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The carnivorans from Cava Monticino (Faenza, Italy; Messinian) revisited

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Abstract

Among the vertebrates found at Cava Monticino, carnivorans are by far the most abundant of all the large mammals. Five different taxa were recovered: one felid, two hyaenids, one canid, and one mustelid. The small-sized felid remains can be attributed to *Felis christoli* and seems to represent one of the earliest records of a true member of the genus *Felis* in Western Europe. Hyaenids at Cava Monticino are represented by the large wolf-sized and cursorial *Lycyaena* cf. *chaeretis*, and by the peculiar small *Plioviverrops faventinus*, the most abundant taxon of all. The latter is one of the most derived species of the genus and the last to appear in the fossil record of these mongoose-like hyaenids. The medium-sized canid recorded at Cava Monticino, *Eucyon monticinensis*, represent one of the oldest, certain record in the Old World of the genus *Eucyon*. It was a mesocarnivorous species that preyed on small vertebrates (abundantly recorded in the area of Cava Monticino during the Late Miocene). Lastly, mustelids are represented by the large relative of the extant honey badger, *Mellivora benfieldi*, whose record at Cava Monticino represents the northernmost record of the species and, presently, the only record of the genus outside of Africa.

Keywords:
Felidae, Hyaenidae, Canidae, Mustelidae, Late Miocene, Messinian.

Introduction

Terrestrial carnivores are an important ecological component in a wide range of biomes, and overall contribute to characterizing faunal assemblage ecology, composition, and structure. In respect to the general structure of other well-known Late Miocene faunas (such as Pikermi and Samos in Greece or Batallones and Venta del Moro in Spain) where the number of recorded species is similar to the high taxonomic diversity seen in modern African or Asian faunas, the carnivore guild documented at Cava del Monticino assemblage is composed by only five taxa (Rook et al. 1991): one felid (the small cat referred to *Felis* ex gr. *attica-christoli*; two hyaenids (the small mongoose-like

Plioviverrops faventinus, and the large-sized meat-eater hyaenid, referred to *Thalassictis* (*Lycyaena*) gr. *macrostoma-chaeretis*); one canid (the primitive dog *Eucyon monticinensis,* and one mustelid (the honey badger *Mellivora benfieldi*). Despite its reduced composition, the carnivorans from Cava Monticino represent one of the best and most abundant association of carnivorans dated to the latest Miocene of Italy and Western Europe, in general. Here we provide an updated revision of these carnivorans, with particular attention to the most problematic ones (the small felid and the large hyaenid) and focusing on the significance of Cava Monticino guild in terms of paleoecology, biochronology and zoogeography.

Materials & Methods

The present study is carried out studying the material of carnivorans housed at the "Museo Civico di Scienze Naturali Malmerendi" of Faenza (Emilia Romagna, Italy) and some isolated teeth and fragmented specimens from the Earth Science Department of the University of Florence. For the Miocene hyaenid discussion, we followed the ecomorphological interpretation by Werdelin and Solounias (1991) and the taxonomic revision by Turner et al. (2008). Metric and morphological comparison was taken by literature (*inter alios* De Beaumont 1961; Ficcarelli and Torre 1975; Morales and Aguirre 1976; de Bonis and Koufos 1991; Werdelin et al. 1994; Werdelin 1999; Salesa et al. 2012, 2019; Robles et al. 2013; Ozkurt et al. 2015; Koufos 2021). Measurements were taken to the nearest 0.1 mm with a digital caliper, following Driesch (1976) and reported in the Supplementary Material.

Systematic Paleontology

Order Carnivora Bowdich, 1821
Family Felidae Fischer, 1817
Sub-Family Felinae Fischer, ,1817
Genus *Felis* Linnaeus, 1758

Felis christoli Gervais in Gervais, 1848-1852
Figure 1A-B, I

Material – *Mandible.* MSF 90 (BRS 27/3), right hemimandible fragment with partial p4 and m1. *Postcranial elements.* MSF 91 (BRS 27/12), third left metatarsus; MSF 467 (BRS 27/sn), four left metatarsus.

Remarks – The generic attribution of the species *F. christoli* has been questioned, relating it to extant forms, like the serval, *Leptailurus serval* (see Gervais 1859), to lynxes (see Morales and

Aguirre 1976), to *Pseudaelurus* or even *Metailurus* (see Ficcarelli and Torre 1975). Other authors left the question open (Werdelin et al. 2010), considering the scantiness of its fossil record. Nevertheless, the comparison of the mandible (e.g., the angle between the ramus and the corpus; reduction of the angular process; height of the condyloid process) and of the m1 (e.g., absence of the talonid; proportion between paraconid and protoconid) with those of the members of the above-mentioned fossil and extant genera does not show any affinity, if not with *Felis sensu stricto*. The phylogenetic relationships and evolutionary history of Miocene felids have been a harshly debated topic in the last century as a consequence of their scarce record especially in the Early-Middle Miocene (see Werdelin et al. 2010 for discussion). We report a resuming map of the occurrences of small felids from the MN10 onward (Figure 2). Some authors, in spite of the initial attribution of Miocene small felid to the genus *Felis* (*sensu lato*), have preferred including these forms into different genera (e.g., Salesa et al. 2012, 2019).

Compared to the old forms attributed to the genera *Pseudaelurus*, e.g., *Pseudaelurus romieviensis* (type locality: La Romieu, France, MN4), *P. quadridentatus* (type locality: Sansan, France, MN6) and *P. turnauensis* (type locality: Göriach, Austria, MN5), MSF 90 lacks the developed talonid on the m1, evident In these primitive forms (De Beaumont 1961; Robles et al. 2013) (Figure 1). This same relevant difference strongly suggests the distinction between the specimen from Cava Monticino and the Spanish MN10 *Leptofelis vallesiensis* (see Salesa et al. 2019) in which the talonid is as marked as in small and primitive *Pseudoaelurus* s.l. Moreover, *L. vallesiensis* shows a short m1 paraconid compared to the protoconid. Several morphologies of the type and hypodigm material of the MN12 *Felis attica* from Pikermi and Samos allow separating the fossils from Cava Monticino from this small felid (de Beaumont 1961; Koufos 2011). For instance, in *F. attica*, the corpus of the mandible is shallower with an inclined ramus, proportionally higher coronoid process but a shorter height between the angular process and the condyloid process. The angular process is smaller and more slender in MSF 90 (Figure 1A-B). Even in dental morphologies, there are differences: *F. attica* shows a shorter blade of the paraconid compared to the protoconid, unlike MSF 90, in which the two cuspids are equally developed (Figure 1). Moreover, MSF 90 shows a very small, but evident, metaconid, whereas *F. attica* does not. Like some specimens of *F. attica*, MSF 90 does not have a talonid, nor distal enlargement or cingulid. For what is visible, the distal portion of the p4 differs from that of *F. attica* for the smaller distal accessory cuspulid and less sharp cingulid; moreover, in occlusal view, the distal portion of the p4 of MSF 90 is more enlarged compared to that of *F. attica* (Figure 1). The overall morphology of the lower m1, with subequal paraconid and protoconid, recalls the morphologies of the MN13-14 *Felis christoli* recovered from the marine sands of Montpellier and described from Venta del Moro (Gervais 1859; Ficcarelli and

Torre 1975; Morales and Aguirre 1976). Other similarities are evident like the position of the mental foramina, the general shape of the m1, with a bulging distobasal portion, instead of a talonid; a small pointy metaconid; and the sharp buccal cingulids on the p4 and the m1. The type mandible is rather shallow and possesses a considerably stout distal accessory cuspulid on the p4 and a visible gap between paraconid and protoconid on the m1, although such gap is not present in MP338 (one of the two specimens housed in the Museum of Basel). More importantly, the available specimens of *F. christoli* do not have any trace of a metaconid, unlike the greatly reduced one of MSF 90. Altogether, the set of features suggests an attribution to a form close to the French and Spanish late Miocene-Early Pliocene *F. christoli*. This interpretation is supported also by the similar size between the specimens of *F. christoli* and those of Cava Monticino, intermediate between large lynxes and smaller feral cats (Figure 3). According to the above-mentioned morphology and overall proportions, we include the Cava Monticino specimens in *Felis christoli*.

Family Hyaenidae Gray, 1821
Sub-Family Ictitheriinae Dietrich, 1927
Genus *Plioviverrops* Kretzoi, 1938

Plioviverrops faventinus Torre, 1989
Figure 4A-B, Figure 5A-B

Material – MSF 62, fossiliferous block with several specimens.

Cranium. MSF 408 (BRS 5/33), palate with left and right P4; MSF 430 (BRS 19/5), left maxillary fragment P3-P4.

Upper teeth. MSF 423_1 (BRS 5/294), right C; MSF 411 (BRS 5/61), right C; MSF 417 (BRS 5/278), right P2; MSF 423_1 (BRS 5/279), left P2; MSF 424_1 (BRS 5/279), left P2; MSF 424_2 (BRS 5/279), left P2; MSF 418 (BRS 5/300), right P3; MSF 425_1 (BRS 5/64), right P3; MSF 425_2 (BRS 5/65), left P3; MSF 425_3 (BRS 5/301), right P3; MSF 425_4 (BRS 5/281), left P3; MSF 426_1 (BRS 5/63), left P3; MSF 415 (BRS 5/165), right P4; MSF 424_2 (BRS 5/297), right P4; MSF 424_3 (BRS 5/162), left P4; MSF 413 (BRS 5/313), left M1; MSF 428_1 (BRS 5/310), right M1; MSF 428_2 (BRS 5/56), right M1; MSF 428_3 (BRS 5/sn), right M1; MSF 414_1 (BRS 5/57), right M2; MSF 414_2 (BRS 5/312), right M2.

Mandible. MSF 92 (BRS 5/34), right hemimandible with p3-m2; MSF 92.1 (BRS 5/34), left hemimandible fragment with p4-m2; MSF 93 (BRS 5/30), left hemimandible with c and p3; MSF 94 (BRS 19/6), right edentulous hemimandible; MSF 407 (BRS 5/158), right hemimandible fragment with p3-m2.

Lower teeth. MSF 412 (BRS 5/sn), left c; MSF 423_1 (BRS 5/16), left c; MSF 423_2 (BRS 5/293), right c; MSF 423_3 (BRS 5/62), right c; MSF 423_4 (BRS 5/279), right c; MSF 409 (BRS 5/167), right p3; MSF 410 (BRS 5/168), right p4; MSF 416 (BRS 5/54), left m1; MSF 417_1 (BRS 5/169), right m1; MSF427_1

(BRS 5/314), left m1;MSF 427_2 (BRS 5/sn), right m1; MSF 427_3 (BRS 5/67), right m1; MSF 427_4 (BRS 5/68), right m1; MSF 429_1 (BRS 5/sn), left m2; MSF 429_2 (BRS 5/sn), right m2; MSF 429_3 (BRS 5/sn), left m2; MSF 429_4 (BRS 5/170), right m2; MSF 429_5 (BRS 5/286), right m2.

Remarks – Remains of a small-sized hyaenid are among the most abundant of all mammals recovered at Cava Monticino. This important record features also some impressive fossils (Figure 1). The species was described extensively by late Danilo Torre, Professor of the University of Florence, in 1989 who was the first to acknowledge the peculiarity of the teeth morphologies of the Cava Monticino small hyaenid (Torre 1989). The cranium morphology, although crushed and deformed in the specimens from Cava Monticino, is somewhat in between that of herpestids and that of a fox, with a longer neurocranium compared to the snout. It has some features that recall modern herpestids, for instance, the posterior portion of the mandible in lateral view or the full dentition with four premolars and two upper and lower molars. Cava Monticino *Plioviverrops* displays crushing-puncturing cusps on its teeth, especially on the molars, like other species of the genus across Europe. For instance, compared to *Plioviverrops guerini* and *Plioviverrops orbignyi* the P4 has a mesiodistally shorter metastyle and, in general, a proportionally larger surface of the upper P4 (for the higher cingulum; the lingually expanded paracone and protocone); the morphology of the M1 is similar in three species but *P. faventinus* has a slender M2, compared to the squared one of *P. guerini* or of *P. orbignyi* (Alcalá 1994; de Bonis and Koufos 1991; Koufos 2011). Compared to both *P. guerini* and *P. orbignyi*, the lower premolars of *P. faventinus* have more developed accessory cuspulids, with larger distal portions, which in the case of the p3 and p4 have the shape of talonid (Torre 1989). Torre (1989) regarded *P. orbignyi* and *P. guerini* as closely-related species, zoogeographic variants of single species dwelling Southern Europe, and *P. faventinus* as derived from *P. orbignyi*. In terms of size, *P. faventinus* is closer to *P. guerini*, as *P. orbignyi* is overall smaller (Figure 6). Nevertheless, in teeth proportions, the similarity of *P. faventinus* lies closer to *P. orbignyi* as *P. guerini* has slender carnassials and upper molars and a proportionally larger m2. These similarities and differences, rather than a true phylogenetic affinity might be a hint of a similar ecological adaptations (as seen in other carnivorans, Bartolini-Lucenti and Rook 2020).

Although *Plioviverrops* is among the earliest hyaenids to appear in the fossil record, as its earliest occurrences are in the MN4-5 (ca. 16.5 Ma) (Turner et al. 2008), *Plioviverrops faventinus* is the youngest species of this mongoose-like genus to appear in the fossil record (Figure 7). The earliest records of *Plioviverrops* are scanty and not well characterized (Turner et al. 2008). *Plioviverrops orbignyi* from numerous localities of Greece dated between 9.7-7.0 Ma (Koufos 2011); and *P. guerini* from Spanish and Greece MN11-12 (8.7-7.0 Ma) sites (Alcalá 1994; Koufos 2011) (Figure 7). The extensive record of Cava Monticino makes *Plioviverrops faventinus* one of the best-known species of the genus. As visible from Figure 6, *P. faventinus* is overall larger compared to *P. orbignyi* and it is more similar to *P. guerini* in this respect. Whereas *P. orbignyi* weighted around 3-4 kg, both *P. guerini* and *P. faventinus* had a probable body mass of ca. 7 kg. Moreover *P. faventinus* is one of the latest species of ecomorph Group 2 to survive the Miocene-Pliocene transition, together with the *P.* cf. *orbignyi* from Çalta-1 (Sen and Saraç 2018). Fossils of *P. faventinus* have been also recovered from the Spanish site of La Gloria 4 (ca. 4.1 Ma).

Sub-family Hyaeninae Mivart, 1882

Genus *Lycyaena* Hensel, 1863

Lycyaena cf. *chaeretis* (Gaudry, 1861)

Figure 4C-D, Figure 5C-F

Material – *Cranium.* MSF 84 (BRS 27/17), cranium with right P3-M1.

Upper teeth. MSF 385 (BRS 27/19), a third upper left incisor; MSF 383 (BRS 8/9), left P3; MSF 401 (BRS 27/18), left M1.

Mandible. MSF 384 (BRS 27/1), juvenile left mandible.

Lower teeth. MSF 83 (BRS 25/20), upper left canine; MSF 86 (BRS 27/2), right p4; MSF 87, right m1 (BRS 27/28).

Postcranial elements. MSF 393, second left metacarpal (BRS 27/35); MSF 394 (BRS 27/36), third right metacarpals; BRS 27/39, third right metacarpals; MSF 395, fifth left metacarpals (BRS 27/36); MSF 396, fifth left metacarpals (BRS 27/37); MSF 64 (BRS 27/31), the proximal part of a left radius; MSF 526, right fragment of pelvis; MSF 404, distal epiphysis of a juvenile right femur; MSF 403 (BRS 27/32), distal fragment of a right tibia; MSF 389 (BRS 27/30), proximal fragment of a right tibia; BRS27/48 (BRS 27/48), a juvenile left tibia; MSF 388 (BRS 27/29), right astragalus and lateral cuneiform; MSF 391(BRS 27/33), left calcaneum; MSF 392 (BRS 27/34), right calcaneum; MSF 398, third metatarsal; MSF 399, first left phalanx; BRS 27/9 (BRS 27/41), first right phalanx; MSF 400 (BRS 27/42), first left phalanges; BRS 27/43, second left phalanges; BRS 27/44, second left phalanges.

Remarks – The morphologies possessed by the large-sized hyaenid from Cava Monticino are a mixture of derived and primitive features for late Miocene Hyaenidae (Figures 4-5): large mesiolingual cuspule on the P3; large paracone on the P4; presence of M1 but absence of the M2; M1 triangular-shaped; the presence of an individualized well developed distolingual cuspulid on the p4; rectangular distal part of the p4; m1 talonid modestly developed, with one large hypoconid and a ridge-like, lingual entoconid; small m1 metaconid (Figure 4-5). A peculiarity of the large hyaenid of Cava Monticino is the prominently developed mesial cuspulid on the P3. The set of morphologies possessed by the specimens of Cava Monticino contrasts with the features of *Thalassictis* s.l., e.g., the dorsoventrally shallow cranium, unlike *Thalassictis robusta* from Kishinev (see Semenov 2008), *Thalassictis montadai* from Hostalets de Pierola; the presence of the M2 (as in *T. robusta* from Kishinev); the absence of a lingual cuspulid on the p4; the larger m1 talonid with developed hypoconid and entoconid. The presence of an m2, is not directly testable on the sample of Cava Monticino, as no m2 nor any mandible of a large hyaenid has been found. The only mandible preserved at Cava Monticino is that of a very young individual with a dp4, but the x-rays image on the mandible has revealed only the roots of the dp4 and the m1, and no m2. These features suggest discarding an attribution to *Thalassictis*. Despite the similarity in size, especially with *Hyaenictis hendey* (Figure 8), an attribution to *Hyaenictis* seems improbable as one of the major diagnostic features of the genus according to Werdelin et al. (1994), i.e., the presence of the m2, is absent in Cava Monticino's hyaenid. Compared to *Hyaenictitherium wongii*, the sample from Cava Monticino is larger (Figure 8) and possesses several features contrasting with the specimens attributed to the former species, e.g., the absence of the M2, the shortened m1, the reduced talonid cuspulids. MSF 84 has a shortened cranium, and especially the muzzle, and contrasts with that of some *Lycyaena* spp., in which is generally more slender and elongated e.g., to *Lycyaena macrostoma* from Dhok Pathan (Pilgrim 1932) and *Lycyaena dubia* from Hayranlı-Sivas (Ozkurt et al. 2015) and Lok. 49 (Zdansky 1924), but it resembles that of *Lycyaena chaeretis* from Samos (unknown locality; Koufos 2021). Another similarity to the sample from Samos is the shape of the M1, although differences from this specimen and from the type (recovered from Pikermi) should be highlighted. The hyaenid from Cava Monticino has a large mesiolingual cuspule on the P3; lowered p4 protoconid contrasting with the slender one of *L. chaeretis*; the p4 distolingual cuspulid is individualized and laterally positioned compared to the distal cingulid; the m1 metaconid is more reduced, and the talonid only presents a large centralized hypoconid and a cristid-like cuspulid on the lingual side. In size, the taxon from Cava Monticino is really large, close to the largest known species of the genus *L. crusafonti* from Bled Douarah (Tunisia) and to *Lycyaena* cf. *chaeretis* from Cerro de la Garita (Alcalá 1994), see Figure 8. For this mixture of similarities and the relevant differences, we prefer to ascribe the taxon from Cava Monticino to *Lycyaena* cf. *chaeretis*, conscious that more research needs to be carried out. The genus *Lycyaena* has a Eurasian and North African distribution (Figure 9): it is known since the MN 9 (a period comprised between 11 and 9.7 Ma) when the species *L. crusafonti* is recovered from the locality 17 of Bled Douarah (Tunisia). Further occurrences are those of the MN 12 (ca 7.75-7.0 Ma): *L. macrostoma* in the Siwalik basin (India-Pakistan); *L. dubia* in several localities of China; and *L. chaeretis* in the famous Greek Miocene sites of Pikermi and Samos. The occurrence at Cava Monticino of this large-sized cursorial hunter is relevant for several reasons. Firstly, this record represents the last occurrence of this genus in the Old World, separated from other congeneric taxa by nearly 1.5 Myr. Furthermore, this of Cava Monticino is one of the largest *Lycyaena* of the fossil record, even larger than the earliest taxon *L. crusafonti* (Figure 8).

Family Canidae Fischer, 1817

Subfamily Caninae Fischer, 1817

Tribe Canini Fischer, 1817

Genus *Eucyon* Tedford and Qiu, 1996

Eucyon monticinensis (Rook, 1992)

Figure 1C-F, K-L

Material – *Cranium.* MSF 466, cranium fragment.

Upper teeth. BRS 27/8, right upper canine; BRS 27/25, right upper canine; BRS 27/26, right upper canine; BRS 27/51, right upper canine; BRS 24/12, right M1.

Mandible. MSF 97 (BRS 27/4), right hemimandible with p2 and m1; MSF 456 (BRS 27/47), a juvenile left hemimandible with p2-p4 in eruption.

Lower teeth. BRS 27/27, three incisors; BRS 27/7, left p2; BRS 27/22, right p2; BRS 27/6, right m1; BRS 27/21, left m1; BRS 27/5; right m2; BRS 27/24; right m2.

Postcranial elements. MSF 100 (BRS 27/16), left humerus; MSF 98 (BRS 27/15), right radius; MSF 99 (BRS 27/14), left ulna; BRS 27/46, right fifth metacarpal; MSF 101 (BRS 27/13), right tibia; BRS27/45, left calcaneum; BRS27/10, right astragalus.

Remarks – The medium-sized canid from Monticino has been described in deep by Rook (1992) as *Eucyon monticinensis*. Its record at Cava Monticino is fairly abundant compared to the other taxa, with cranial and postcranial elements of at least 5 individuals. The type, the right mandible MSF 97 with p2 and m1 (Figure 1E-F, L), shows all the peculiar features that support distinction of *E. monticinensis* from other similar sized and coeval species, like the proportionally stout and deep corpus, m1with developed trenchant portion but also developed talonid one (crushing surface). The genus *Eucyon* is a rather diverse genus of canids that arrived in the Old World between at the end of the Miocene (ca. 7 Ma) and disappeared during the Early Pleistocene (Figure 10). The occurrence of *E. monticinensis* is really important in the Eurasian record as it is the second earliest canid to reach Western Europe, after *Eucyon cipio* (Rook 2009) (Figure 10). Other occurrences of *E. monticinensis* are those of Verduno (Alba, Piedmont) and of the upper cycle of Casino Basin (Siena, Tuscany) (Figure 10). Surely, this species represents nowadays the only species of *Eucyon* yet discovered in Italy. Rook (1992) recognized an affinity between *E. monticinensis* and the sample of the medium-sized canid from Venta del Moro (a coeval site to Cava Monticino). The latter has been recently revised and ascribed to the species *Eucyon debonisi* (see Montoya et al. 2009). The two sample differ for a slight difference in size, as *E. debonisi* is overall smaller (Figure 11). There are also some dentognathic features that distinguish the material from Venta del Moro from that of Cava Monticino, buccolingual margin of the M1 (sharp in *E. debonisi* and rounded in *E. monticinensis*), the robustness of the corpus (stronger in *E. monticinensis*), shape of the m1 (more slender and buccolingually compressed in *E. debonisi*, with a mesiodistally short paraconid and an elongated talonid). Such features are evident although the scarcity of adequately abundant material to assess the entity of intraspecific variability of those two forms leaves the question of their real distinction open.

Family Mustelidae Swainson, 1835

Sub-Family Mellivorinae Gray, 1865

Genus Mellivora Storr, 1780

Mellivora benfieldi Hendey, 1978

Figure 1C, J

Material – *Mandible.* MSF 88 (BRS 25/19), left hemimandible with p3-m1.

Remarks

The extant honey-badger, *Mellivora capensis*, is the only living representative of Mellivorinae although the fossil record of the subfamily is much more abundant (Valenciano and Govender 2020). The earliest occurrences of mellivorines are at MN7-8 (ca 12 Ma) from the Ngorora formation in Kenya, and MN12 (ca. 7 Ma) from Toros Menalla 192 (Chad) and Lothagam (Kenya). The genus *Mellivora* seems to appear around 6.0 Ma, and the species *M. benfieldi* it is indeed the earliest species of the genus. It was described for the first time from the latest Miocene-earliest Pliocene site of Langebaanweg (South Africa; Hendey 1978) (Figure 12). During the Pliocene, the extant species *M. capensis* arose in Africa whereas in Eurasia and North America appeared the large-sized genus *Eomellivora* (Valenciano and Govender 2020). The sample of Cava Monticino is composed of a single left mandible with p3-m1. As Rook et al. (1991) noted the specimen is really similar to the original material of *M. benfieldi* from Langebaanweg if not for minor dental features. This interpretation was followed by a recent restudy by Valenciano and Govender (2020). The record from in the Italian Messinian locality is relevant as it testifies to the northern-most occurrence of this species in the Old-World and the first occurrence on the genus out of the African continent (Figure 12). The only other occurrence of the species is the Late Miocene site of Middle Awash.

Concluding remarks

The carnivoran assemblage recovered from Cava Monticino is, although limited in species richness, relevant in terms of the peculiar composition and different ecology. Of the carnivorans there recorded, the top predator was surely the large-sized *Lycyaena* cf. *chaeretis*. Although size estimations for the other species of the genus are around 50 kg, the individuals of Cava Monticino weighted more than 60 kg. Considering its morphological features (Rook et al. 1991 and the present study) and enamel structure (Ferretti 2007), this hyaenid was interpreted as a hypercarnivorous species referred to the ecomorph group 4 by Werdelin and Solounias (1991). Like others of this ecomorph group, *L.* cf. *chaeretis* from Cava Monticino was a cursorial wolf-like, meat- and bone-eater capable of hunting down large ungulates, like for instance hipparions, probably after tiring them out with long runs, like modern canids do (the African hunting dog or wolves). *Lycyaena* cf. *chaeretis* is also the only large-sized carnivorans yet recovered from Cava Monticino. The other carnivorans are all small- or medium-sized. The felid *Felis christoli* was more similar to a modern small lynx than to feline cats, and, therefore a similar hunting strategy to that of modern *Lynx* can be hypothesized. The dental and mandibular morphology of *Plioviverrops faventinus* are closely resembling those of extant Herpestidae, as identified by Werdelin and Solounias (1991) who classifies the species of this genus in the ecomorph group 2 (mongoose-like Hyaenidae). Ferretti (2007) remarked the omnivorous nature of *Plioviverrops*'s diet pointing out macroscopic and microscopic features like the crushing-puncturing dentition and the outlines of the Hunter-Schreger bands. Studying mandibular and dental proportions, Bartolini Lucenti and Rook (2020) found that *E. monticinensis* probably was able to hunt larger prey compared to other Mio-Pliocene eucyons, up to ca. 5 kg in size. The great variety of small mammals found at Cava Monticino might give us a hint of the diet of this canid: from mice, dormice and hamsters to lagomorphs (like *Prolagus* or *Trischizolagus*), and probably not distasting some herpetofaunal species as well (Villa et al. 2021). *E. monticinensis* represents an important element of the fauna of Cava Monticino and also for other European Messinian localities. This medium-sized canid probably occupied an ecological niche intermediate between the small-sized *Plioviverrops faventinus* and the large-sized *Lycyaena* cf. *chaeretis*, filling the empty place of medium-sized hyenas, as none of them have been discovered in the fossil record of Cava Monticino. Ecologically speaking, *M. benfieldi* was probably very similar to the extant *M. capensis* as few dental differences can be pointed out between the two. *M. benfieldi* could have been a stout omnivorous carnivorans preying on small vertebrates like amphibians, reptiles, birds, and mammals but also insects. Like the extant species it could also eat bulbs, berries, and fruits. The peculiar affection of extant *M. capensis* for honey and bee larvae cannot be proved in the fossil taxon but the possibility cannot be ruled out either.

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Figure Caption

Figure 1 Carnivoran materials from Cava Monticino (Brisighella, RA, Italy). *Felis christoli*: A-B, I - MSF 90 (BRS 27/3), right hemimandible with p4-m1 in lateral (A), occlusal (B) and detailed occlusal photographic and 3D model views (I). *Eucyon monticinensis*: C-F, K-L – BRS 24/12, right M1 in photographic and 3D model occlusal (C) and detailed occlusal (K) views; BRS 27/21, left m1 in photographic and 3D model buccal views (D); MSF 97 (BRS 27/4), right hemimandible with p2 and m1 in lateral (E), occlusal (F) and detailed occlusal (L) views. *Mellivora benfieldi*: G-H, J - MSF 88 (BRS 25/19), left hemimandible with p3-m1 in photographic and 3D model lateral (G), occlusal (H) and detailed occlusal (J) views.

Figure 2 Map of the occurrence of the small felids of the Old World. Localities are ordered in chronological order. *Leptofelis vallesiensis*: MN10 localities, (1) Batallones 1, (2) Batallones 3, Spain. *Felis attica*: MN11 localities, (3) Dorn Dürkheim 1, Germany; (4) Middle Maragheh, Iran; MN12 localities, (5) Akkaşdağı, (6) Karain 2, Turkey; (7) Upper Maragheh, Iran; (8) Molayan, Afghanistan, (9) Pikermi, Greece; (10) Taraklia, Moldavia; (11) Thermopigi, Greece; (12) Valdecebro 5, Spain; (13) Morskaya 2; MN13 localities, (16) Las Casiones, Spain; (17) Dzedzvtakhevi, Georgia. *Felis christoli*: MN13 localities, (14) Cava Monticino, Italy; (15) Venta del Moro, Spain; MN14 locality: (18) Montpellier sands, France. *Felis silvestris*: (19) Ahl al Oughlam, Morocco (earliest *F. silvestris*); (20) Olivola, Italy (type locality of *F. silvestris lunensis*). Data from Ficcarelli and Torre (1975); Koufos (2011); Salesa et al. (2012, 2019).

Figure 3 Biplot of the lower carnassial variables in extant and fossil small-/medium-sized felids and in the specimen from Cava Monticino.

Figure 4 Carnivoran materials from Cava Monticino (Brisighella, RA, Italy). *Plioviverrops faventinus*: A-B – MSF 62, fossiliferous block with several cranial and postcranial elements of two or more individuals in lateral (A) and detailed photographic and 3D model views (B). *Lycyaena* cf. *chaeretis*: C-D – MSF 84 (BRS 27/17), cranium in right photographic and 3D model lateral (C) and ventral (D) views.

Figure 5 Carnivoran materials from Cava Monticino (Brisighella, RA, Italy). *Plioviverrops faventinus*: A-B – MSF 92 (BRS 5/34), right hemimandible with p3-m2 in lateral photographic view (A); MSF 92.1 (BRS 5/34), left hemimandible with p4-m2 in 3D model occlusal view (B). *Lycyaena* cf. *chaeretis*: C-F – MSF 87 (BRS 27/28), right m1 in photographic buccal (C) and in 3D model occlusal (E) views; D, F, MSF 86 (BRS 27/2), right p4 in buccal view (D) and in 3D model occlusal (F) views.

Figure 6 Log-ratio diagram on log-transformed dental variables of Mio-Pliocene species of *Plioviverrops* (namely *Plioviverrops gaudryi*, *Plioviverrops gervaisi*, *Plioviverrops guerini*, *Plioviverrops orbignyi* and *Plioviverrops* cf. *orbignyi*) in comparison to *Plioviverrops faventinus* used as a standard comparison.

Figure 7 Map of the occurrence of *Plioviverrops* in the Miocene of Europe. Localities are ordered in chronological order. *Plioviverrops gervaisi*: MN5, (1) Vieux Collonges, France; MN6, (2) Calatayud, Spain. *Plioviverrops gaudryi*: MN7/8, (3-4) La Grive 1-2, France. *Plioviverrops orbignyi*: MN11, (5) Ravin des Zouaves 5, Greece; (11) Gorna Sushitsa, Bulgaria; MN12 localities, (12) Los Aljezares, Spain; (13) Pikermi, (14) Samos, (15) Vathylakkos-2, (16) Perivolaki, (17) Prochoma, Greece; (18) Kalimantsi 2, (19) Kalimantsi 4, Bulgaria. *Plioviverrops guerini*: MN11, (6) Piera, (7) Crevillente 2, (8) Puente Minero, (9) Viveros de Pinos, (10) Los Aguanaces, Spain; MN12, (20) Cerro de la Garita, Spain; MN 13, (21) Los Mansuetos, (22) Concud, (24) La Alberca, (25) Las Casiones, Spain. *Plioviverrops faventinus*: MN13, (23) Cava Monticino, Italy; MN14, (26) La Gloria 4, Spain. *Plioviverrops* cf. *orbignyi*: MN15, (27) Çalta-1, Turkey. Data from Werdelin and Solounias (1991); Turner et al. (2008).

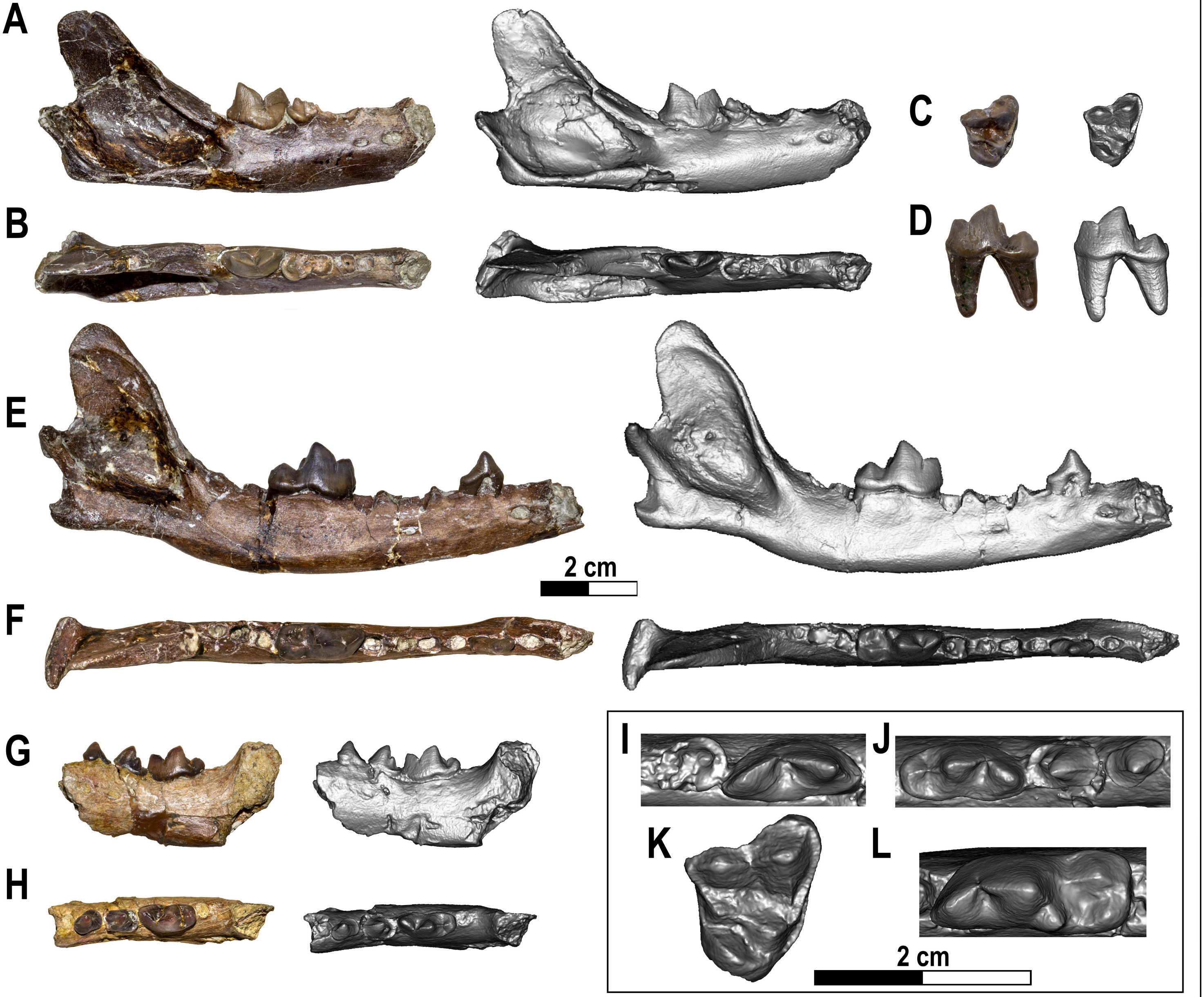
Figure 8 Biplot of the lower carnassial variables of selected fossil hyaenids as compared to the specimen from Cava Monticino.

Figure 9 Map of the occurrence of *Lycyaena* in the Miocene of Europe. Localities are ordered in chronological order. *Lycyaena crusafonti*: MN9, (1) Bled Douarah, Loc. 17, France. *Lycyaena chaeretis*, MN10, (3) La Roma 2, Spain; MN11, (4) Hidiraga, Turkey; MN12, (5) Pikermi, (11) Samos, Greece; (12) Taraklia, Moldavia; (13) Valdecebro 5, Spain; MN13, (15) El Arquillo 1, (16) Los Mansuetos, Spain. *Lycyaena* aff. *chaeretis*: MN10, (2) Los Valles de Fuentidueña, Spain. *Lycyaena* cf. *chaeretis*: MN10, (10) Cerro de la Garita, Spain; (17) Cava Monticino, Italy. *Lycyaena macrostoma*: MN12, (6) Dhok Patan, (7) Hasnot, (8) Jabi, (9) Wadia, Pakistan. *Lycyaena dubia*: late MN12-MN13, Pao-Te-Lok.49, Wenquan-dakusitai, China. Data from Werdelin and Solounias (1991); Turner et al. (2008).

Figure 10 Biplot of the lower carnassial variables of Mio-Pleistocene *Eucyon* species as compared to the sample of *E. monticinensis* from Cava Monticino.

Figure 11 Map of the occurrence of *Eucyon* in the Miocene-Early Pleistocene times of Europe. Localities are ordered in chronological order. *Eucyon cipio*: MN 13, (1) Los Mansuetos, (2) Concud, Spain. *Eucyon monticinensis*: MN13, (3) Cava Monticino, (4) Casino, (6) Verduno, Italy. *Eucyon debonisi*: MN13, (5) Venta del Moro, Spain. ‘*Eucyon*’ *khoikhoi*: MN13, (7) Langebaanweg, South Africa. *Eucyon davisi*: MN13, (8) Khirgis Nur 2 Loc. 5-37, Mongolia; MN14, (10) Khirgis Nur 2 Loc. 51-55, (11) Sangin Dalay Nur, Mongolia; (17) Gusinyi Perelet, Kazakhstan; (19) Olkhon 520 level B, Russia; MN15-16a, (27) Xiakou, (28) Liujiagou, China. *Eucyon intrepidus*: MN13, (9) Lukeino, Kenya. *Eucyon kuta*: MN 15, (21) Aralee Issie, Ethiopia. *Eucyon marinae*: MN15, (22) Muhor-Erig, Mongolia. *Eucyon adoxus*: MN14-15, (18) La Calera, Spain; (23) St. Estève, France; (24) Red Crag, UK. *Eucyon odessanus*: MN14, (13) Beresti, Romania; (14) Etulia, (15) Nikolskoe, (16) Novaja Karbolia, Moldavia; MN15, (20) Odessa Catacombs, Ukraine; (25) Malusteni, Romania; (26) Megalo Emvolon, Greece; MN 17, (34) Sarikoltepe, Turkey. *Eucyon zhoui*: MN14, (12) Gaozhuang, MN16, (29) Yinjiao, (30) Zhaozhuang, China. *Eucyon minor*: MN16a, (31) Shamar, (32) Beregovaya, (33) Udunga, Russia; MNQ18, (36) Xiashagou, China. ‘*Eucyon*’ *kuruksaensis*: MN17, (35) Kuruksay, Tajikistan. Data from Rook (2009); Valenciano et al. (2021).

Figure 12 Map of the known occurrences of *Mellivora benfieldi* in the Old World in comparison to the extant distribution of the extant *Mellivora capensis* (shaded area). (1) Langebaanweg, South Africa; (2) Cava Monticino, Italy; (3) Middle Awash, Ethiopia. Data from Valenciano and Govender (2020).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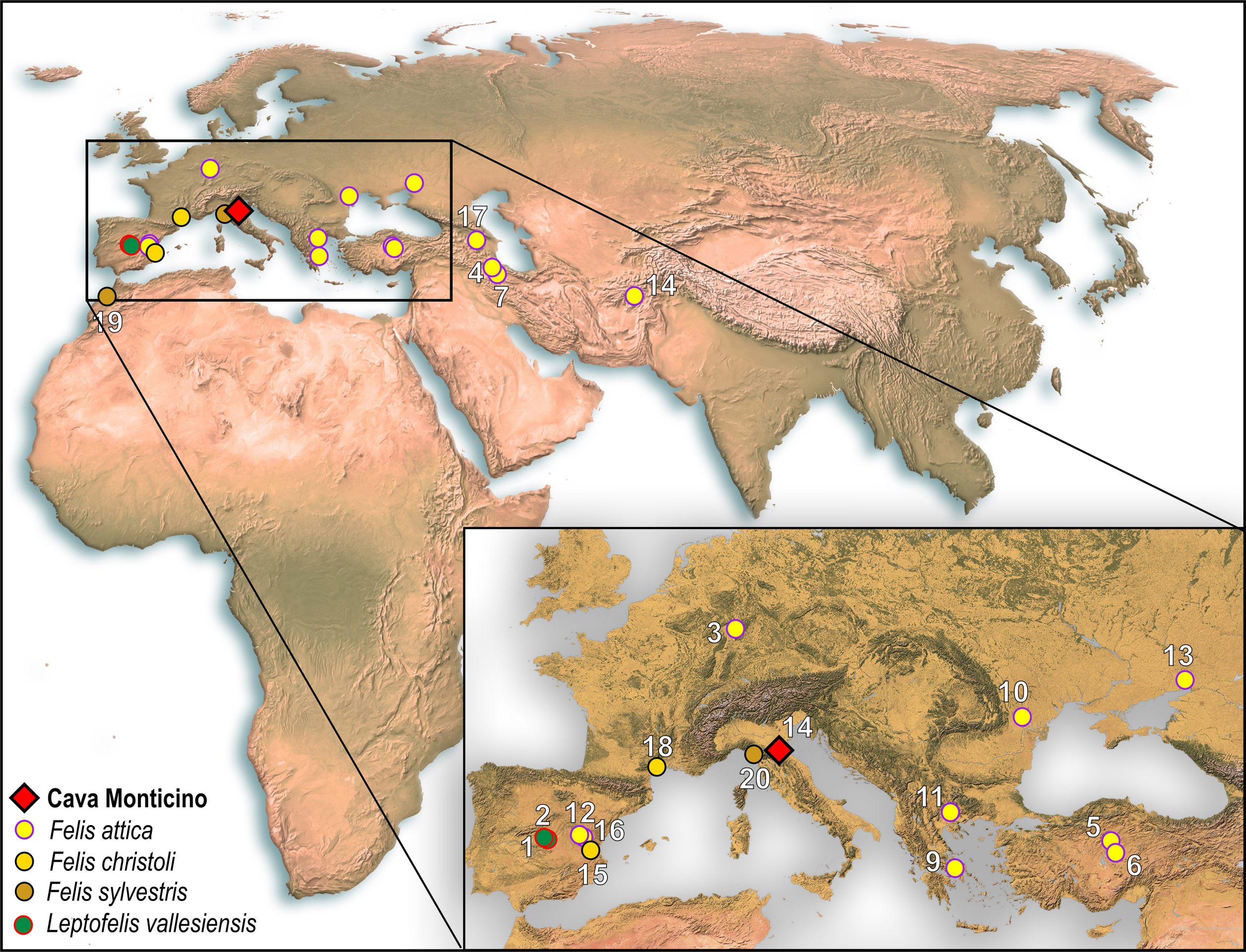
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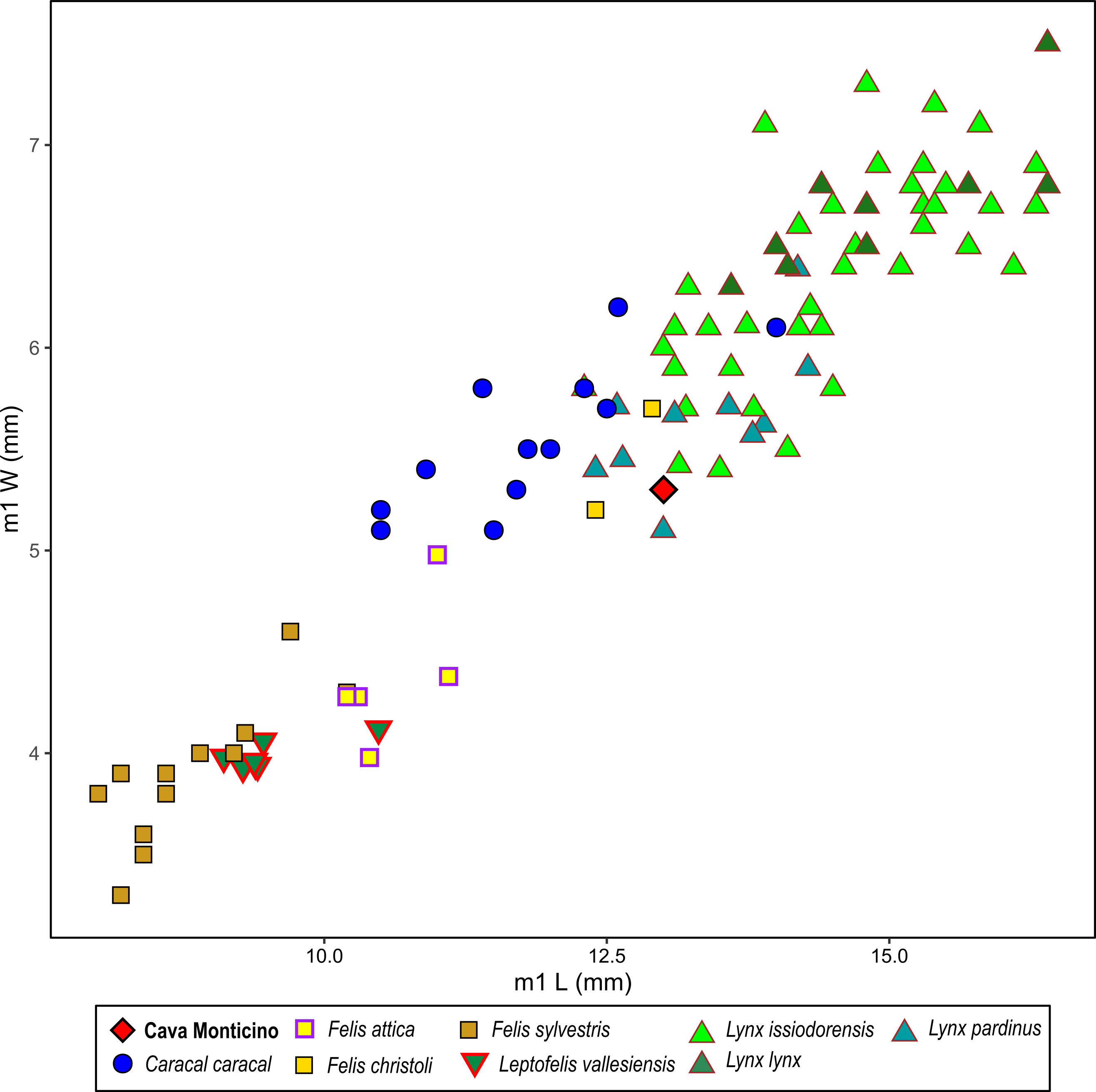
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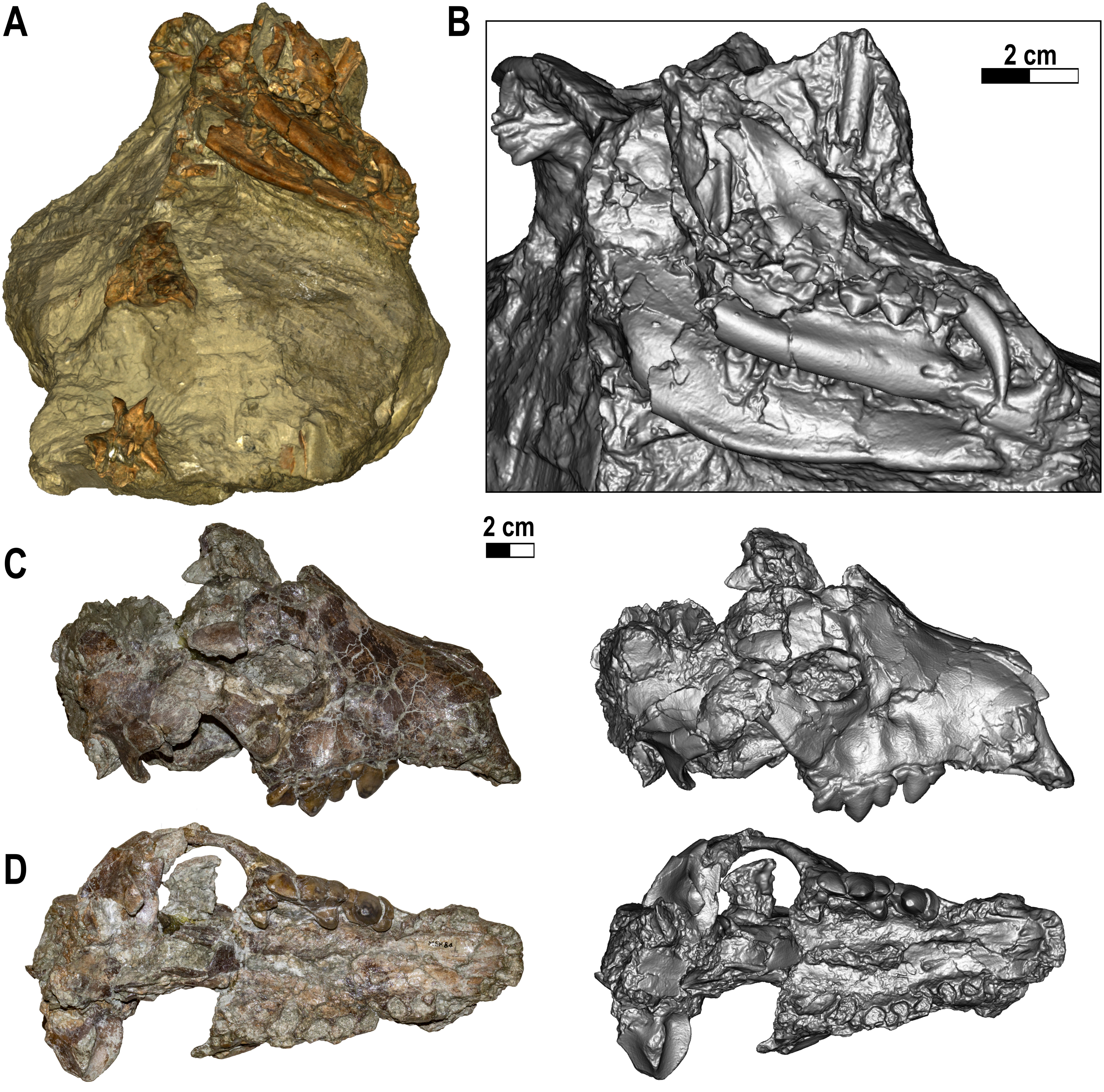
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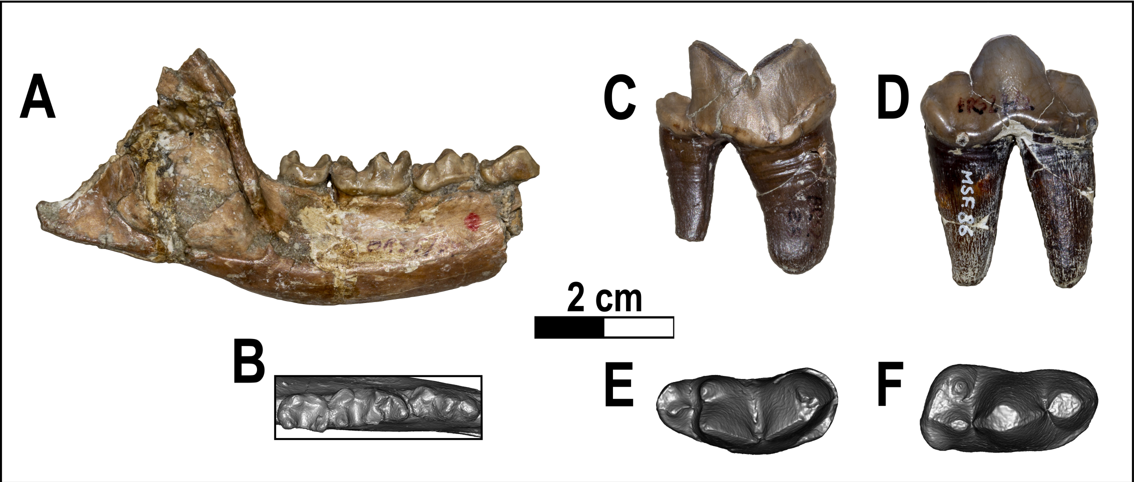
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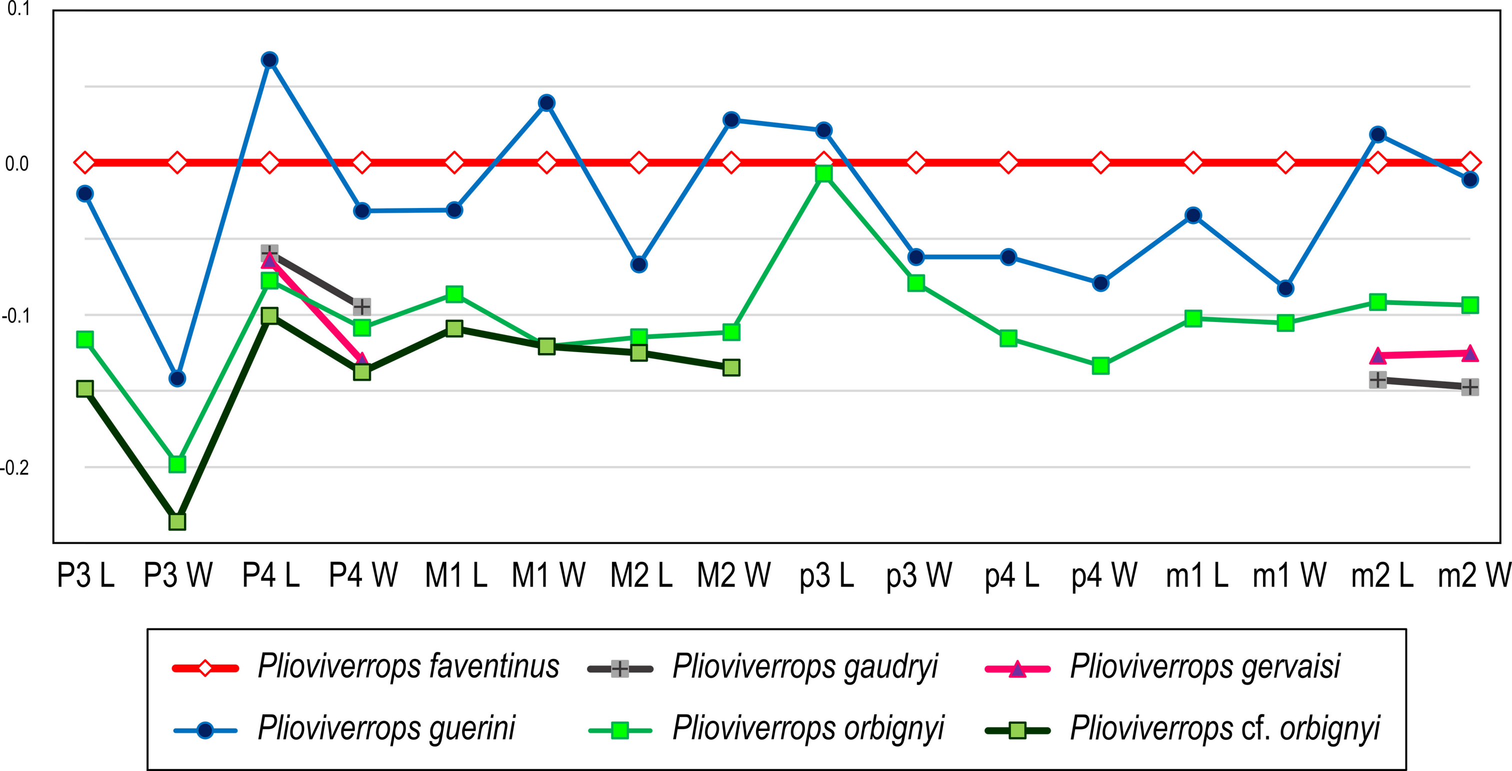
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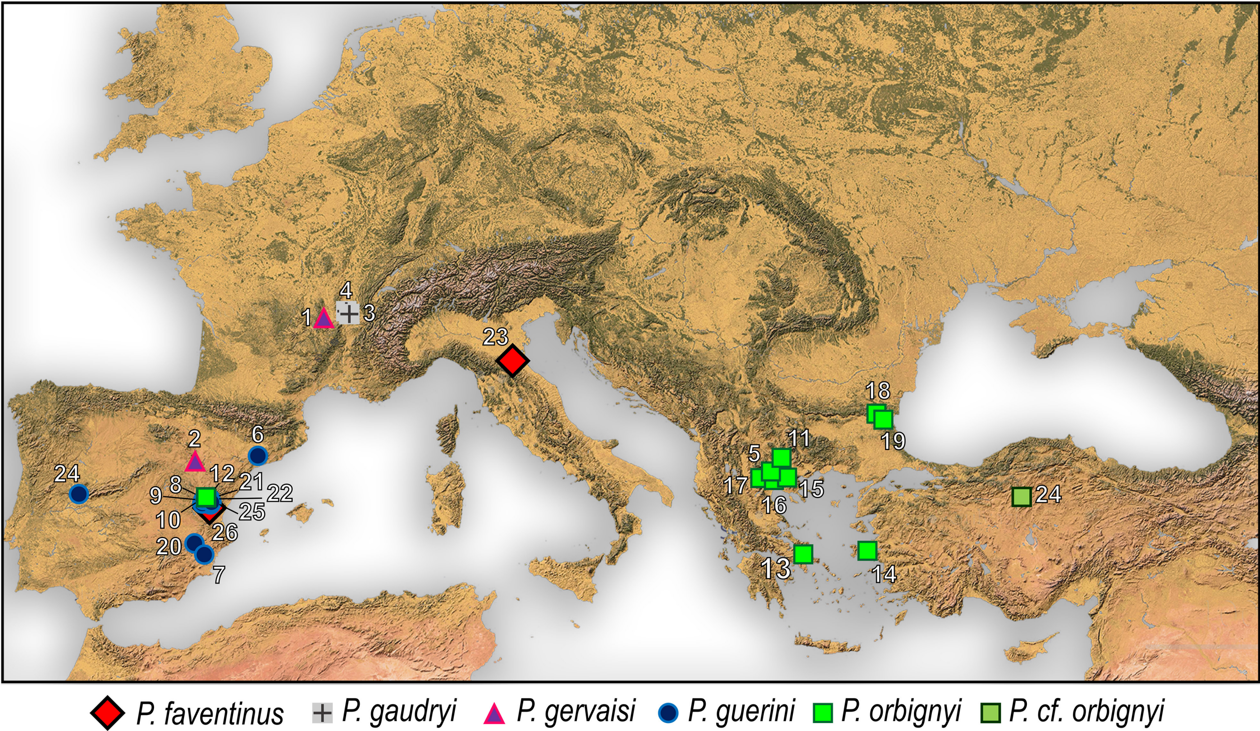
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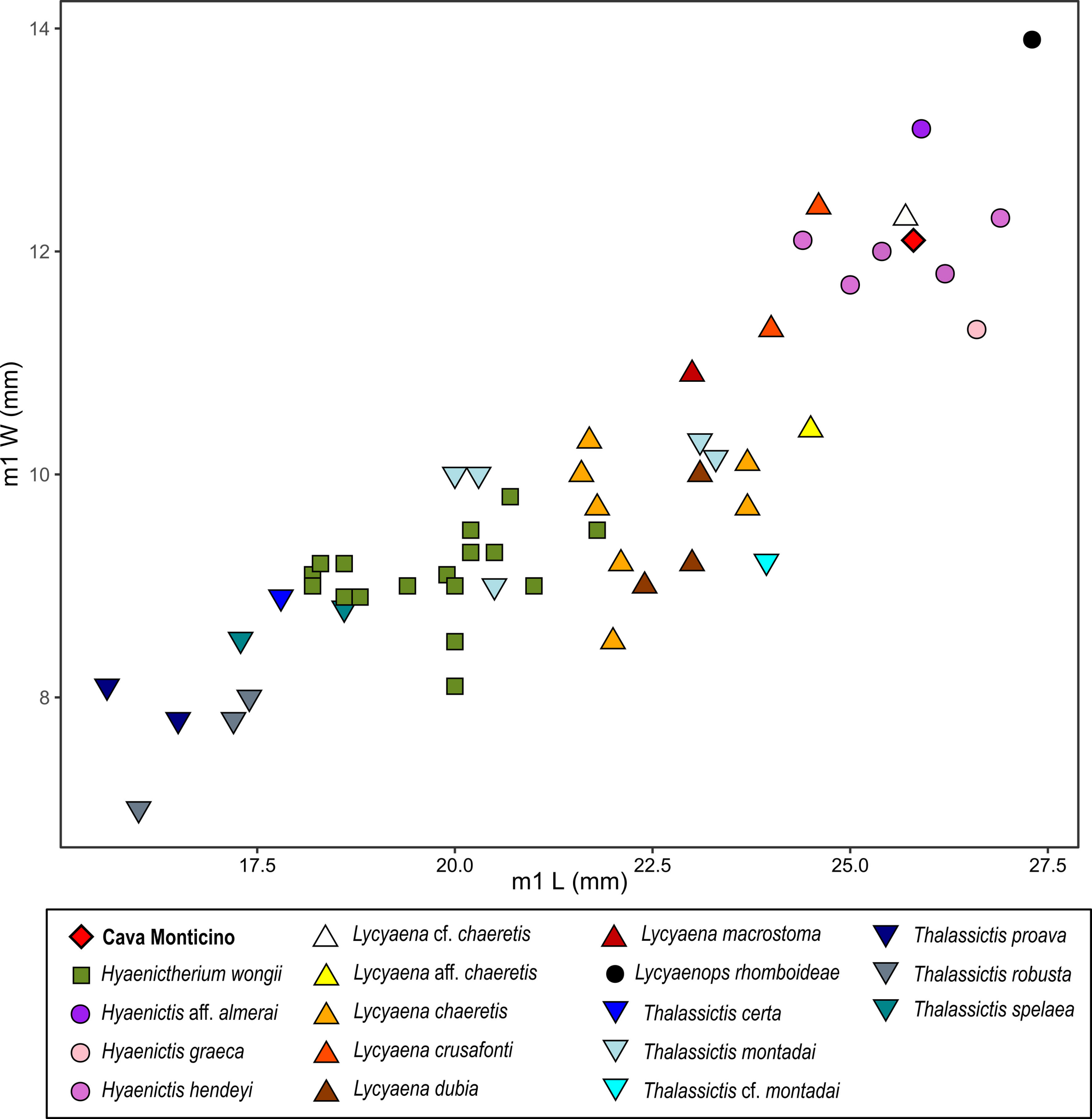
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Lycyaena aff. chaeretis
Lycyaena chaeretis
Lycyaena crusafonti
Lycyaena dubia
Lycyaena macrostoma
Lycyaenops rhomboideae
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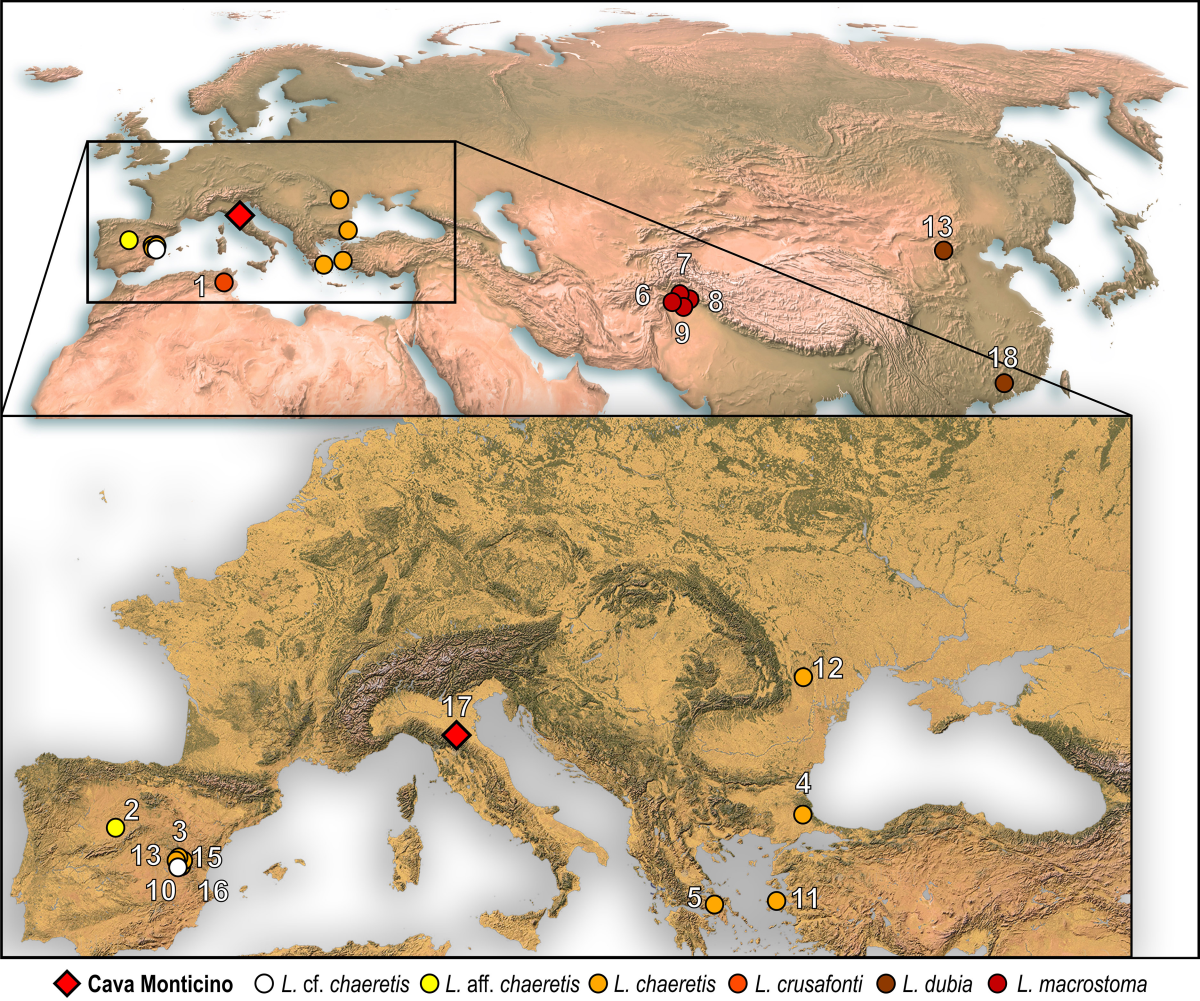
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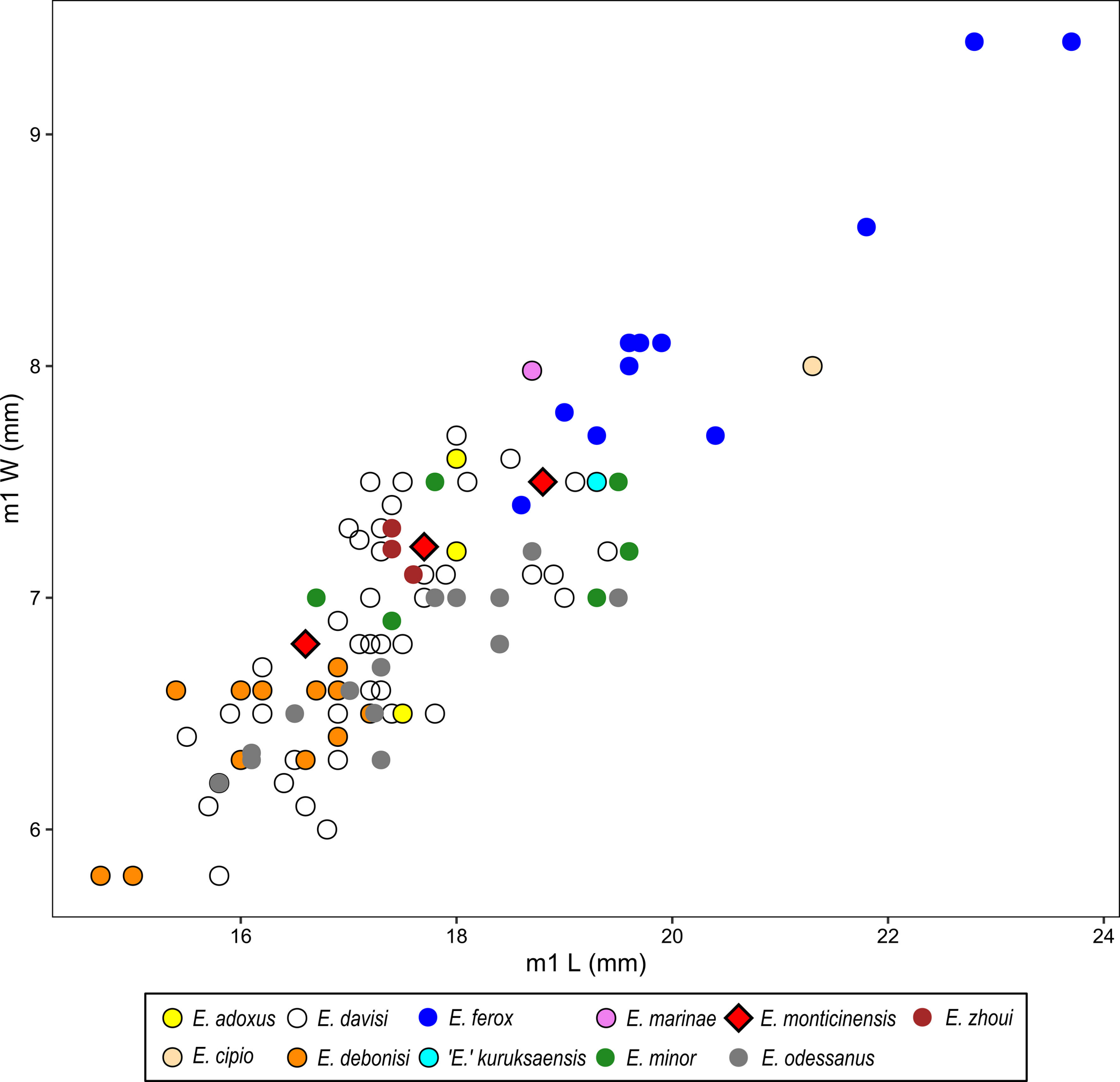
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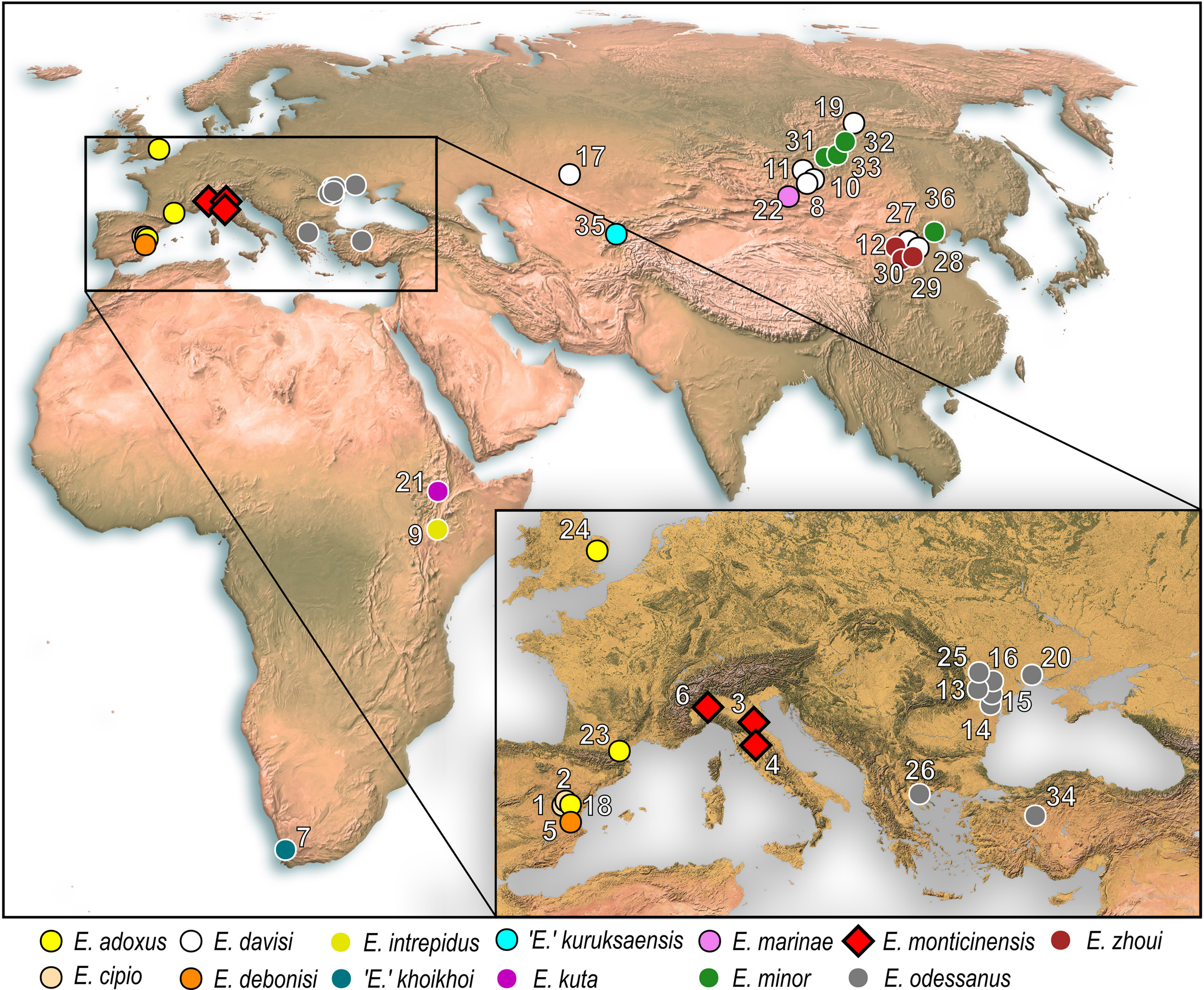
E. minor
E. odessanus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1
18
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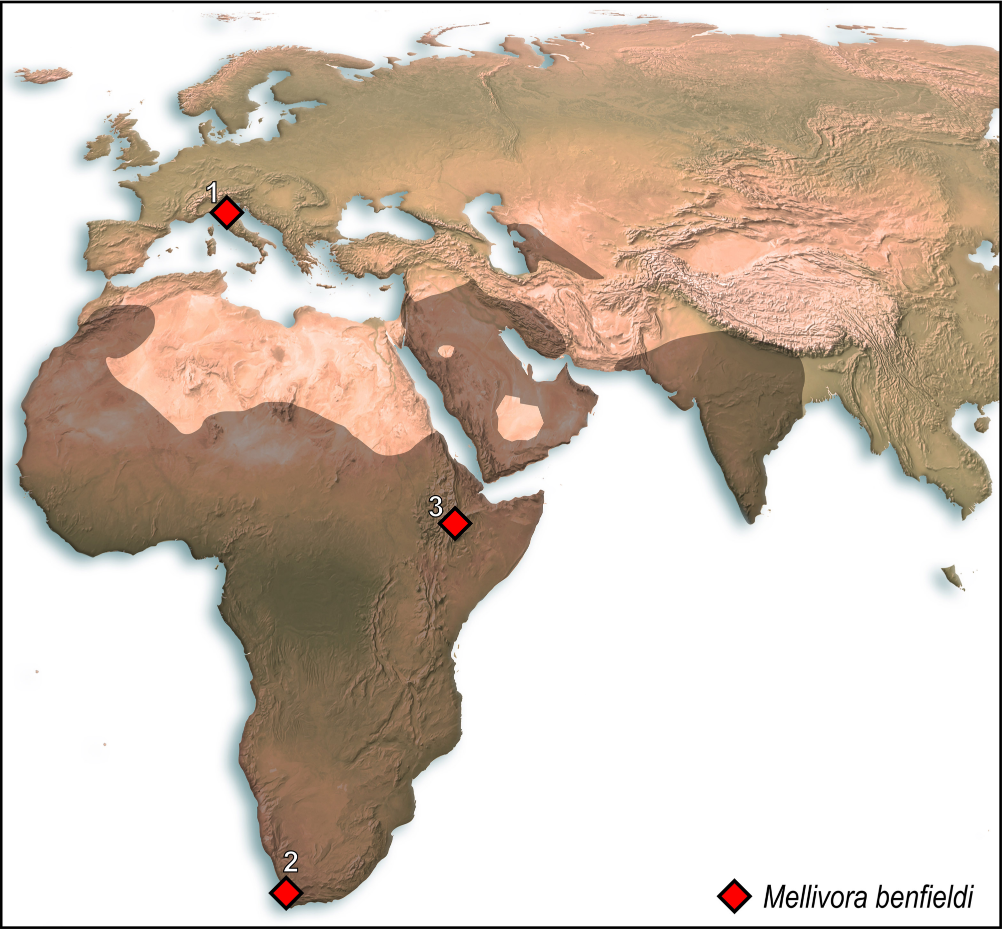
E. adoxus
E. davisi
E. intrepidus
'E.' kuruksaensis
E. marinae
E. monticinensis
E. zhoui
E. cipio
E. debonisi
'E.' khoikhoi
E. kuta
E. minor
E. odessanus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◆ *Mellivora benfieldi*