocene amphisbaenian *Terastiodontosaurus marcelosanchezi* Georgalis et al., 2024 (Fig. 11E, F). Both *Malleodectes mirabilis* and *Terastiodontosaurus marcelosanchezi* have been interpreted as having fed primarily on snails (Arena et al. 2011; Archer et al. 2016; Georgalis et al. 2024; Churchill et al. 2025). The parallel teeth morphology of *T. cyamoides* to these land-dwelling, snail-eating specialists, as well as the lack of postcranial material that would support a semi-aquatic lifestyle (Qiu and Schmidt-Kittler 1982), leads us to suggest that this carnivoran may have fed primarily on terrestrial gastropods, but we cannot completely rule out a diet based on aquatic invertebrates, such as that seen in the extant herpestid *Atilax paludinosus* Cuvier, 1829, or the procyonid *Procyon cancrivorus* (Nowak 1999).

Conclusions

The description of new fossils of *Trochotherium cyamoides* from La Grive-Saint-Alban and Kleineisenbach, alongside the re-evaluation of all the known material of this species, contributes to a better understanding of this enigmatic carnivoran and expand its geographical range. We observed variability in the position of the P4 protocone, consisting of a mesial position of this cusp in specimens from Anwil and a more central position in those from Steinheim am Albuch. Additionally, the width of the m1 talonid varies in the populations from La Grive-Saint-Alban and Steinheim am Albuch. The Steinheim am Albuch population, which is the most well-documented one, also exhibits the greatest variability in size. All these differences are interpreted as intraspecific variation, primarily reflecting phenotypic plasticity.

Based on its dental characteristics, we consider *T. cyamoides* to be a stem Mephitidae, as it displays a combination of diagnostic traits of this family (e.g., the distally placed protocone of the P4, larger M1 than P4, single-rooted m2) alongside derived traits (e.g., bunodont dentition, enlarged cusp in the M1 instead of shearing crests, shortened m1 talonid, and absence of metaconid and entoconid) that do not appear in other extinct and extant mephitids. *Miomephitis pilgrimi* and *Neoyunnanotherium* spp. should also be considered stem Mephitidae due to their similarities with *T. cyamoides*. The peculiar morphology of the dentition of *T. cyamoides*, which resembles that of certain snail-eating extinct marsupials and lizards, suggests that this carnivoran may have fed on terrestrial gastropods by occluding the hyperdeveloped M1 paracone with the distal wall of the m1 protoconid.

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