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RESEARCH

The last of Europe: systematics and palaeoecology of the ictitheres (Hyaenidae) from Venta del Moro (Spain)

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Abstract

Venta del Moro is one of the most exceptional localities in the Miocene of Europe due to its chronostratigraphic position and its unusual fauna, which includes taxa of African and Asian origin. The hyaenids of this locality belong to the group of ictitheres, dog-like hyenas that roamed Eurasia and Africa until their sudden decline at the latest Miocene and their subsequent ecological replacement by the canids. The ictithere record of Venta del Moro is crucial to our understanding of hyaenid evolution, since it represents the last accurately dated occurrence of ictitheres in Europe, and one of the very few cases of coexistence between ictitheres and canids. The bulk of the discovered craniodental material is identified as *Hyaenictitherium wongii*, an abundant species with a wide distribution and morphometric range in the Turolian of Eurasia. However, four isolated teeth correspond to a larger, unidentified ictithere that may represent one of the Asian immigrants present at the locality. A preliminary review of the genus *Hyaenictitherium* is conducted, emphasising the importance of intraspecific variability throughout its temporospatial range. This allows us to discuss the validity of several species, noting that a thorough review with firsthand study of old material is required. In palaeoecological terms, *H. wongii* was, according to our current knowledge, a coyote-like, cursorial animal, with advanced adaptations for durophagy, larger and more robust than the coexisting *Eucyon debonisi*. This relationship between canids and ictitheres is seen in other localities in Eurasia and Africa, showing that the dynamics of the aforementioned transition are complex and cannot be explained solely by the Eurasian dispersal of canids.

Keywords Canidae · Carnivora · *Hyaenictitherium* · Miocene · Ventian

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Introduction

The locality of Venta del Moro

The palaeontological site of Venta del Moro (Valencia, Spain) is one of the most significant continental Miocene localities in the Iberian Peninsula, due to the richness and diversity of its fossil assemblage. First reported by Aguirre et al. (1973) and Robles (1974), the site is located 2 km southeast of the village of the same name (UTM Zone 30 S, 642494 E, 4370967 N) within the Cabriel Basin (Fig. 1). Fossil remains recovered from the site include charophytes, pollen, macroflora, foraminifera, aquatic and terrestrial molluscs, ostracods, fish, amphibians, reptiles, and both small and large mammals (e.g., Morales 1984; Montoya et al. 2006; Abella et al. 2014; Casas-Gallego et al. 2015; Delfino et al. 2021; Guillem et al. 2022). The site has been correlated with the upper Turolian (MN13 biozone; Mein 1990, 1999; Van Dam 1997) and has been magnetostratigraphically dated to approximately 6.23 million years ago (Gibert et al. 2013), near the Miocene/Pliocene boundary. Venta del Moro has also yielded the first European occurrences (FADs) of the ursoid *Agriotherium* (Morales 1984; Abella et al. 2014, 2019), the canid *Eucyon* (Montoya et al. 2009), the camel *Paracamelus* (Morales et al. 1980; Morales 1984; Pickford et al. 1993, 1995; van der Made and Morales 1999; Caballero et al. 2021), and the murid *Paraethomys* (Gibert et al. 2013; Mansino et al. 2017).

Due to its exceptional fossil record and its status as the type locality for multiple species —including the macromammals *Agriotherium roblesi*, *Paracamelus aguirrei*, *Tragoportax ventiensis*, and *Parabos soriae* (Morales and Aguirre 1976; Morales 1984)— Venta del Moro has been designated as a Site of Special Interest in the Geoscientific Map of the Province of Valencia. It is also included in the Geological Heritage Catalogue of Valencia and in the Palaeontological Map of the Valencian Community (Robles et al. 1983). Recent work has described five new species of macro- and micromammals from the site: *Eucyon debonisi*, *Martes ginsburgi*, *Eliomys yevesi*, *Rhinolophus antonioi* and *Pipistrellus rouresi* (Montoya et al. 2009, 2011; Mansino et al. 2015a; Crespo et al. 2018).

The site's faunal assemblage suggests that it played a crucial role in major dispersal events of Asian (camels, canids, colobines, ursoids) and African (hippos, crocodiles) taxa into Western Europe during the Late Miocene (Pickford and Morales 1994; Agustí et al. 2006; van der Made et al. 2006; Minwer-Barakat et al. 2009, 2018; Gibert et al. 2013; Alba et al. 2015; Mansino et al. 2015b; García-Alix et al. 2016; Delfino et al. 2021). Additionally, Venta del Moro records other taxa with African affinities, such as the murid rodent *Paraethomys meini* (Michaux 1969) and the chiropteran *Myotis podlesicensis* (Mansino et al. 2017; Crespo et al. 2018). Aguirre et al. (1976) proposed Venta del Moro as the reference locality for a new mammalian age, the Ventian, later refined by Alberdi et al. (1977) and Alberdi and Bonadonna (1988), though this designation has seen limited use in recent studies (Morales et al. 2013).

Late Miocene ictitheres

The family Hyaenidae is today represented by only four species that are found in Africa and south/southwestern Asia. However, during the Miocene, the hyaenids displayed an astonishing range of ecomorphs, from small opportunistic omnivores like *Plioviverrops* to giant crocutoid bone-crackers such as *Adcrocuta* (Werdelin 1991; Werdelin and Solounias 1991; Turner et al. 2008; Coca-Ortega and Pérez-Claros 2019). Between these two ends of the hyaenid ecomorphological spectrum is the group of ictitheres, which included medium-sized genera with moderate adaptations for bone crushing and many cranial and postcranial similarities with the extant canids (Crusafont Pairó and Petter 1969; Werdelin and Solounias 1991; Ferretti 2007; Turner et al. 2008; Coca-Ortega and Pérez-Claros 2019; Koufos 2021; Kargopoulos et al. 2023a). Some of these species were extremely abundant during the Miocene and have been found in numerous localities in Eurasia, often ranging from Spain to China, such as *Ictitherium viverrinum* and *Hyaenictitherium wongii* (Gaudry 1862–1867; Zdansky 1924; Solounias 1981; Werdelin 1988a, b; Werdelin and Solounias 1991; Tseng and Wang 2007; Kargopoulos et al. 2023b). However, despite their long reign over the Miocene faunas of Eurasia and Africa, ictitheres suddenly disappear from the fossil record at the end of the Late Miocene, with very scarce records in the Early Pliocene of Africa and Asia (Hendey 1978; Werdelin et al. 1994; Tseng and Wang 2007; Iurino et al. 2022). Their ecological niches were gradually filled by the canids, which became increasingly abundant and diverse during the Pliocene and the Pleistocene (e.g., Rook 2009; Valenciano et al. 2022).

Even though there have been many valuable efforts to review the systematics and evolution of ictitheres over the recent decades (Crusafont Pairó and Petter 1969; Kurtén 1982; Werdelin 1988a, b; Semenov 1989, 2008; Werdelin and Solounias 1991; Tseng and Wang 2007), an in-depth revision of this group and the details of its Late Miocene radiation is herein considered necessary to resolve the lingering doubts about taxonomy and to clarify the evolutionary relationships between the included taxa. Despite some occasional doubts regarding the family attribution of this group, it is now securely considered as part of the hyaenid family. It can be differentiated by the more plesiomorphic forms of the family, such as *Plioviverrops*, based on larger

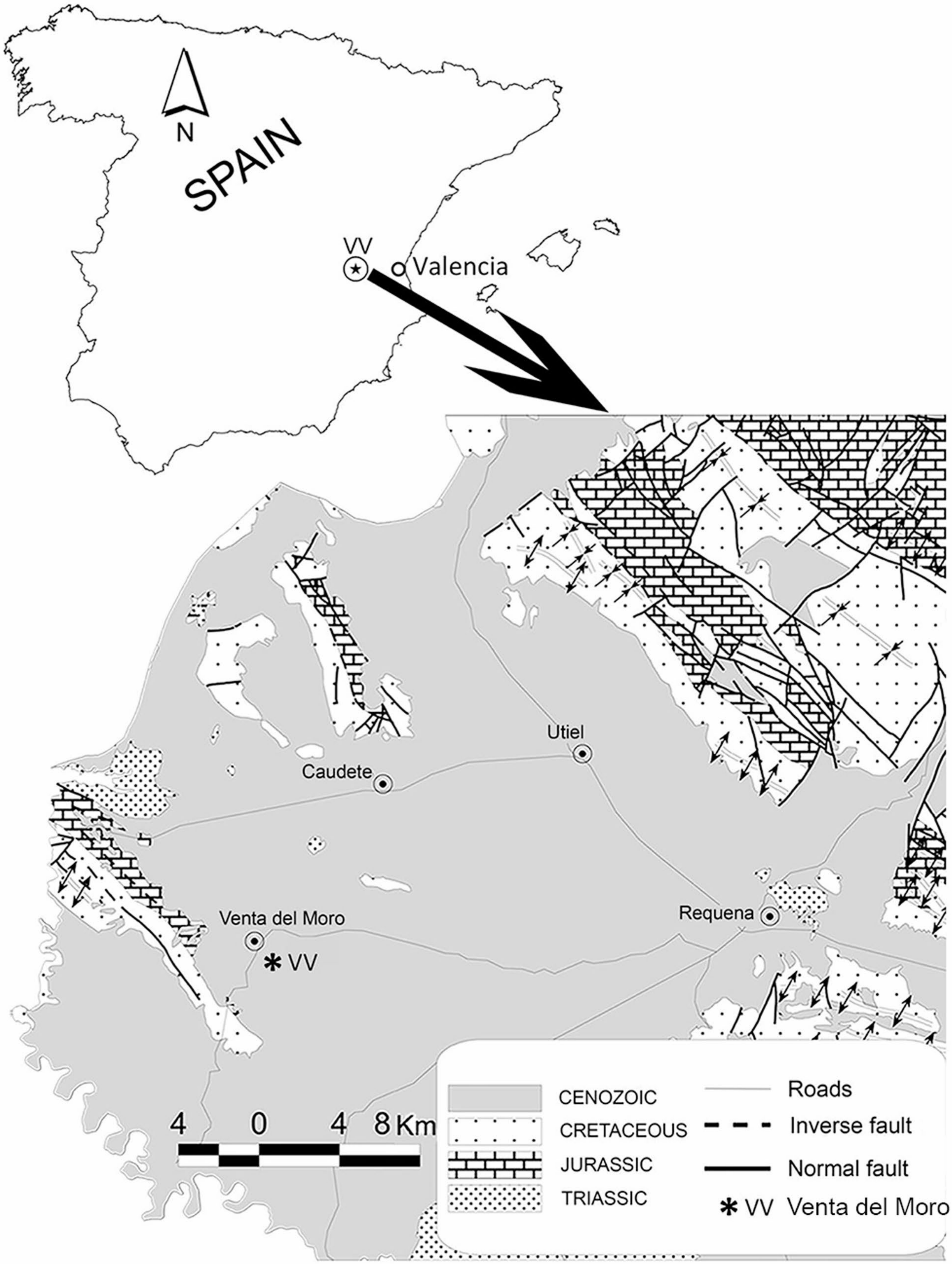

Fig. 1 Geological map of the area of Venta del Moro (Cabriel Basin, Valencia, Spain) with the geographical situation of the palaeontological site (modified from Gibert et al. 2013)

size, higher cranial vault, wider zygomatic arches, more developed tympanic, more robust mandibular ramus and cheek teeth, gradually less developed upper molars as well as the m1 talonid and m2, and m1 talonid cuspids lower than the trigonid ones. On the other end, it can be differentiated from the more derived hyenas, such as *Adcrocuta*, in the smaller size, the longer rostrum, the less developed tympanic, the slenderer mandibular ramus and cheek teeth, the presence of P1/p1 and M2/m2 and the relatively larger upper molars and m1 talonid.

The hyaenid material from Venta del Moro was first reported by Morales and Aguirre (1976) as *Ictitherium sivalense*. Some years later, Soria (1979) attributed it to *Thalassictis* aff. *hyaenoides*, a taxonomic referral also followed by Morales (1984) and Fraile et al. (1997). The material of these publications is hosted in Madrid and Barcelona. New material hosted in Valencia was preliminary identified as *H. wongii* by Morales Flores (2024).

Therefore, the purpose of the present work is to critically review all the available hyaenid material from Venta del Moro, to clarify its taxonomic identity, and to discuss the palaeoecological, biogeographical and evolutionary implications of this record.

Materials and methods

In total, there are 64 dentognathic specimens of hyenas from Venta del Moro: 34 upper teeth and 30 lower teeth. The material is housed in the collections of the Museu de Geologia de la Universitat de València (MGUV, Valencia, Spain), the Museo Nacional de Ciencias Naturales (MNCN-CSIC, Madrid, Spain), and the Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA, Cerdanyola del Vallès, Spain). The present article reviews the previously published material (Morales and Aguirre 1976; Soria 1979; Morales 1984; Morales Flores 2024) and reports some additional specimens, allowing for wider taxonomic comparisons and ecomorphological implications.

Institutional abbreviations: **AMNH**, American Museum of Natural History; **GPIMH**, Geological and Palaeontological Institute and Museum, Hamburg; **HLD**, Hessisches Landesmuseum Darmstadt; **ICP**, Institut Català de Paleontologia Miquel Crusafont; **MGL**, Musée Cantonal de Géologie, Lausanne; **MGUV**, Museu de Geologia de la Universitat de Valencia; **MHNG**, Musée d'Histoire Naturelle de Geneve; **MNCN**, Museo Nacional de Ciencias Naturales; **MNHN**, Musée Nationale d'Histoire Naturelle; **NHMUK**, Natural History Museum of the United Kingdom; **NHMA**, Natural History Museum of the Aegean; **NMW**, Naturhistorisches Museum Wien; **SARA**, Supervisory Authority for Regulatory Affairs.

Metric abbreviations: **H**, maximum height of the dental crown from the dentine-enamel juncture until the dental tip; **L**, maximum mesiodistal length of the dental crown; **Lb**, maximum mesiodistal length of the dental crown on its buccal side; **Ll**, maximum mesiodistal length of the dental crown on its lingual side; **Ltr**, maximum mesiodistal length of the lower carnassial trigonid; **W**, maximum buccolingual width of the dental crown; **Wb**, maximum buccolingual width of the upper carnassial blade. Raw data on the measurements of the specimens are provided in Online Resource 1.

Systematic Palaeontology

Order Carnivora Bowdich, 1821
Family Hyaenidae Gray, 1821
Subfamily Ictitheriinae Trouessart, 1897

Included genera: *Ictitherium* Wagner, 1848; *Thalassictis* Gervais, 1850, ex von Nordmann; *Protictitherium* Kretzoi, 1938; *Hyaenictitherium* Kretzoi, 1938; *Miohyaenotherium* Semenov, 1989.

Remarks: Herein, the term Ictitheriinae is used in a relatively strict sense. Alternative views on the included genera of this group might also include *Lycyaena* Hensel, 1862.

Emended subfamily diagnosis: Hyaenids of moderate size, auditory bullae with developed tympanic but also with developed caudal entotympanic, rostrum long and slender, P1/p1 and M2/m2 present, moderately robust cheek teeth, slightly reduced P4 protocone, m1 trigonid cuspids higher than the talonid ones.

Genus *Hyaenictitherium* Kretzoi, 1938

Emended generic diagnosis: Member of Ictitheriinae with large size, derived auditory bulla with very extended tympanic, present posterior lip of the external auditory meatus, straight or concave ventral profile of the mandibular corpus and presence of a mental edge, robust premolars, P4 protocone level or more distal than the parastyle, P4 metastyle elongated, reduced upper molars and m2, reduced m1 talonid, m1 hypoconid larger than the entoconid, and relatively elongated limb bones.

Included Species: *Hyaenictitherium wongii* (Zdansky, 1924) (=*Hyaenotherium magnum* Semenov, 1989), *Hyaenictitherium hyaenoides* (Zdansky, 1924) (= *Hyaenictitherium venator* Semenov, 1989, and *Lycyaena parva* Khomenko, 1914, at least partly), *Hyaenictitherium namaquensis* (Stromer, 1931), *Hyaenictitherium pilgrimi* Werdelin and Solounias, 1991, *Hyaenictitherium ebu* (Werdelin, 2003), *Hyaenictitherium minimum* de Bonis et al., 2005.

Remarks: Many species of *Hyaenictitherium* sensu lato from Europe, Asia, and Africa have been described over the years, and there is an ongoing dispute about the taxonomic validity of many of them (Semenov 1989, 2008; Werdelin 1988a; Werdelin and Solounias 1991; Tseng and Wang 2007). In this work we recognize the aforementioned species, noting that a thorough review is needed to clarify the exact relationships within the genus. The justification for this preliminary framework and the particular differences between the species are provided in the following paragraphs. See also Online Resources 2–4 for information about the intraspecific morphological variability of *H. wongii* from Samos and *H. hyaenoides* from China, based on the material from AMNH, as discussed below.

Hyaenictitherium minimum from Toros Menalla (ca. 7.0 Ma; Chad) can be differentiated from all other species of the genus based on its small size (P4L around 19.0 mm; m1L around 15.5 mm) and the small/absent mesial accessory cuspids of the premolars (de Bonis et al. 2005, 2010). Werdelin and Peigné (2010) suggest that the three specimens from Lothagam published by Werdelin (2003) ascribed to *H.* cf. *parvum* could in fact belong to *H. minimum*, but the size of this material is considerably larger than that of *H. minimum*. The mesial accessory cuspids of the premolars are indeed small, but not to the extent seen in the Toros Menalla specimens. Additionally, the height of the main cuspids of the premolars is very different from that seen in *Hyaenictitherium*. Semenov (2008) suggests that these specimens could be attributed to *Hyaenictis* sp., also reported by Werdelin (2003) from Lothagam. This genus is relatively rare, but the existing specimens show a much more robust mandibular corpus and a long and narrow p2 (e.g., Gaudry 1862–1867; Villalta Comella and Crusafont Pairó 1943; Vinuesa et al. 2017). Another hyaenid from this period from Africa is *Belbus djurabensis*, also from Toros Menalla (de Bonis et al. 2010). Despite the poor preservation of the Toros Menalla specimens, some similarities with the Lothagam hemimandible (e.g., the overall size, the relative slenderness of the mandibular corpus, the high main cuspids and the small accessory cuspids of the premolars) are evident, but on the other hand the teeth are slightly slenderer. Without careful re-examination of the material, it is not easy to attribute it to any of the known species, but it is concluded that it differs significantly from *H. minimum*.

Geraads (1997) erected a new species from the Late Pliocene (MN 16, 2.19–1.8 Ma) of Ahl Al Oughlam (Morrocco):?*Hyaenictitherium barbarum* Geraads, 1997, based on four specimens of upper and lower dentition. However, Werdelin and Dehghani (2011) argue that this is a synonym of *Ikelohyaena abronia*, which was already implied in Geraads (2008). We agree with this suggestion, and we will not consider this form as a member of the genus *Hyaenictitherium*.

The species *H. parvum* and *H. venator* have been a subject of debate concerning their validity as distinct species and their generic attribution (Semenov 1989, 2008; Werdelin and Solounias 1991; Tseng and Wang 2007). Werdelin and Solounias (1991) and Tseng and Wang (2007) synonymize these two names and highlight that they could be a separate species (under the name *H. parvum*), or that it could belong to one or both of the two well-known species *H. wongii* and *H. hyaenoides*. Semenov (1989) considered "*H. venator*" to be more similar to *H. hyaenoides* than to *H. wongii*. Its differentiation from *H. hyaenoides* was based on its larger size, the long and pointed postorbital processes and the higher mandibular angle. The postorbital processes are usually broken in skulls, but in the *H. hyaenoides* sample from China hosted in the AMNH, there are some specimens (such as AMNH 14-L31, AMNH 144879, and AMNH 144880) that show moderate to developed postorbital processes. Therefore, such variability is seen in *H. hyaenoides*. As also pointed out by Werdelin and Solounias (1991), the mandibular angle can change drastically during ontogeny, so it is not always a reliable character for taxonomic distinctions, at least without large samples. In terms of size differentiation, the morphometric review by Werdelin (1988a) for the two main species considerably expanded the known ranges for both. Even though the mean and highest values of "*H. venator*" fit very well with those of *H. hyaenoides*, the lowest values could also fit into the ranges of *H. wongii*. The coexistence of the two species in the same locality is not uncommon (e.g., Zdansky 1924; Qiu 1985; Werdelin 1988a), so the possibility that at least some of these specimens could belong to *H. wongii* cannot be excluded. Nevertheless, the existence of large specimens more similar to *H. hyaenoides* than to *H. wongii* based on the comparisons of Semenov (1989) cannot be doubted for any of the localities included in the distribution of this taxon: Novoelisavetovka (Ukraine, MN11), Novaja Emetovka 2 (Ukraine, MN11), Belka (Ukraine, MN12), Taraklia (Republic of Moldova, MN12), Tudorovo (Republic of Moldova, MN12), and Pavlodar (Kazakhstan, MN13). For all these localities there are specimens that exceed the size ranges given by Werdelin (1988a) for *H. wongii*, especially in the P3 and p4, which is interpreted herein as evidence for the existence of *H. hyaenoides* in Eastern Europe during the Turolian.

The nomenclatural and taxonomic history of two ictithere forms from the Siwaliks has been rather unusual. Concerning the first one, Lydekker (1877) erected a new species, *Ictitherium sivalense*, based on two hemimandibles from Hasnot. In a subsequent study, he attributed it to a new genus, *Lepthyaena* (Lydekker 1884). Additional material was later published by Pilgrim (1932) and Colbert (1935).

The combination of primitive and derived features of this species is explained in Werdelin and Solounias (1991), noting that its exact phylogenetic position is uncertain. However, as discussed below, there appears to be some metrical and morphological heterogeneity between the upper and lower dentition of this form. The lower dentition is unfortunately poorly preserved, but from the figures of Lydekker (1884), Pilgrim (1932) and Colbert (1935), and from the measurements noted therein this species fits very well to the morphology of *H. wongii*. The m1 talonid is restricted in length, width, and height, whereas the trigonid is relatively high and elongated. The p4 is robust with a very strong distal accessory cuspid and a restricted mesial one (variable in *Hyaenictitherium*; Online Resource 2). The mandibular corpus is also relatively robust, high below the m1. Rather than showing a strong ventral expansion (resembling the subangular lobe of canids) followed by a convex profile that gradually leads to a very narrow mandibular corpus below p1 and c (which is typical for *Ictitherium*; Semenov 1985, 2008), the mandibular corpus is relatively high throughout the cheek teeth row, with a slightly skewed mental edge (even though it shows evidence of periodontitis), which is more typical of *Hyaenictitherium* (e.g., Qiu 1985; Werdelin 1988a; Semenov 2008). On the other hand, the maxillae from Hasnot (the type locality) published by Pilgrim (1932) and Mahmood and Khan (2020) are relatively smaller, especially the P3, which fits more to the size group of *H. minimum*. Additionally, these maxillae show a combination of an *Ictitherium*-like P4 and *Hyaenictitherium*-like molars, as observed by Werdelin and Solounias (1991). Therefore, they may not correspond to the specimens with the lower dentition and may represent instead a smaller taxon with this mix of characters resembling a *Thalassictis*-like stage. Furthermore, the hemimandible published by Colbert (1935) is considerably larger than the other specimens (especially in comparison to the maxillae) and it is herein believed that it also differs from the type material of *I. sivalense*. In a lumping classification point of view, the lower dentition specimens published by Lydekker (1877, 1884) and Pilgrim (1932) could correspond to *H. wongii*, the hemimandible of Colbert (1935) could belong to *H. hyaenoides*, and the two maxillae by Pilgrim (1932) could represent a different form. If so, *H. sivalense* should take priority over *H. wongii*, as it is the older name. However, as we have not studied this material first hand and these assumptions are based on measurements and sketches from old literature, we do not want to disrupt the current taxonomic framework. In terms of comparisons with the material from Venta del Moro, *I. sivalense* is perfectly comparable with the smaller specimens, fitting into the morphometrical range of *H. wongii*. This is an interesting matter that is definitely worth reviewing in the future.

Another species from the Siwaliks, *Palhyaena indica*, was erected by Pilgrim (1910) based on a maxilla from Hasnot with at least the P3 and the P4. He noted that this could be the same species as a hemimandible (GSI – D 53) of *Hyaena sivalensis* (not to be confused with *I. sivalense*, which was discussed above; this is a different form) published by Lydekker (1884). However, this maxilla from Hasnot was never figured or described properly, nor was an inventory number given. Pilgrim (1910) only noted that the premolars are wide and that the P3L and P4L are nearly equal. However, a few years later, Pilgrim (1932) surprisingly stated that the right hemimandible published by Lydekker (1884) as *H. sivalensis* is in fact the holotype, admitting that he had been "mistaken in quoting a maxilla as the holotype of the genus" and adding that "the only upper teeth of the species known are the two specimens of P4 mentioned below". Nonetheless, holotypes and taxonomic names are tightly connected, so it is not possible to change the holotype of a taxon. This confusion, also mentioned in Colbert (1935), led Werdelin and Solounias (1991) to create the name *Hyaenictitherium pilgrimi* for this material, since *P. indica* corresponded to a non-existing holotype (the maxilla from Hasnot). Once this nomenclatural issue was resolved, the only known specimens of this form were those mentioned by Pilgrim (1932) (two P4s, two fragmentary hemimandibles, and one isolated m1), the hemimandible reported in Lydekker (1884), and one maxilla published by Ghaffar and Akhtar (2012). These specimens are very similar in morphology and size to *H. hyaenoides* from China (also noted by Pilgrim [1932] himself). Ghaffar and Akhtar (2012) based their identification on the relatively posterior placement of the protocone of the P4. However, as can be seen in Online Resource 2, there seems to be significant variability in *H. hyaenoides* when regard to this character (especially in AMNH 14-L31). From Pilgrim´s (1932) descriptions, depictions, and diagnosis, most of the characteristics of *H. pilgrimi* also tend to be identical to those of *H. hyaenoides*. The only interesting trait is the short premolar tooth row in the hemimandible from Nila (GSI – D 211), depicted in Pilgrim (1932: pl. IV, Fig. 12 and a), which is mainly expressed by the short diastema between the premolar row and the canine. Even though there is a degree of variability in the Chinese specimens of this character too (and it may be also affected by ontogenetic changes), such a close proximity between the premolars and the canines is indeed exceptional. However, since the figures of Pilgrim (1932) are sketches and not photographs, it is difficult to make a direct comparison. In general, this species seems to be very similar, if not identical, to *H. hyaenoides*, but as was also the case with *Ictitherium sivalense*, this is merely a preliminary note without close examination of the actual specimens.

Werdelin (2003) erected a new species of ictithere, *Ictitherium ebu*, based on a complete skeleton from Lothagam (Kenya). He attributed it to the genus *Ictitherium* due to the relatively unreduced M1 and m2, and the short P4 metastyle. However, he noted that the talonid of the m1 is markedly reduced. This species is characterised by its extremely long limbs (Werdelin 2003), which is interpreted as evidence of ecomorphological convergence with the extant maned wolf (van der Hoek and Werdelin 2024). Semenov (2008) argued that many characteristics of the dentition, cranial and postcranial anatomy suggest that this is a member of the Hyaenotheriini, and more particularly of the genus *Hyaenotherium*, noting similarities with *H. wongii* and *H. magnum*, which are herein considered conspecific (also considered as such in Semenov 2001), since the characters separating them are either ontogenetically driven (such as the zygomatic width, the premolar length, and the skull length), taphonomically biased (such as the length and width of the palate), or have considerable overlap if the Chinese specimens are taken into account (such as the condylobasal length, the incisor arch, the I3 width, and the molar angle). Concerning the form from Lothagam, we agree with Semenov (2008) in placing *Ictitherium ebu* in the genus *Hyaenictitherium* sensu lato. The P4 metastyle is indeed slightly short, but the P4 protocone is slightly posteriorly positioned, the molars are reduced (even though not drastically), the mandibular corpus is straight, and the braincase (occipital crest, sagittal crest, temporal lines, alisphenoid canal, auditory bullae) more resembles that of the genus *Hyaenictitherium*, and especially the dentition is not considerably different from that of *H. wongii*. However, we consider that the dorsal outline of the braincase differs from that of the latter species. In *H. ebu*, the braincase is relatively short in height and long without a sudden uplift in front of the orbits, while the sagittal crest expanding distally forming a relatively straight line. On the other hand, in *H. wongii* and *H. hyaenoides*, the braincase is higher, shorter in length, there is a sudden uplift in front of the orbits, and the sagittal crest is more expanded dorsally (e.g., AMNH 144883 and AMNH 144879 for *H. hyaenoides*; AMNH 20555 and AMNH 23031 for *H. wongii*). There are some intermediate stages for *H. wongii* (such as AMNH 22878), but in general these two species already show a tendency towards a crocutoid lateral outline of the skull (also seen in Werdelin and Solounias, 1991: Fig. 48). In this respect, the skull of *H. ebu* more closely resembles the skull of the type material of *I. viverrinum* from Pikermi (SNSB-BSPG-AS-II-604). Unfortunately, since no braincase or postcranial material of the hyaenids from Venta del Moro are preserved, it is not possible to distinguish them from *H. ebu* with certainty. However, considering that its only known occurrence is Lothagam, it is much more plausible that the smaller specimens from Venta del Moro correspond to *H. wongii*, which is known from numerous localities in Eurasia.

Finally, the last species of the genus is *H. namaquensis*, an African form from the latest Miocene and Early Pliocene of Libya, Kenya, and South Africa. This species has only been found in four localities: Kleinzee (Stromer 1931; type locality), Langebaanweg (Hendey 1978), As Sahabi (Howell and Petter 1980; Howell 1987; Iurino et al. 2022), and Tugen Hills (Morales et al. 2005). An additional possible occurrence comes from the Middle Awash (Haile-Selassie and Howell 2009). Its size and morphology are very similar to those of *H. hyaenoides*, and in particular to the largest and most robust specimens of this taxon, since the m1 talonid is very short, the premolars are very robust, and the mandibular corpus is very deep. This close relationship is also mentioned by Tseng and Wang (2007), who conclude that this could be a sister taxon to *H. pilgrimi* (possibly conspecific with *H. hyaenoides*, as discussed above), but state that the premolars of *H. namaquensis* are relatively wider than those of *H. hyaenoides*. However, their dimensions follow the same pattern as that of the latter species. Tseng and Wang (2007) mention several differences between the two species in their matrix, noting the derived stage of *H. namaquensis*. However, the statistical ranges of *H. hyaenoides* are considerably wide, leading to overlap. In any case, considering the temporospatial difference and the average morphotypes of the two species, we agree that they are indeed distinct, albeit a revision of the material from Langebaanweg would be crucial for our understanding of the morphological range of *H. namaquensis* and its evolutionary relationship with *H. hyaenoides*.

Therefore, it is concluded that within this genus there are three size groups: the smallest is *H. minimum*, the intermediate is similar to *H. wongii*, and the largest is similar to *H. hyaenoides*. This transition is also marked by a gradual increase in the robustness of the dentition towards a more crocutoid form, characterised by wider premolars, and a reduction of the M1, M2, m1 talonid, and m2. Other species, regardless of their taxonomic validity, mostly fall (sometimes with considerable overlap) into one of these three categories. *Ictitherium sivalense*, *H. ebu*, and *H. magnum* are comparable to *H. wongii*, whereas *H. venator*, *H. pilgrimi* and *H. namaquensis* are comparable to *H. hyaenoides*.

Hyaenictitherium wongii (Zdansky, 1924)

Emended diagnosis: Species of *Hyaenictitherium* with moderate size; accessory cusps of premolars developed; premolars moderately robust; upper molars, m1 talonid, and m2 moderately reduced; not extremely long limb bones.

Differential diagnosis: Differs from *H. minimum* in larger size, the more developed accessory cusps and cuspids of the premolars, and the more robust premolars. Differs from *H. ebu* mainly in the less elongated limbs. Differs from *H. hyaenoides*, *H. pilgrimi*, and *H. namaquensis* in the smaller size, less robust premolars, and the larger M1, M2, m1 talonid, and m2.

Lectotype: PMUU-M3707-9 (Ex. 14), skull and mandible, designated by Solounias (1981).

Type locality: Loc. 109 (Huan Lou Kou), Baode, China.

Temporospatial range: MN9–14 of Eurasia, from Spain to China. A review of the localities can be found in Semenov (1989), Werdelin and Solounias (1991), and Tseng and Wang (2007).

New material: MGUV-16945 (mentioned as MGUV-11032 in Morales Flores 2024), right I3; MGUV-24296, left I3; MGUV-18470, right C; IPC-IPS-143204, right C; MGUV-14799, left P1–3; MGUV-15756, left P1; MGUV-16942, right P2; MGUV-16941, right P2; MGUV-15934, right P2; MGUV-14808, left P2; MGUV-15960, left P2; MNCN-71966, right P3; MGUV-14798, right P3; MGUV-19192, right P3; MGUV-24146, mesial part of a right P3; MGUV-16944, distal part of a right P3; MGUV-24144, distal part of a right P3; MGUV-18466, left P3; MGUV-16943, left P3; MGUV-14807, mesial part of a left P3; MGUV-24145, mesial part of a left P3; MGUV-19189, right P4; MGUV-15933, protocone and lingual cingulum of a right P4; MGUV-14801, left P4; MGUV-15932, left P4; MGUV-24141, left P4; MGUV-15759, mesial part of a left P4; MGUV-15999, mesial part of a left P4; MGUV-18467, right M1; MGUV-25994, right M1; MGUV-16946, left M1; MGUV-14797, right DP3; MGUV-16947, left hemimandible with c–m1; MGUV-19193, right hemimandible with c–m1 and the alveoli of i1–2 and m2; MGUV-15760, right c; MGUV-24149, right c; MGUV-15937, right c; MGUV-24150, right c; MGUV-14789, left c; MGUV-18469, right p2; MGUV-14795, left hemimandible with p2–4 and the alveoli of p1 and m1; MNCN-71967, left p3; MNCN-71972, left p3; MNCN-71973, right p3; MGUV-14809, right p3; MGUV-14794, right hemimandible with p3–4; MGUV-15755, distal part of a left p3; MNCN-71969, right p4; MNCN-71970, right p4; MNCN-71971, left p4; MGUV-18468, right p4; MGUV-15758, left p4; MNCN-71968, right m1; MGUV-19190, partial trigonid of a right m1; MGUV-24147, partial trigonid of a right m1; MGUV-14796, distal part of a right m1; MGUV-24148, left m1 and mesial part of P3; IPC-IPS-33071 (cast MGUV-14806), left m1; MGUV-25902, left m1; MGUV-14800, distal part of a left m1.

Description: A minimum number of six individuals of *H. wongii* have been discovered in Venta del Moro based on six right p4s. Most of the material consists of isolated teeth, but also a maxilla and four hemimandibles are available. The descriptions are based on the whole sample and particular deviations are noted.

The crown of the I3 consists of a single cusp which is moderately elongated and curved (Fig. 2a). It is not widened or significantly robust. The base of the tooth is surrounded by a cingulum which is very asymmetrical. On its lingual side, it is much more developed, creating a wide crest, while its height from the apex of the tooth is lower. On the other hand, the cingulum on the buccal side of the tooth is much less developed and it expands slightly more towards the root. A crest runs from the apex of the crown towards the distobuccal corner of the dental outline. A narrow basin is formed between the lingual cingulum crest, the curve of the main cusp, and the longitudinal buccal crest, without forming a heel.

The upper canines are badly preserved and show advanced dental wear (Fig. 2b). They are slightly compressed buccolingually, but their crown is curved and robust. Not much is retained from their morphology, but similarly to the I3, the cingulum is more expanded on the buccal side of the tooth.

The P1 is unicuspid and its outline is almost oval-shaped (Figs. 2c and 3a). It is very low and positioned slightly mesially form the centre of the tooth. The distal crest is concave and longer than the convex mesial one. The distal arch of the P2 outline is almost semicircular, whereas the mesial part is more angled. The P2 is much larger than the P1 but much smaller than the P3 (Fig. 2c, d). Its main cusp is much larger than the accessory one, but it forms a slightly obtuse angle. A moderately developed distal accessory cusp is present, approximately in line with the main cusp on the tooth row axis. Even though there is no mesial accessory cusp, there is a crest that starts from the apex of the tooth and ends on the mesiolingual border of the cingulum. The end of this crest is slightly enlarged resembling a cusp. The cingulum is developed, especially on its distolingual part. The outline of the tooth is highly asymmetrical. On each side of the tooth there are two expansions interrupted by a constriction. On the buccal side, this constriction is slightly distally located, whereas it is more mesially located on its lingual side. The widest level of the tooth could be either on its mesial or distal expansions. The main cusp of the P3 is much higher than the moderately developed distal accessory cusp, whereas there is no mesial accessory cusp (Fig. 2c, e). The crista that runs mesiolingually from the apex of the main cusp is slightly wider in its mesial end, creating a cuspule-like structure, in similar manner as in P2. There are two lingual expansions of the tooth's outline, one mesial and one distal, whereas the latter could sometimes show another constriction in its middle. The mesiolingual extent of the distal one (or the position of the middle one if there are three) varies, but in general is moderately developed and located slightly

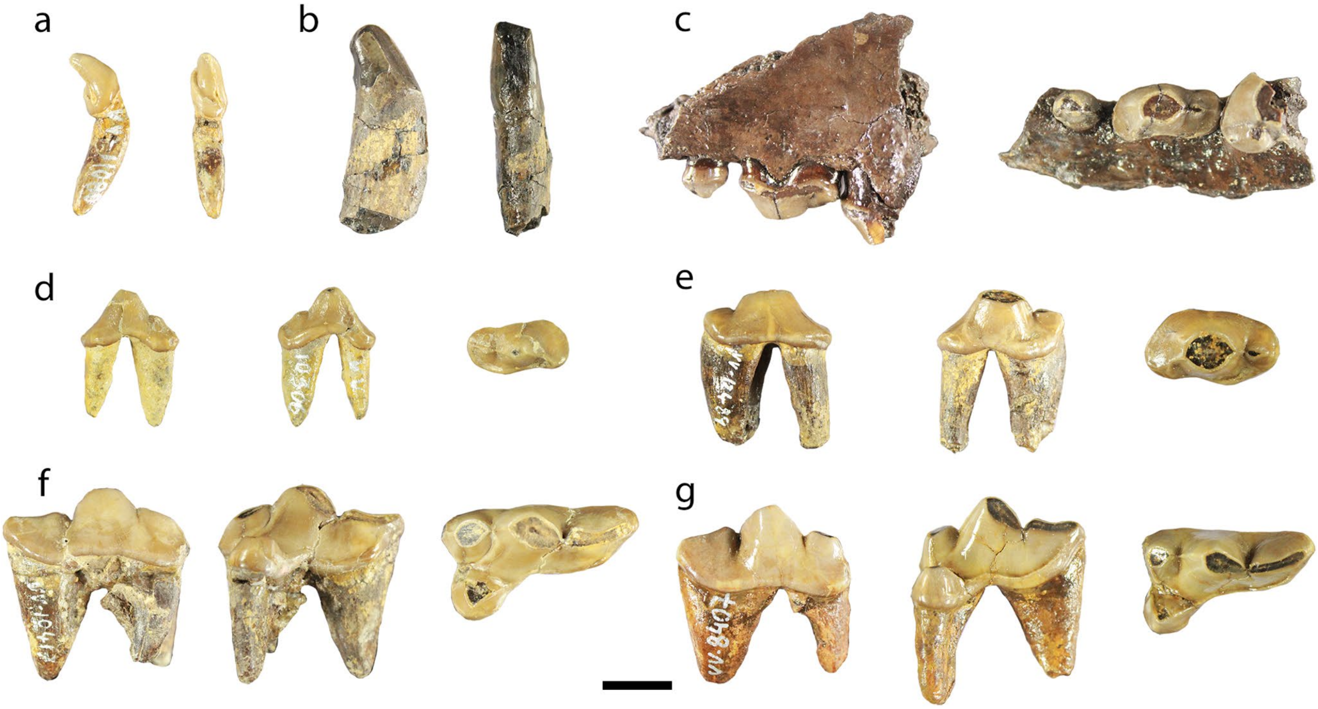

Fig. 2 Upper dentition of *Hyaenictitherium wongii* from Venta del Moro. **a**. MGUV-24296, left I3 in buccal (left) and distal (right) views; **b**. MGUV-18470, right C in lingual (left) and distal (right) views; **c**. MGUV-14799, left maxilla with P1–P3 in buccal (left) and occlusal (right) views; **d**. MGUV-15934, right P2 in buccal (left), lingual (middle), and occlusal (right) views; **e**. MGUV-18466, left P3 in buccal (left), lingual (middle), and occlusal (right) views; **f**. MGUV-15932, left P4 in buccal (left), lingual (middle), and occlusal (right) views; **g**. MGUV-14801, left P4 in buccal (left), lingual (middle), and occlusal (right) views. Scale bar equals 1 cm

distally. The cingulum is more developed distally, especially on the distolingual border of the tooth.

The upper carnassial (P4) has four cusps that show some degree of variability with the two ends of the range seen in Fig. 2f, g. The paracone is always the highest cusp, considerably higher and more robust than the rest of the cusps. There is a very strong parastyle, which could be higher (Fig. 2f) or lower (Fig. 2g) than the metastyle, depending on their development and the particular stage and manner of dental wear. The metastyle is also variable in terms of its length, as it can be longer (Fig. 2f) or shorter (Fig. 2g). The protocone is well developed and it is situated more or less at the level of the parastyle, but again it shows some degree of variability from more distal (Fig. 2f) to more mesial (Fig. 2g) positions. The cingulum of the P4 is very developed, especially on its distolingual border.

The M1 (Fig. 3b) is formed by three cusps and has a narrow outline. The two buccal cusps, the paracone and the metacone, are asymmetrical, with the paracone being slightly longer and wider, also showing a much more developed buccal outline. The lingual protocone is considerably high, hook-like and rugose, merged with the lingual cingulum. It is positioned between the two buccal cusps and between them there is a clear basin.

The only deciduous tooth that can be attributed to this hyaenid is a right DP3 (Fig. 3c). This is formed by five cusps. The paracone is centrally located and is the largest cusp, much larger than the others. The metastyle is well developed, but relatively shorter than the respective structure in the adult upper carnassial. The parastyle is much smaller than in the P4 and is restricted to a small, pointy elevation on the mesial end of the tooth. An additional cusp is present between the paracone and the parastyle, here interpreted as a paraconule. This is higher and wider than the parastyle and it is slightly more lingually positioned than the other three cusps. The metastyle, paracone, and parastyle are aligned on the axis of the tooth. The protocone is long and narrow and stems from the middle point of the paracone forming an almost right angle. It is moderately high, and a shallow basin is formed between it and the paracone. The cingulum is moderately developed with the distolingual border being much more robust.

The mandibular ramus is better preserved in the specimen MGUV-19193 (Fig. 4a), but a larger part of it is also visible in MGUV-16947 (Fig. 4b). The coronoid process and the mandibular condyle are missing. The angular process is relatively short and slightly curved dorsally. The mandibular fossa is relatively deep and extends mesially until the level of m2. The height of the mandibular corpus

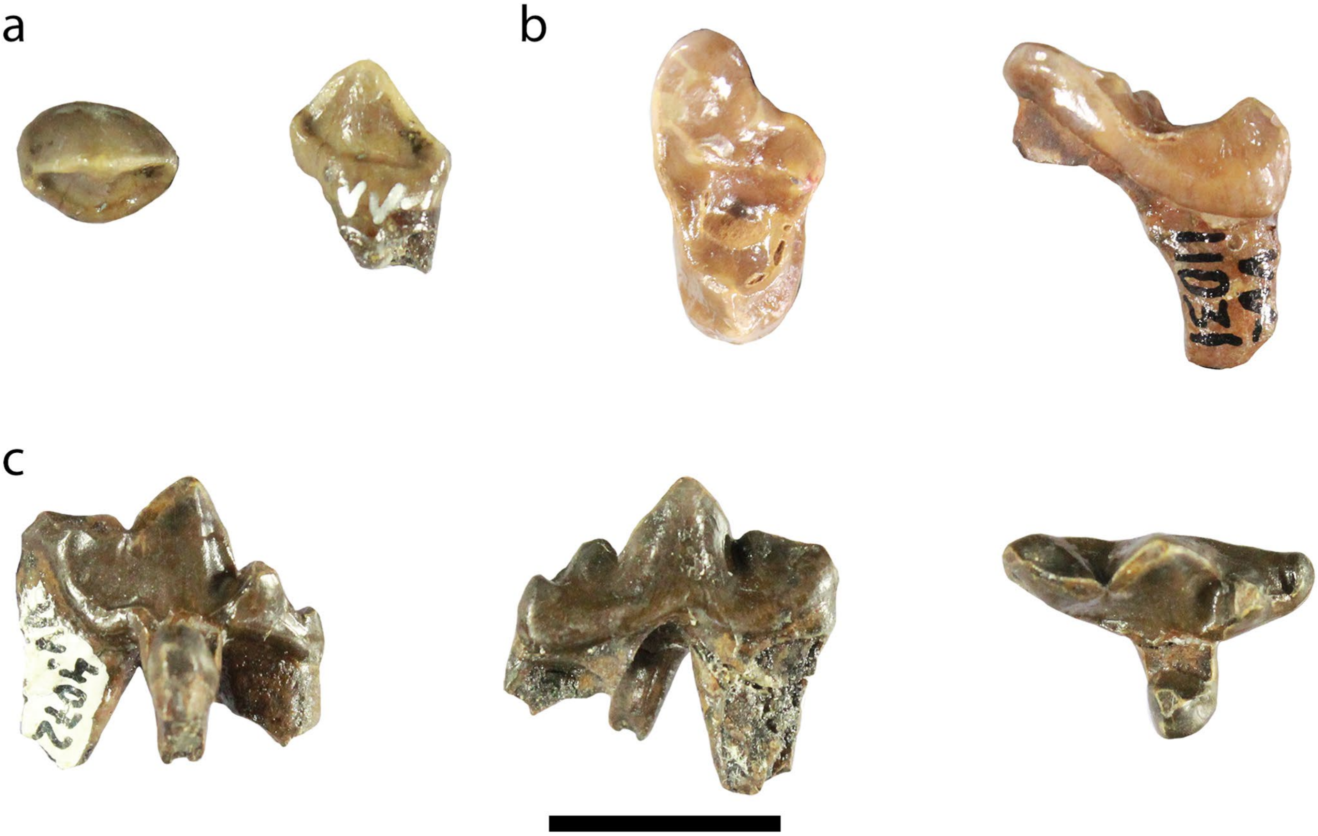

Fig. 3 Upper dentition of *Hyaenictitherium wongii* from Venta del Moro. **a**. MGUV-15756, left P1 in occlusal (left) and lingual (right) views; **b**. MGUV-16946, left M1 in occlusal (left) and mesial (right) views; **c**. MGUV-14797, right DP3 in lingual (left), buccal (middle), and occlusal (right) views. Scale bar equals 1 cm

becomes gradually lower towards the symphysis. However, the ventral outline of the mandible is not smooth, because there is a mental edge at the distal plane of p2, so that the height below p2 is slightly higher than below p3. There is only one mental foramen, relatively large and circular, situated below p2. A long diastema is present between the p1 and the c, but no other diastema is noted. On the contrary, there is some overlap between most of the cheek teeth with the mesial end of the distal one being positioned lingually to the distal end of the mesial one. The symphysis is long and extends distally until the middle plane of p2.

The only lower incisor is that of MGUV-19193 (Fig. 4a). The central part of this tooth is formed by a large main cuspid, which is lower than that of the I3 and not curved, but more spatulate-shaped. The lingual cristid of this cuspid is much higher and robust than the buccal one. On the buccal side of the tooth, there is a laterally diverging cuspid. The cingulid is very mild, not creating a crest as in the I3. The lower canine is long, robust, and curved, not very different from the upper one (Figs. 4 and 5a). The border of the enamel of the crown is extended more towards the root on its buccal side. There is a cristid stemming from the apex of the crown towards the distolingual end of the dental border. The distal base of the tooth forms a faint heel.

The only p1 found is on the right hemimandible MGUV-19193 (Fig. 4a). It is very similar to the P1, but much smaller in length and width (almost half), its single cuspid is slightly higher than the main cusp of the P1, and the outline is more circular. The p2 is smaller and narrower in comparison to the p3 (Figs. 4 and 5b). The main cuspid is moderately high and forms a relatively obtuse angle. It is slightly mesially placed and there is no mesial accessory cuspid. The mesial cristid is parallel to the axis of the tooth and at its mesial end, it forms a faint heel. A small distal accessory cuspid is present. The cingulid is moderately developed and the outline of the tooth is almost oval shaped with the lateral and buccal sides being parallel. The p3 is very similar to the p2, but it differs from the latter on a larger and more robust main cuspid, a more developed cingulid, a more robust mesial cristid, and a wider outline (Figs. 4 and 5c). In contrast to the two former premolars, the p4 has a strong mesial accessory cuspid (Figs. 4 and 5d and e). The mesial accessory cuspid, even though it is developed, is smaller than the distal one. However, the distal accessory cuspid is still the highest of the accessory cuspids of the premolar. The three cuspids are

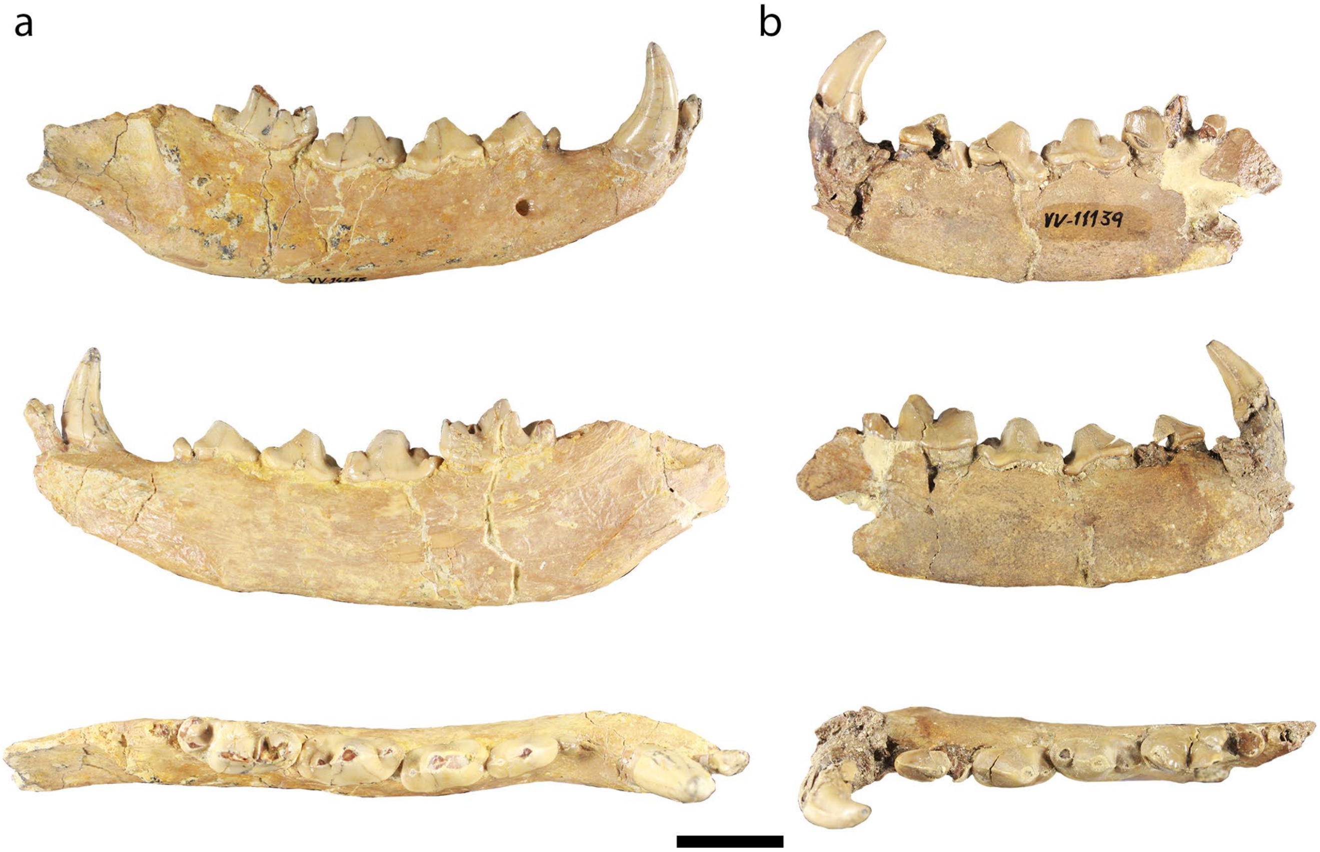

Fig. 4 Hemimandibles of *Hyaenictitherium wongii* from Venta del Moro. **a**. MGUV-19193, right hemimandible with i3–m1 in buccal (upper), lingual (middle), and occlusal (lower) views; **b**. MGUV-16947, left hemimandible with c–m1 in buccal (upper), lingual (middle), and occlusal (lower) views. Scale bar equals 2 cm

aligned and the lingual and buccal borders of the tooth are either parallel or slightly converging mesially.

The lower carnassial (m1) is the largest tooth of the lower tooth row (Figs. 4 and 5f and g). The trigonid is much larger than the talonid, which is restricted in length, width, and height. The protoconid is the largest cuspid, followed by the paraconid (in some cases subequal to the protoconid), and then by the (relatively large) metaconid, which is oriented lingually but is still clearly lower than the two other trigonid cuspids. The angle between the protoconid and the paraconid is moderately strong. There are three cuspids on the border of the talonid: a lingual entoconid, a distal hypoconulid, and a buccal hypoconid, with the latter being the highest of the three. There is a short and shallow basin among them. The cingulid is moderately developed and it is more marked mesiobuccally.

Ictitheriinae indet.

Referred material: MGUV-24142, right P3; MGUV-14810, left P3; MGUV-15935, right p4; MGUV-15757, right p4.

Remarks: Two P3s and two p4s are reported separately from the material already described, mainly because of their size, which is slightly larger than that of the other specimens from the locality (Fig. 6).

Description: Specimens MGUV-14810 (right) and MGUV-14810 (left) are extremely worn and may belong to the same individual based on their stage of wear and dimensions. Despite the advanced wear, there are relatively large distal and mesial wear facets, indicating that a cusp may have been present on each of them, with the mesial one being slightly centrally located. The mesial expansion of the tooth outline is moderately developed and distally located. The two p4s are slightly larger than the corresponding teeth of *H. wongii* from Venta del Moro, especially MGUV-15935. The main cuspids and the mesial and distal accessory cuspids are relatively high and placed in line. In MGUV-15757 the mesial accessory cuspid is approximately as high as the distal one, whereas in MGUV-15935 it is slightly lower. However, in the latter specimen, the distal cingulid is very developed, forming a crest-like wall that is stronger distolingually, creating a cuspid-like structure that provides a wider outline on the distal part of the tooth.

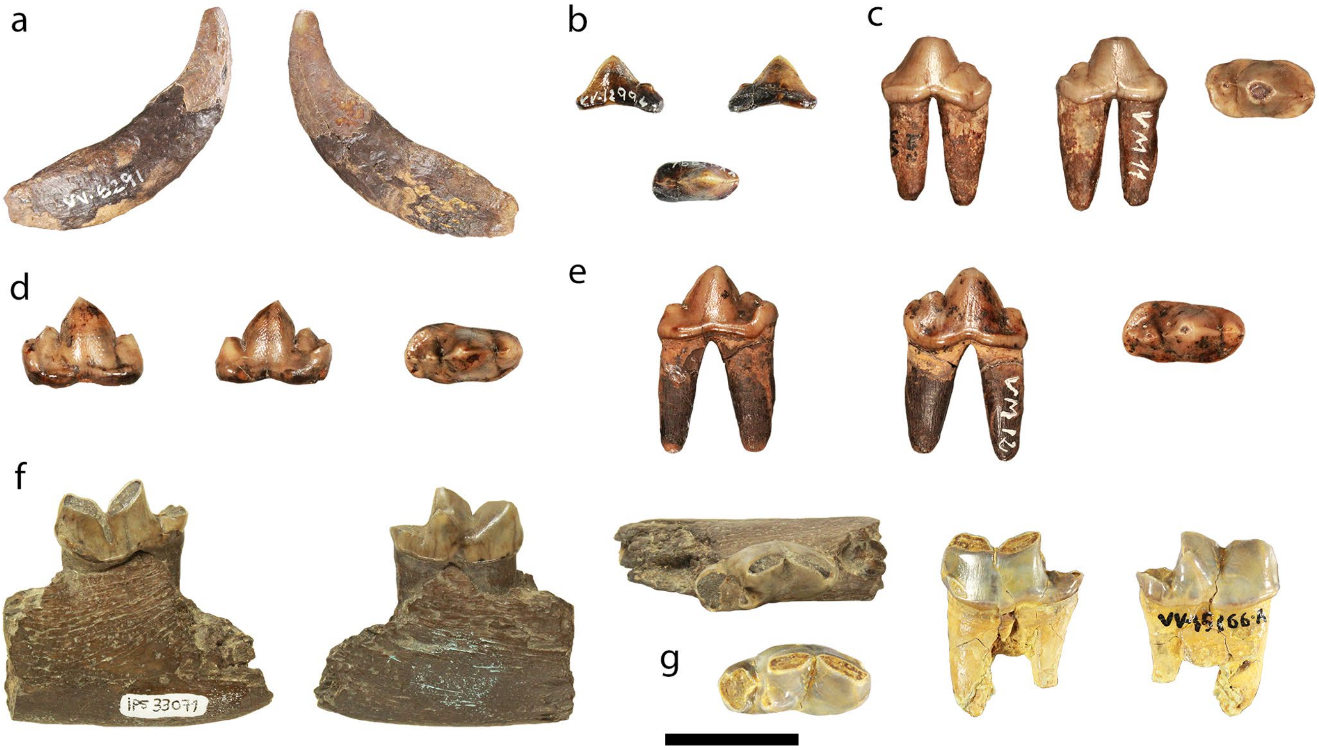

Fig. 5 Lower dentition of *Hyaenictitherium wongii* from Venta del Moro. **a**. MGUV-14789, left c in lingual (left) and buccal (right) views; **b**. MGUV-18469, right p2 in lingual (upper left), buccal (upper right), and occlusal (lower) views; **c**. MNCN-71967, left p3 in buccal (left), lingual (middle), and occlusal (right) views; **d**. MNCN-71970, right p4 in buccal (left), lingual (middle), and occlusal (right) views; **e**. MNCN-71969, right p4 in lingual (left), buccal (middle), and occlusal (right) views; **f**.IPS33071, left m1 in buccal (left), lingual (middle), and occlusal (right) views; **g**. MGUV-24148, left m1 in occlusal (left), buccal (middle), and lingual (right) views. Scale bar equals 2 cm

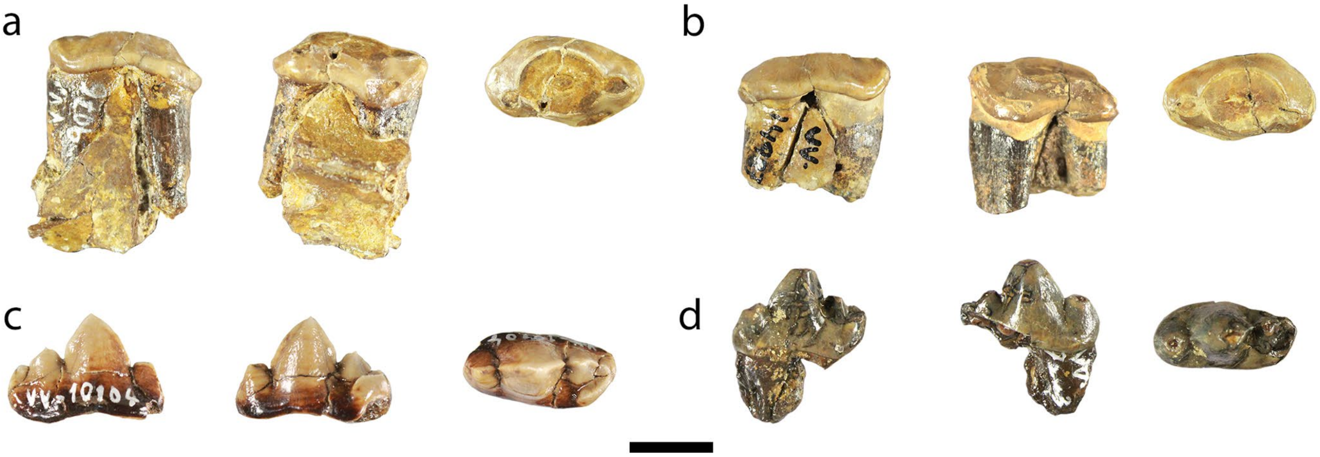

Fig. 6 The dental material of the larger Ictitheriinae indet. **a**. MGUV-14810, left P3 in buccal (left), lingual (middle), and occlusal (right) views; **b**. MGUV-24142, left P3 in buccal (left), lingual (middle), and occlusal (right) views; **c**. MGUV-15935, right p4 in buccal (left), lingual (middle), and occlusal (right) views; **d**. MGUV-15757, right p3 in buccal (left), lingual (middle), and occlusal (right) views. Scale bar equals 1 cm

Discussion

Comparisons of the Venta del Moro material: differentiation between *H. wongii* and *H. hyaenoides*

Even though there is some degree of variability in the studied dataset of Venta del Moro, it is clear that the specimens correspond to one or maybe two closely related species. The size and relative dimensions of the teeth show that the material belongs to a medium-sized ictithere. This is smaller than more derived hyenas such as *Adcrocuta*, *Allohyaena*, *Lycyaenops*, *Leecyaena*, *Hyaenictis*, and *Chasmaporthetes*, but larger than smaller opportunistic forms such as *Protictitherium*, *Gansuyaena*, *Tungurictis*, and *Plioviverrops* (e.g., Howell and Petter 1985; Kurtén and Werdelin 1988; Werdelin and Solounias 1990, 1991; Werdelin et al. 1994; Werdelin 1999; Werdelin and Kurtén 1999; Fraile 2016; Vinuesa et al. 2017; Wang et al. 2020; Galiano et al. 2022). In the Late Miocene of Eurasia, there are many hyaenid genera that belong to this size-group (e.g., Semenov 1989, 2008; Werdelin and Solounias 1991; Turner et al. 2008). The presence of developed accessory cusps and cuspids on the premolars, as well as the restricted m1 talonid with relatively low cuspids, shows that this material differs from the usual morphology of *Ictitherium* (e.g., Kurtén 1954, 1982; Semenov 1985, 1989, 2008; Werdelin 1988b). This aspect will be discussed further. The material also differs from *Lycyaena* in its slightly smaller size, wider premolars with lower and obtuse main cusps/cuspids, and the larger m1 metaconid (Zdansky 1924; Pilgrim 1931; Qiu 1985; Werdelin 1988a). Compared to the genera *Metahyaena*, *Palinhyaena*, and *Belbus*, it is also distinguishable by the development of the accessory cusps/cuspids of the premolars and the concave/straight profiles of their margins (Qiu 1985; Werdelin 1988a; Werdelin and Solounias 1991; Viranta and Werdelin 2003; de Bonis et al. 2010). The genus *Ikelohyaena*, which is known from the Late Miocene to the Late Pliocene of Africa, exhibits an intermediate morphology between ictitheres and bone-crushing crocutoid hyenas (Hendey 1974, 1978; Werdelin and Solounias 1991; Werdelin et al. 1994; Coca-Ortega and Pérez-Claros 2019). In general, the dentition of this species is more massive, with wider premolars, higher and wider main cusps/cuspids, slightly smaller mesial accessory cusps/cuspids, and slightly larger size. The cingula/cingulids are more developed and particularly in the p4 the distal cingulid is robust, especially on its buccal side, creating a strong cristid. The taxonomy of the genus *Thalassictis* has been problematic in the past, but its classification is now much more restricted. Although the dentition of this genus is not very different from that of *Miohyaenotherium* and *Hyaenictitherium*, it shows some more primitive characteristics, such as the larger m1 talonid and the slightly larger M2 and m2 (Kurtén 1982; Qiu 1985; Werdelin 1988b; Semenov 1989, 2008; Werdelin and Solounias 1991; Kargopoulos et al. 2022). While the differences between the remaining genera *Miohyaenotherium* and *Hyaenictitherium* are not striking in terms of isolated dentition, the former is characterised by a mesially protruding P4 protocone and a developed m1 entoconid that is higher than the hypoconid (Semenov 1989, 2008). This genus will be discussed further later on. The genus *Hyaenotherium* Semenov, 1989, was erected to highlight the evolutionary differences between the *wongii*- and *hyaenoides*-size groups. Even though these differences are indeed present, the overlap between the two groups can be very significant, while other suggested differences (such as the presence of pterygoid hooks, the inflation degree of the auditory bulla, or the tip of the jugular processes) can be affected by taphonomy. Therefore, we prefer to refer to both forms under the name *Hyaenictitherium*, noting that they indeed correspond to distinct ecomorphological (and possibly evolutionary) stages. Considering these comparisons, the material from Venta del Moro is consistent with the size and morphology of the genus *Hyaenictitherium*.

As the specimens from Venta del Moro are clearly larger and more robust than *H. minimum*, with much more developed premolar accessory cusps and cuspids, the following comparisons focus on the morphometric differences between *H. hyaenoides* and *H. wongii* sensu lato. Even though most of the material from Venta del Moro corresponds perfectly with the morphology of *H. wongii*, a well-known species from the Late Miocene of Europe, a few specimens described above as Ictitheriinae indet. (Fig. 6) indicate the potential occurrence of a larger form, possibly attributed to *H. hyaenoides*. Morphological and metrical comparisons between the two species are based on the material of *H. hyaenoides* from China hosted in the AMNH (based on the identifications of Werdelin 1988a) and the material of *H. wongii* from Samos hosted in various collections in Europe and the AMNH, accompanied by the metrical range shown in China (Solounias 1981; Werdelin 1988a; Koufos 2009). The taxonomic identification of both samples is not currently disputed, and we believe they demonstrate the morphometric range of the two main ictithere species adequately.

In general, *H. hyaenoides* is considered to be slightly more derived than *H. wongii*, as it is larger and possesses more robust dentition (Zdansky 1924; Qiu 1985; Werdelin 1988a; Tseng and Wang 2007). The differences suggested by Qiu (1985) for *H. hyaenoides* are the following: larger size, more derived ear region, stouter mandibular corpus with straight ventral outline, large and mesially placed mental foramen(s), absence of p1, more robust canine. According to Werdelin (1988a), *H. hyaenoides* differs from *H. wongii* in the following characteristics: larger size, broader premolars, relatively longer p4 main cuspid and m1 trigonid, and reduced M1, M2, and m2. Tseng and Wang (2007) represented some of these differences in their cladistic matrix as LP4/WM1 = 1.84 instead of 1.70, Wp3/Lp3 = 0.54 instead of 0.48, Wp4/Lp4 = 0.50 instead of 0.48, and WP3/LP3 = 0.58 instead of 0.54~0.55. However, as also pointed out in Kargopoulos et al. (2023b), these metrical differentiations serve more as expressions of evolutionary trends and less as clear taxonomic criteria. In this sense, considering the variability of both species and the fact that most of the specimens from Venta del Moro are isolated teeth, this study attempts to review the morphological and metrical differences of the two species for each of the main cheek teeth separately, in order to accurately identify the material.

Although there are some metrical differences between the P3 and P4 of the two species, they are not easily distinguishable in morphological terms, partly because of the considerable variability observed in both (Table 1; Online Resource 2). Concerning the P3, variability exists in the degree of development of the mesial region, including the mesial crest, as well as in the development of the cingulum and the lingual expansion of the tooth, which can be vestigial (e.g., AMNH 144879 for *H. hyaenoides* and MGL-39697 for *H. wongii*) or large and pointy (e.g., AMNH 144884 for *H. hyaenoides* and AMNH 23031 for *H. wongii*). The development of the lingual expansion also affects the total width of the tooth, showing that metrical comparisons can also incorporate this factor of variability. The size and position of the protocone of the P4 also vary. In some cases, it is well developed (as in AMNH 20554), whereas in others it is much smaller (e.g., AMNH 144879). There is a trend towards a slightly larger protocone in *H. wongii* than in *H. hyaenoides*, but there is considerable overlap. Most of the time, the protocone is at the level of the parastyle, but it can be slightly more mesially or (more commonly) distally positioned. The metastyle is also very variable in terms of its length (e.g., shorter in MGL-82849), outline (in some specimens it is curved, e.g., AMNH-144883) and development of the lingual cingulum (e.g., more developed in AMNH 20555). Considering this variability, it is unclear whether the two species can be distinguished in morphological terms without metric comparisons. While there are some trends, such as the wider P3 and the less developed P4 protocone in *H. hyaenoides*, there is significant morphological variability that prevents the establishment of clear separating characters.

Concerning the p4, there is significant variability in both species (Table 2; Online Resource 3) in terms of absolute

Table 1 Comparison of the upper teeth dimensions of the sample from Venta Del Moro to that of other hyenas. Data sources: Kretzoi (1952), Semenov (1985), and Werdelin (1988a). Abbreviations: **H**, height; **L**, length; **Lb**, buccal length; **Ll**, lingual length; **n**, number of specimens; **W**, width; **Wb**, blade width. Ranges represent minimum and maximum values

	H. wongii Venta del Moro	Ictitheriinae indet. Venta del Moro	*H. wongii*	*H. hyaenoides*	*I. pannonicum*
I3L	5.3–6.2 5.8 (*n*=2)				
I3W	5.0–5.3 5.2 (*n*=2)				
CL	8.0–9.5 8.8 (*n*=2)				13.6
CW	6.5 (*n*=2)				8.9
CH	18.2				
P1L	5.8–6.3 6.1 (*n*=2)		4.8–6.2 5.4 (*n*=12)		5.7
P1W	4.8–5.0 4.9 (*n*=2)		3.8–4.8 4.4 (*n*=10)		4.2
P2L	12.7–13.7 13.1 (*n*=4)		11.1–15.1 13.3 (*n*=83)	14.0–17.2 15.4 (*n*=19)	14.3
P2W	6.4–7.5 6.7 (*n*=5)		5.4–7.7 6.5 (*n*=99)	7.4–10.0 8.6 (*n*=19)	7.0
P3L	16.1–17.2 16.7 (*n*=4)	17.5–18.2 17.9 (*n*=3)	14.3–19.0 16.7 (*n*=91)	18.0–22.5 19.7 (*n*=19)	18.0–18.5 18.3 (*n*=2)
P3W	9.3–10.8 9.7 (*n*=6)	9.6–11.0 10.5 (*n*=3)	7.4–10.8 9.0 (*n*=108)	9.8–13.1 11.4 (*n*=22)	10.0–10.2 10.1 (*n*=2)
P4L	21.8–26.0 23.7 (*n*=4)		23.1–29.2 25.5 (*n*=100)	27.4–33.4 30.0 (*n*=17)	26.3–27.5 26.8 (*n*=3)
P4W	13.8–15.4 14.3 (*n*=5)		11.2–16.8 14.0 (*n*=92)	15.5–19.2 17.0 (*n*=21)	15.0–16.2 15.8 (*n*=3)
P4Wb	8.2–9.0 8.6 (*n*=4)		7.2–10.6 8.6 (*n*=107)	9.1–11.8 10.4 (*n*=19)	
M1Lb	7.1–7.9 7.5 (*n*=2)		6.0–9.2 7.9 (*n*=82)	7.0–8.9 8.0 (*n*=14)	13.3–13.4 13.4 (*n*=2)
M1Ll	5.2–5.9 5.6 (*n*=2)				
M1W	12.7–13.4 13.1 (*n*=2)		13.2–18.1 15.0 (*n*=82)	14.3–18.7 16.3 (*n*=14)	19.5–19.7 19.6 (*n*=2)
DP3L	14.0				
DP3W	9.2				
DP3Wb	4.1				

Table 2 Comparison of the lower teeth dimensions of the sample from Venta Del Moro to that of other hyenas. Sources of comparative data: Kretzoi (1952), Semenov (1985), Adrover et al. (1986), Werdelin (1988a), Alcalá (1994), and Roussiakis and Theodorou (2003). Abbreviations: **H**, height; **L**, length; **Ltr**, trigonid length; **n**, number of specimens; **W**, width. Ranges represent minimum and maximum values

	H. wongii Venta del Moro	Ictitheriinae indet. Venta del Moro	*H. wongii*	*H. hyaenoides*	*I. pannonicum*
i3L	5.3				
i3W	5.0				
cL	10.3–12.9 11.1 (*n*=7)				10.6–12.6 11.4 (*n*=2)
cW	6.7–8.0 7.6 (*n*=7)				7.5–8.3 8.0 (*n*=5)
cH	16.8–20.6 18.9 (*n*=4)				
p1L	3.2				
p1W	3.3				
p2L	12.3–12.5 12.4 (*n*=3)		10.6–13.6 12.2 (*n*=77)	12.4–15.7 14.3 (*n*=14)	11.3–13.5 12.8 (*n*=7)
p2W	5.6–6.3 6.0 (*n*=3)		5.0–7.0 5.9 (*n*=83)	7.1–8.8 7.7 (*n*=15)	6.2–7.1 6.6 (*n*=5)
p3L	14.2–16.1 15.0 (*n*=7)		13.4–17.1 15.3 (*n*=77)	15.5–19.2 17.5 (*n*=14)	14.8–17.2 16.0 (*n*=11)
p3W	6.9–8.7 7.7 (*n*=9)		6.2–8.5 7.3 (*n*=85)	8.2–10.3 9.5 (*n*=16)	7.0–8.3 7.8 (*n*=7)
p4L	15.6–17.5 16.4 (*n*=9)	18.3–19.7 19.0 (*n*=2)	14.7–19.0 17.0 (*n*=66)	18.3–21.8 20.1 (*n*=13)	16.0–19.7 17.3 (*n*=10)
p4W	7.7–9.1 8.4 (*n*=8)	8.7–8.9 8.8 (*n*=2)	7.1–10.3 8.2 (*n*=74)	8.8–11.3 10.1 (*n*=18)	7.7–9.5 8.6 (*n*=8)
m1L	19.5–20.8 19.9 (*n*=6)		17.7–23.1 20.3 (*n*=66)	19.0–25.1 22.9 (*n*=14)	19.3–21.0 20.1 (*n*=9)
m1Ltr	13.9–15.9 15.1 (*n*=6)		13.0–14.9 14.1 (*n*=14)	13.7–19.6 17.6 (*n*=14)	13.9–15.4 14.7 (*n*=6)
m1W	7.9–9.7 9.0 (*n*=6)		7.4–10.2 8.6 (*n*=63)	9.0–11.2 10.1 (*n*=15)	8.4–10.0 9.3 (*n*=8)

and relative dimensions, size and shape of the cuspids, development of the cingulid and shape of the outline of the tooth. In general, the p4 of *H. hyaenoides* has a more massive (higher, longer, and wider) main cuspid, even though the distinction can be less clear in some cases. The clearest difference is possibly the size of the mesial accessory cuspid. Especially in *H. wongii*, there is considerable variability, and dental wear can affect visibility, but in general it is smaller (shorter, narrower, and lower) in *H. wongii* than in *H. hyaenoides*. Concerning the outline, the tooth is usually wider in *H. hyaenoides*, and the edges are more rounded, creating a smoother outline than the angular one seen in *H. wongii*. This is most evident on the distolingual edge of the tooth.

Finally, significant variability is also evident in the lower carnassial of both species in terms of absolute and relative size, size of the cuspids, relative size of the talonid, outline of the tooth, and development of the cingulid (Table 2; Online Resource 4). The relative size of the m1 talonid is considerably variable, but it shows a trend to be shorter in *H. hyaenoides* and longer in *H. wongii*. This is more evident in the worn talonids. As with the premolars, the m1 of *H. hyaenoides* is slightly wider than that of *H. wongii*, even though there are some slender specimens of *H. hyaenoides* and some wide carnassials of *H. wongii*.

From the aforementioned comparisons between *H. wongii* and *H. hyaenoides*, it is clear that their huge intraspecific variability in Eurasia, mainly expressed in the Chinese samples in Qiu (1985); Werdelin (1988a), is so substantial that it encompasses many other taxa (including *I. sivalense*, *H. pilgrimi*, *H. venator*, and *H. magnum*). This would result in a relatively continuous distribution of the two hyaenids from Spain to China during the Late Miocene. This is not an unusual situation, as a similar temporospatial taxonomic homogeneity has been established for other fossil hyenas, such as *Adcrocuta eximia* (Werdelin and Solounias 1990), *I. viverrinum* (Werdelin 1988b; Semenov 1989, 2008) and possibly *Lycyaena chaeretis* (Werdelin 1988b; Werdelin and Solounias 1991), but it is also seen in extant medium- to large-sized carnivorans, such as the brown bear (Pasitschniak-Arts 1993), the grey wolf (Mech 1974), and the red fox (Larivière and Pasitchniak-Arts 1996). As Werdelin (1988a) emphasized, in the case of *Hyaenictitherium*, taxonomic separations should be based on several characteristics concerning many anatomical elements. This secures their stable application in small sample sizes and allow us to detect deviations and evolutionary trends without compromising taxonomic clarity. A renewed study including as many specimens as possible to demonstrates the full range of *Hyaenictitherium* morphometric variability is deemed necessary to reveal the true extent of this genus´s taxonomic, palaeoecological, and evolutionary position.

Regarding the material from Venta del Moro, it is clear that the bulk of the specimens can be confidently attributed to *H. wongii*. However, the identification of the specimens described as Ictitheriinae indet. remains unclear (Figs. 6, 7 and 8). They are slightly larger and more robust, with more marked accessory cusps/cuspids. The most unusual specimen in terms of size and morphology is MGUV-15935.

After the detailed comparisons above, there are many possible attributions for all these specimens. Firstly, they could potentially belong to *H. wongii*, which appears to be a very plastic species in size and morphology. This seems more possible for the upper premolars than the lower ones. Another interpretation is that they belong to the larger and more robust *H. hyaenoides*, which was present in Eastern Europe and the Asian influences on the fauna of Venta del Moro are well-documented (Morales et al. 2013). In a similar manner, another possible species could be *Miohyaenotherium bessarabicum*. Even though there are no MN13 records of this species, the morphology of its P3 and p4 is practically identical to that of *Hyaenictitherium*, and a dispersal to Western Europe in MN13 cannot be excluded. Considering the potential African faunal elements in the locality (African-Iberian Dispersals 1 and 2 in Gibert et al. 2013), the presence of *H. namaquensis* is also possible, even though the teeth are relatively narrower and smaller than those of the latter species. Finally, the species *Ictitherium pannonicum*, already reported in Spain at the sites of Valdecebro (Adrover et al. 1986) and Cerro de la Garita (Alcalá 1994) and in Hungary at Polgárdi (MN13) (Kretzoi 1952; Semenov 1985), is also not very different in terms of morphology and size. In general, the premolars of *Ictitherium* are less derived with smaller accessory cusps/cuspids than those of *Hyaenictitherium*, but *I. pannonicum* is larger and more robust, and phenotypic plasticity cannot be ruled out given the variation ranges seen in *H. wongii* and *H. hyaenoides*. Therefore, in the absence of more diagnostic teeth of this larger form, it is herein referred to Ictitheriinae indet. until more material is discovered.

The last ictitheres of Europe

The ictitheres are not represented in any Pleistocene or Holocene faunas. Based on current data, the last ictitheres are *H. namaquensis* from the Early Pliocene of Africa (Stromer 1931; Hendey 1978; Howell and Petter 1980; Howell 1987; Morales et al. 2005; Iurino et al. 2022), and possibly *H. hyaenoides* and *H. wongii* from the Early Pliocene Gaozhuang Formation in China (Qiu and Qiu 1995; Tseng and Wang 2007). Concerning the latest Miocene (MN13) occurrences of ictitheres and related forms in Europe, very few can be comparable to those of Venta del Moro. The type locality of *Ictitherium pannonicum* is Polgárdi in Hungary (Kretzoi 1952). This locality belongs to MN13 but, according to van der Made et al. (2013, and references therein), it should correspond to either early stages of MN13 or even MN12. Sardella (2008) attributed the dental material from Gravitelli (Italy) published by Seguenza (1902) to *H. hyaenoides* (*Ictitherium hipparionum* in the original text). This is an interesting report but, considering that the material is now lost and that the isolated upper teeth of *Hyaenictitherium* are not very different from that of *Lycyaena* (Werdelin 1988a), it is not easy to ascertain the affinities of these specimens. Nevertheless, the age of the locality is definitely older than that of Venta del Moro, since the review of Iannucci (2024) concluded that it predates 7.0 Ma. One tooth from Verduno (MN13 of Italy) was reported by Sardella (2008) as a P3 of *Hyaenictitherium* sp. However, this tooth shows parallel buccal and lingual borders, without expansions or constrictions. Therefore, it is identified here as a lower premolar and not an upper one, and since there is no mesial accessory cuspid, it should be a p3 and not a p4. However, the dimensions given by Sardella (2008) for the specimen (22.5 × 11.6 mm) exceed the metrical range of p3 not only for *Hyaenictitherium*, but also for larger hyenas, even though its morphology is not crocutoid. This specimen is intriguing, but without more material and no solid stratigraphical framework for the locality, an accurate identification is not possible. The material attributed to *Ictitherium ibericum* by Meladze (1967), considered as conspecific with *I. viverrinum* by Semenov (2008), comes from the locality of Bazaleti in Georgia. This locality has been considered possibly MN13 (Werdelin and Solounias 1991), but Vangengeim and Tesakov (2013) state that magnetostratigraphically it aligns with chron C3Br (7.21–7.53 Ma), therefore belonging to MN12. The MN13 localities of Kalmakpai and Pavlodar have also yielded *Hyaenictitherium* material (Semenov 1989; Werdelin and Solounias 1991), but these sites are situated at the far east of Kazakhstan, being significantly different in terms of space and possibly also time from Venta del Moro. Finally, the Spanish localities of El Arquillo, Las Casiones, and Milagros, have all yielded ictithere material (Alcalá 1994; Fraile et al. 1997; personal observations) and are very similar in age to Venta del Moro. However, according to Morales et al. (2013), these three localities belong to the biostratigraphical subzone M2, which is slightly older than the subzone M3 of Venta del Moro. Two reports of species that are sometimes included in the group of ictitheres, depending on the definition chosen by each scholar, are also noted in the MN13 of Europe. *Lycyaena chaeretis* has been found in Brisighella (Italy) (Sardella 2008), dated to ca. 5.6–5.33 Ma, which is indeed younger than Venta del Moro (Rook et al. 2015). The genus *Lycyaena* has been considered to be very closely

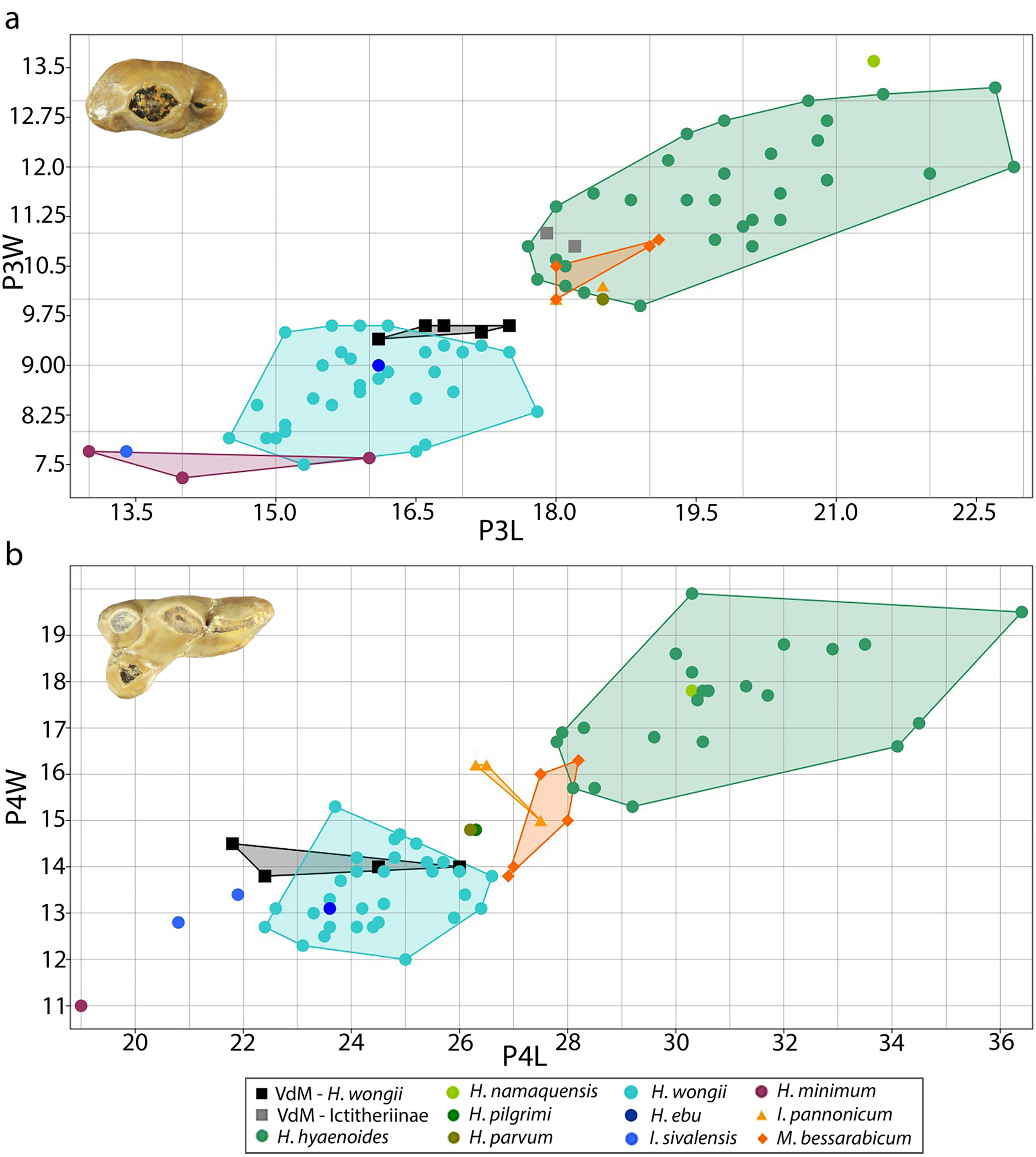

Fig. 7 Upper premolar dimensions (in mm) of specimens of Venta del Moro (VdM) and related ictithere taxa. **a**. P3; **b**. P4. Data sources: Khomenko (1914), Pilgrim (1932), Hendey (1978), Semenov (1985, 1989), Werdelin (2003), de Bonis et al. (2005, 2010), Mahmood and Khan (2020), Iurino et al. (2022), and personal measurements

related to *Chasmaporthetes*, which has also been reported from the faunas of Maramena (Schmidt-Kittler 1995) and Dytiko-1 (Koufos 1987), but the latter genus is much more derived than the Middle Turolian ictitheres (e.g., Antón et al. 2006). Another species that possibly survived beyond the age of Venta del Moro is *Protictitherium crassum*, a small hyaenid with a very extensive temporal range in Europe. This species was reported in the fauna of Dytiko-3 (Greece)

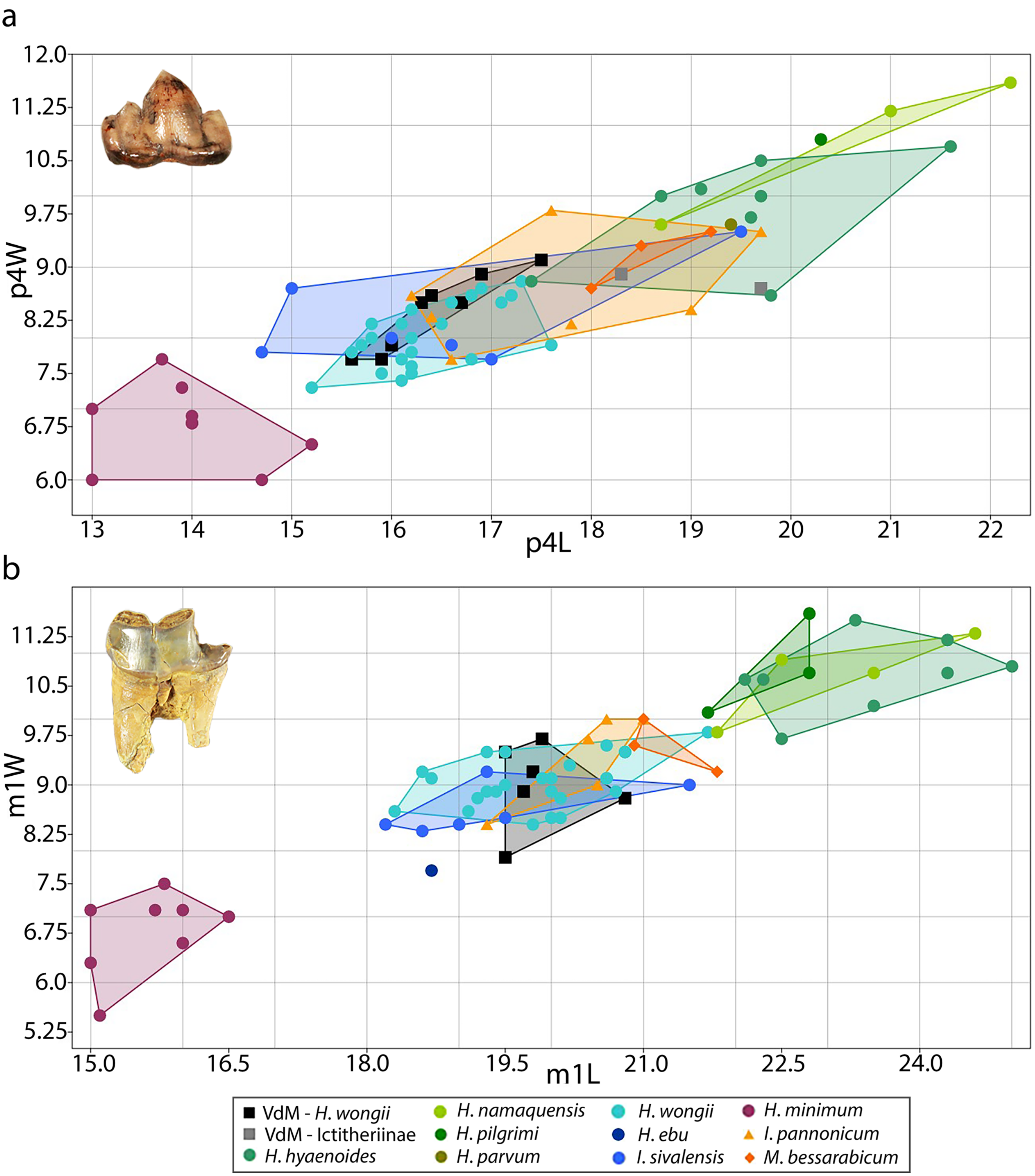

Fig. 8 Metrical comparison (in mm) of the specimens of Venta del Moro (VdM) and related ictithere taxa. **a**. p4; **b**. m1. Data sources: Khomenko (1914), Pilgrim (1932), Hendey (1978), Semenov (1985, 1989), Adrover et al. (1986), Howell (1987), Alcalá (1994), Werdelin (2003), de Bonis et al. (2005, 2010), Iurino et al. (2022), and personal measurements

by de Bonis and Koufos (1991), a locality that has not been accurately dated, but estimations suggest a range between 7.0 and 6.0 Ma (Koufos and Vasileiadou 2015). Consequently, the hyaenid record from Venta del Moro represents the last accurately dated evidence of ictitheres sensu stricto in Europe.

Palaeoecology, coexistence with Canidae, and competitive exclusion

Our knowledge of the palaeoecology of ictitheres comes from ecomorphological comparisons with modern analogues. Over the years, many different approaches have been used to understand the ecological role of the ictitheres, with *Hyaenictitherium* being among the most commonly studied hyaenids in such research efforts. Werdelin and Solounias (1991) followed by Werdelin and Solounias (1996) and Turner et al. (2008) established six ecomorphological groups for fossil hyenas based on their anatomical characteristics and concluded that *Hyaenictitherium* belongs to the "jackal- and wolf-like meat and bone eaters" group. This attribution was verified by Coca-Ortega and Pérez-Claros (2019) based on the dimensions of the cheek teeth, with the sole exception of *H. namaquensis*, which appears to be slightly more derived and similar to cursorial meat and bone eaters, such as *Lycyaena* and *Chasmaporthetes*. Semenov (1989, 2008) states that *Hyaenictitherium* is characterised by elongated limbs, even though a more detailed taxonomic and ecomorphological comparison has yet to be conducted. The ecomorphological comparison of *H. ebu* by van der Hoek and Werdelin (2024) showed that this is definitely true at least for this species, since it resembles the maned wolf. As noted by Werdelin (1988a); Spassov et al. (2019), and based on personal preliminary observations (NK) of material from Samos, it can be said that the postcranial elements of *H. wongii* are indeed long, but not to the same extent as in *H. ebu*. The semi-cursorial body plan of *Hyaenictitherium* consists of a fitting adaptation to relatively open environments (Kargopoulos et al. 2023a) and is consistent with the palaeoenvironment of Venta del Moro (Casas-Gallego et al. 2015). Joeckel (1998) studied the frontal sinuses of fossil hyaenids and pointed out their considerable expansion, initially seen as an elongation in intermediate forms (including *Hyaenictitherium*) and interpreted as an adaptation that reduces resistance to high mechanical stress in the skull (such as bone-cracking). Stefen and Rensberger (1999), followed by Ferretti (2007) and Tseng (2011, 2012), compared the Hunter-Schreber bands (HSB) of several fossil hyaenids and showed that *Hyaenictitherium* presents zigzag HSBs, which is another dental adaptation towards durophagy. Nagel and Koufos (2009) discussed the carnivoran guild of Samos and Greece and considered *H. wongii* to be a 30–100 kg, generalised terrestrial and carnivorous species. A couple of years later, Koufos (2011) and Koufos and Konidaris (2011) followed the same ecomorphological attributions but changed the body mass class to 10–30 kg. Kargopoulos et al. (2023a) compared the ecomorphological proxies (body mass, relative rostrum width, endocranial volume, bite force, dental morphology) of *I. viverrinum* and *H. wongii* concluding that, even though there are some differences, both species occupy a position more similar to extant coyotes than to jackals and wolves, respectively. They also concluded that *H. wongii* had a body mass of around 20 kg and a brain volume quotient of approximately 100, which indicate a carnivoran of relatively average brain size, similar to that of a canid (Damasceno et al. 2013). Summarising, our current knowledge of this species shows that *H. wongii* was a coyote-sized animal with relatively long legs adapted for cursoriality in open environments, as well as several craniodental adaptations for durophagy.

The presence of two ictitheres in the same locality is surprisingly common, even if they belong to the same genus. In the initial publication of *H. wongii* and *H. hyaenoides*, Zdansky (1924) mentions both of them from the localities 30, 43, 44, 49, 108, 109, and 116. As indicated before, the same could be true for some localities of Eastern Europe where the material was published by Semenov (1989) as *H. venator*. Coexistence of closely related durophagous species has also been observed in other carnivoran groups, such as in borophagines (Wang et al. 1999). The dynamics between sympatric ictitheres can vary depending on the foraging strategies of each taxon (Kargopoulos et al. 2023a).

The faunal list of Venta del Moro includes an astonishing plethora of different species, revealing a flourishing ecosystem with complex interspecific relationships (Morales and Aguirre 1976; Morales 1984; Pickford et al. 1995; Montoya et al. 2006, 2009, 2011; Pesquero et al. 2007; Salesa et al. 2010; Mansino et al. 2014, 2015a, b, 2017, 2018; Alba et al. 2015; Crespo et al. 2018, 2021; Caballero et al. 2021; Delfino et al. 2021; Guillem et al. 2022). Among the vertebrates discovered in the locality, the possible prey of the ictitheres could include the hipparions (Pesquero et al. 2007), the pig, the bovids, and the cervids (Morales 1984), while if social behavior is taken into account hunting larger animals such as the camelid (Pickford et al. 1995) cannot be excluded. Occasional consumption of smaller prey, such as rodents, lagomorphs, and reptiles (Montoya et al. 2006), as well as scavenging on even larger animals, such as the rhino or *Anancus* (Morales 1984), could also be considered possible.

The diversity of hyenas reached its peak during the Turolian, with many genera found throughout Eurasia and Africa, ranging from small opportunistic species to canid-like ictitheres and bone-cracking crocutoids, such as *Plioviverrops*, *Hyaenictitherium*, and *Adcrocuta*, respectively (Werdelin

1991; Werdelin and Solounias 1991; Turner et al. 2008; Koufos 2021). However, almost all ictitheres went extinct at the end of the Miocene, with *H. namaquensis* and the record of Gaozhuang being the sole exception, as discussed previously. The extinction of the canid-like ictitheres coincided with the arrival and gradual dominance of the true canids in Eurasia and Africa. However, it is unclear whether this happened due to competitive exclusion, or whether ictitheres became extinct before the arrival of canids, which subsequently occupied the empty ecological niches (Werdelin 1991). There are some rare cases in Europe and Africa in which ictitheres coexist with canids in the same locality and the ictithere genus that is most often sympatric with canids is *Hyaenictitherium* (Fig. 9).

Even though the actual stratigraphic attribution of "*Canis*" *cipio* is doubted, the two specimens of this species have been found at the localities of Cerro de la Garita in Concud (Crusafont Pairó 1950; Alcalá 1994) and Los Mansuetos (Pons Moyà and Crusafont Pairó 1978) (in Teruel), and both sites contain ictitheres (Alcalá 1994). If this canid record is indeed accurate and the maxilla from Cerro de la Garita comes from the same fossiliferous layers as the other specimens of this locality, then *Ictitherium* aff. *pannonicum* published by Alcalá (1994) is the only non-*Hyaenictitherium* ictithere to have coexisted with a canid. Another example is of course Venta del Moro, where *Hyaenictitherium* coexists with the slightly smaller-sized *Eucyon debonisi* (Montoya et al. 2009). That is, the last ictithere of Europe coexists with the first *Eucyon* of Europe. Similarly, in Langebaanweg *H. namaquensis* coexists with *Eucyon khoikhoi* (Hendey 1974, 1978; Valenciano et al. 2022). Based on the length of skull and the lower carnassial these two canids are similar in size to *Canis adustus*, so they are smaller than their sympatric ictitheres. Interestingly, a third canid-like taxon has been discovered recently in the locality (Churcher et al., 2025). *Civettictis vulpidens*, a giant viverrid could overlap ecomorphologically with both the hyaenid and the canid. In the locality of Verduno, where the enigmatic large hyena discussed above has been found, there is also the species *Eucyon monticinensis* (Rook, 1992) described recently by Azzarà et al. (2025). In Middle Awash (Ethiopia), *Hyaenictitherium* sp. coexists with *Eucyon intrepidus* (*Eucyon* sp. in Haile-Selassie and Howell 2009). Again, the latter is much smaller, although both forms are poorly recorded (Haile-Selassie and Howell 2009; Valenciano et al., 2022). In Toros-Menalla (Djurab, Chad), *H. minimum* (de Bonis et al. 2005, 2010) coexists with the considerably smaller *Vulpes riffautae* (de Bonis et al. 2007). Apart from direct sympatry, there is also indirect evidence of possible co-occurrence, at least temporally in broader regions. For instance, in the Lukeino Formation of Kenya the species *E. intrepidus* (Morales et al. 2005) is found during a time period (6.1–5.8 Ma) when ictitheres were still present in East Africa (Werdelin and Peigné 2010).

Even though the canids eventually covered the niche of ictitheres, the patterns of this transition are not clear. The coexistence of ictitheres and canids in the same locality shows that sympatry was at least occasionally possible. With the exception of the obscure "*Canis*" *cipio* record, the other recorded cases show that ictitheres were larger than their sympatric canids. A comparison of the hemimandibles of *Hyaenictitherium* and *Eucyon* (Fig. 10) shows differences in size, but also in the robustness of the mandibular corpus and dentition. The mandibular corpus of *E. debonisi* is short and slender, whereas that of *H. wongii* is much deeper and wider. Additionally, the lower premolars of *Hyaenictitherium* are much larger and more robust, and have more developed accessory cuspids and cingulids, as well as more rugose and wide enamel, making them much more suitable for bone consumption. Also considering the potential social behaviour of ictitheres (Werdelin and Solounias 1991; Kargopoulos et al. 2023a) and their relatively advanced adaptations for durophagy discussed above, it is possible that the two groups engaged niche partitioning and subsequent balanced sympatry. However, it must be noted that no medium-to small-sized hyaenids, such as *I. viverrinum* or *P. crassum*, have been found together with canids. Therefore, bilateral exclusion for this size group of hyenas is possible. On the other hand, the record of canids in Europe in MN13 and MN14 is limited, since they have only been recorded in very few sites, with Venta del Moro and Brisighella being the only localities with more than a handful of specimens (Rook 2009). In other words, this record is hardly comparable to the extreme abundance and diversity of ictitheres seen in MN12. Presently, it is not impossible that the dominance of ictitheres in Eurasia and Africa formed an ecological barrier to the western expansion of canids, and that the extinction of the former for unknown reasons enabled the canids to gradually occupy their ecological niche. Therefore, even though the dispersal of canids could have contributed to the sudden extinction of most ictitheres, this process appears to have been much more complex, being influenced by other possible factors, particularly the climatic and tectonic changes in Europe during the latest Miocene, such as a global warming, the Messinian Salinity Crisis and the Rhodanian tectogenic phase (Aguirre 2003; Morales et al. 2013). All these led to profound environmental changes in terrestrial ecosystems that may have affected the ictitheres and related groups. Hopefully, the discovery of more fossils from the MN13/14 transition and the conduction of more detailed palaeoecological comparisons will clarify the exact conditions surrounding this replacement.

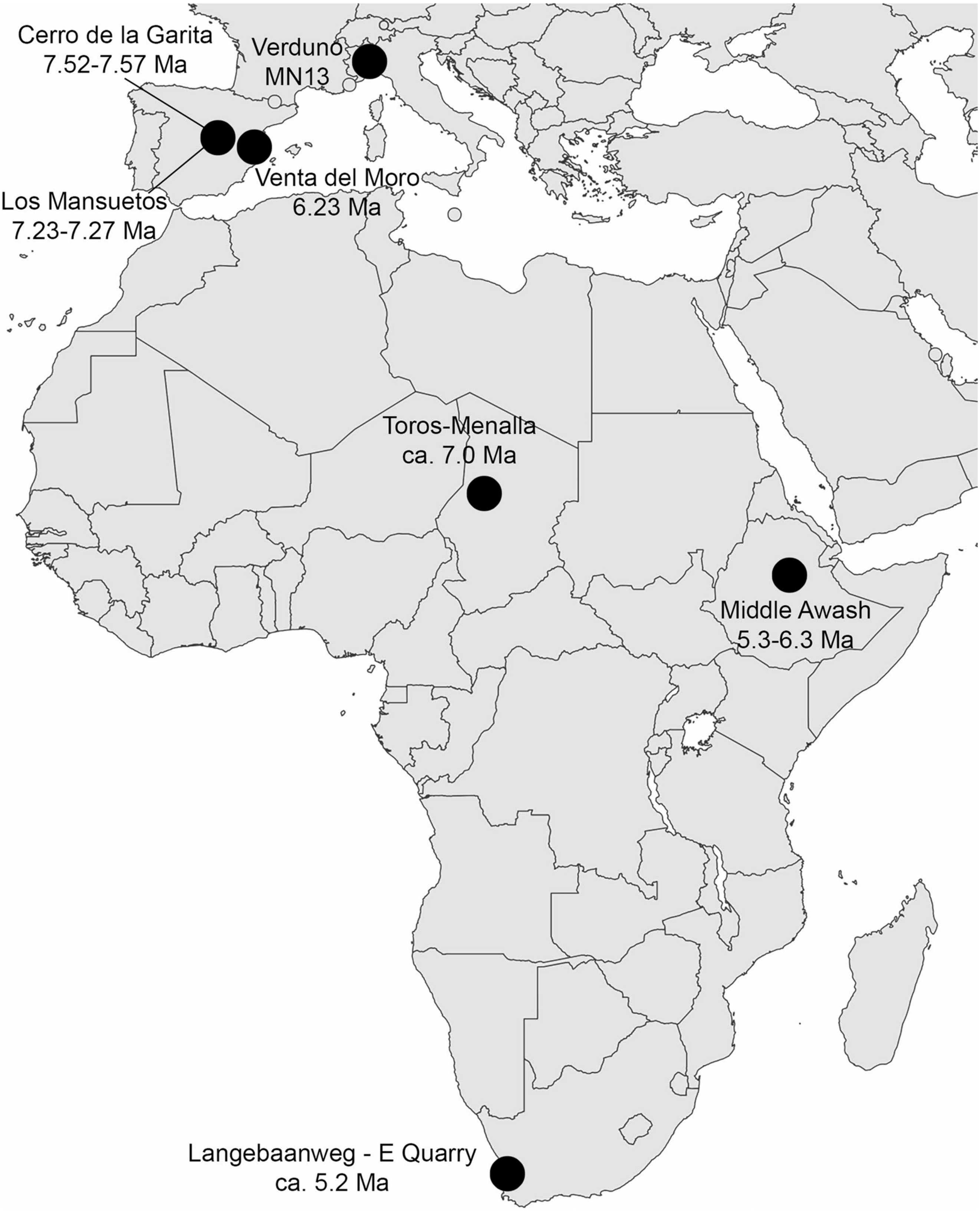

Fig. 9 Map depicting the cases of coexistence between canids and ictitheres in Europe and Africa. Map source: mapchart.net

Fig. 10 Comparison of the right hemimandibles of *Eucyon debonisi* and *Hyaenictitherium wongii*. **a**. *Eucyon debonisi* from Venta del Moro (composite of the specimens MGUV-14787, MGUV-24125, and MGUV-14791, published in Montoya et al. 2009); **b**. *Hyaenictitherium wongii* from Venta del Moro (MGUV-19193 - flipped); **c**. *Hyaenictitherium wongii* form Samos (AMNH 20586 - flipped). *Hyaenictitherium* specimens were reversed for better comparison with the *Eucyon* hemimandible. Scale bar equals 2 cm

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Declarations

Competing interests The authors declare no competing interests.

References

Abella J, Montoya P, Morales J (2014) Paleodiversity of the Superfamily Ursoidea (Carnivora, Mammalia) in the Spanish Neogene, related to environmental changes. J Iber Geol 40:11–18. https://doi.org/10.5209/rev_JIGE.2014.v40.n1.44083

Abella J, Hontecillas D, Valenciano A, Montoya P, Morales J, Pesquero MD, Alcalá L (2019) The last record of an ailuropod bear from the Iberian Peninsula. In: de Bonis L, Werdelin L (eds) Memorial to Stéphane Peigné: Carnivores (Hyaenodonta and Carnivora) of the Cenozoic. Geodiversitas 41(23):797–809. https://doi.org/10.5252/geodiversitas2019v41a23

Adrover R, Alcalá L, Mein P, Moissenet E, Orrios J (1986) Mamíferos del Turoliense medio en la Rambla de Valdecebro (Teruel). Estud Geol 42:495–509. https://doi.org/10.3989/egeol.86426781

Aguirre E (2003) Messiniense: compleja y grave crisis ecologica. Estud Geol 59:205–212. https://doi.org/10.3989/egeol.03591-499

Aguirre E, Robles F, Thaler L, López Martínez N, Alberdi MT, Fuentes C (1973) Venta del Moro, nueva fauna finimiocena de moluscos y vertebrados: Estud Geol 29:569–578

Aguirre E, López N, Morales J (1976) Continental faunas in southeast Spain related to the Messinian. In: Cita MB (ed) Il Significato Geodinamico della Crisis di Salinita del Miocene Terminale nel Mediterraneo. Messinian Seminar 2, Gargano, pp 62–63

Agustí J, Garcés M, Krijgsman W (2006) Evidence for African-Iberian exchanges during the Messinian in the Spanish mammalian record. Palaeogeogr Palaeoclimatol Palaeoecol 238:5–14. https://doi.org/10.1016/j.palaeo.2006.03.013

Alba DM, Montoya P, Pina M, Rook L, Abella J, Morales J, Delson E (2015) First record of *Mesopithecus* (Cercopithecidae, Colobinae) from the Miocene of the Iberian Peninsula: J Hum Evol 88:1–14. https://doi.org/10.1016/j.jhevol.2015.08.003

Alberdi MT, Bonadonna FP (1988) Is the "Ventian" a real stratigraphic stage? Mediter Ser Geol 7:65–77

Alberdi MT, López N, Mazo AV, Morales J (1977) Venta del Moro y las faunas de vertebrados finimiocenas de España. Estud Geol 33:589–591.

Alcalá L (1994) Macromamíferos Neógenos de la Fosa de Alfambra-Teruel. Instituto de Estudios Turolenses, Museo Nacional de Ciencias Naturales–CSIC, Teruel

Antón M, Turner A, Salesa MJ, Morales J (2006) A complete skull of *Chasmaporthetes lunensis* (Carnivora, Hyaenidae) from the Spanish Pliocene site of La Puebla de Valverde (Teruel). Estud Geol 62(1):375–388.

Azzarà B, Cherin M, Iurino DA, Colombero S, Panetta D, Pavia M, Sardella R, Sorbelli L, Werdelin L, Carnevale G (2025) An articulated skeleton of *Eucyon monticinensis* (Carnivora: Canidae) from the latest Miocene of Verduno (Italy). Zool J Linnean Soc 203(4):zlaf016. https://doi.org/10.1093/zoolinnean/zlaf016

Bowdich TE (1821) An Analysis of the Natural Classifications of Mammalia, for the Use of Students and Travellers. J. Smith, Paris

Caballero Ó, Montoya P, Crespo V, Morales J, Abella J (2021) The autopodial skeleton of *Paracamelus aguirrei* (Morales 1984) (Tylopoda, Mammalia) from the late Miocene site of Venta del Moro (Valencia, Spain). J Iber Geol 47:483–500. https://doi.org/10.1007/s41513-020-00144-x

Casas-Gallego M, Lassaletta L, Barrón E, Bruch AA, Montoya P (2015) Vegetation and climate in the eastern Iberian Peninsula during the pre-evaporitic Messinian (late Miocene). Palynological data from the Upper Turolian of Venta del Moro (Spain). Rev Palaeobot Palynolog 215:85–99. https://doi.org/10.1016/j.revpalbo.2015.01.001

Churcher CS, Hurlburt GR, Govender R, Valenciano A (2025) Cranial and endocranial morphology of a new species of giant civet (Carnivora, Viverridae) from the early Pliocene of Langebaanweg 'E' Quarry, South Africa. Palaeontogr Abt A Palaeozool Stratigr 329 (1–3):151–199. https://doi.org/10.1127/pala/2025/0157

Coca-Ortega C, Pérez-Claros JA (2019) Characterizing ecomorphological patterns in hyenids: a multivariate approach using postcanine dentition. PeerJ 6:e6238. https://doi.org/10.7717/peerj.6238

Colbert EH (1935) Siwalik mammals in the American Museum of Natural History. Trans Am Phil Soc 26:1–401 https://doi.org/10.70249/9798893981964

Crespo VD, Sevilla P, Mansino S, Montoya P, Ruiz-Sánchez FJ (2018) Bats from the classical site of Venta del Moro (late Miocene, eastern Spain). Hist Biol 30:317–326. https://doi.org/10.1080/08912963.2016.1277995

Crespo VD, Montoya P, Marquina-Blasco R, Ruiz-Sánchez FJ (2021) *Parasorex ibericus* from Venta del Moro (late Miocene, Iberian Peninsula): a new light on the tribe Galericini. Palaeontogr Abt A: Palaeozool Stratigr 320 (1–3):65–86. https://doi.org/10.1127/pala/2021/0116

Crusafont Pairó M (1950) El primer representante del género *Canis* en el Pontiense eurasiático (*Canis cipio* nova sp.). Bol Real Soc Esp Hist Nat 48:43–51.

Crusafont Pairó M, Petter G (1969) Contribution a l'étude des Hyaenidae. La sous-familie des Ictitheriinae. Ann Paleontol 55:89–127.

Damasceno EM, Hingst-Zaher E, Astúa D (2013) Bite force and encephalization in the Canidae (Mammalia: Carnivora). J Zool 290(4):246–254. https://doi.org/10.1111/jzo.12030

de Bonis L, Koufos G (1991) The Late Miocene small carnivores of the lower Axios Valley (Macedonia – Greece). Geobios 24(2):361–379. https://doi.org/10.1016/S0016-6995(09)90015-8

de Bonis L, Peigné S, Likius A, Mackaye HT, Vignaud P, Brunet M (2005) *Hyaenictitherium minimum*, a new ictithere (Mammalia, Carnivora, Hyaenidae) from the late Miocene of Toros-Menalla, Chad. C R Palevol 4(8):671–679. https://doi.org/10.1016/j.crpv.2005.09.020

de Bonis L, Peigné S, Likius A, Mackaye HT, Vignaud P, Brunet M (2007) The oldest African fox (*Vulpes riffaeutae* n. sp., Canidae, Carnivora) recovered in the late Miocene deposits of the Djurab desert, Chad. Naturwissenschaften 94:575–580. https://doi.org/10.1007/s00114-007-0230-6

de Bonis L, Peigné S, Guy F, Mackaye HT, Likius A, Vignaud P, Brunet M (2010) Hyaenidae (Carnivora) from the late Miocene of

Toros-Menalla, Chad. J Afr Earth Sci 58(3):561–579. https://doi.org/10.1016/j.jafrearsci.2010.06.003

Delfino M, Luján À, Abella J, Alba D, Böhme M, Pérez-Ramos A, Tschopp E, Morales J, Montoya P (2021) Late Miocene remains from Venta del Moro (Iberian Peninsula) provide further insights on the dispersal of crocodiles across the late Miocene Tethys. J Paleontol 95(1):184–192. https://doi.org/10.1017/jpa.2020.62

Ferretti M (2007) Evolution of bone-cracking adaptations in hyaenids (Mammalia, Carnivora). Swiss J Geosci 100:41–52. https://doi.org/10.1007/s00015-007-1212-6

Fraile S (2016) Estudio de *Protictitherium crassum* del Cerro de los Batallones (Torrejón de Velasco, Madrid): aportación a la filogenia y evolución de la familia Hyaenidae. Dissertation, Universidad Complutense de Madrid

Fraile S, Pérez B, De Miguel I, Morales J (1997) Revisión de los carnívoros presentes en los yacimientos del Neógeno español. In: Calvo JP, Morales J (eds) Avances en el Conocimiento del Terciario Ibérico. Universidad Complutense de Madrid, Madrid, pp 77–80

Galiano H, Tseng ZJ, Solounias N, Wang X-M, Qiu Z-X, White SC (2022) A new aardwolf-line fossil hyena from Middle and Late Miocene deposits of Linxia Basin, Gansu, China. Vertebr PalAsiatica 60(2):81–116. https://doi.org/10.19615/j.cnki.2096-9899.211025

García-Alix A, Minwer-Barakat R, Martín Suárez E, Freudenthal M, Aguirre J, Kaya F (2016) Updating the Europe-Africa small mammal exchange during the late Messinian. J Biogeogr 43:1336–1348. https://doi.org/10.1111/jbi.12732

Gaudry A (1862–1867) Animaux Fossiles et Geologie de l 'Attique. F. Savy, Paris

Geraads D (1997) Carnivores du Pliocène terminal de Ahl Al Oughlam (Casablanca, Maroc). Geobios 30(1):127–164. https://doi.org/10.1016/S0016-6995(97)80263-X

Geraads D (2008) Plio-Pleistocene Carnivora of northwestern Africa: A short review. C R Palevol 7:591–599. https://doi.org/10.1016/j.crpv.2008.09.008

Gervais P (1848–1852, 1859) Zoologie et Paléontologie françaises (Animaux Vertébrés) ou Nouvelles Recherches sur les Animaux Vivants et Fossils de la France. Arthus Bertrand, Paris

Ghaffar A, Akhtar M (2012) New fossil record of *Hyaenictitherium pilgrimi* (Carnivora: Hyaenidae) from Dhok Pathan Formation of Hasnot, Pakistan. Swiss J Palaeontol 131:275–281. https://doi.org/10.1007/s13358-012-0042-y

Gibert L, Scott GR, Montoya P, Ruiz-Sánchez F, Morales J, Luque L, Abella J, Lería M (2013) Evidence for an African-Iberian mammal dispersal during the pre-evaporitic Messinian. Geology 41:691–694. https://doi.org/10.1130/G34164.1

Gray JE (1821) On the natural arrangement of vertebrose animals. Long Med Repos 15:296–310

Guillem J, Blázquez AM, Mesquita-Joanes F, Montoya P, Usera J (2022) Environmental evolution of the Miocene palaeolake of Venta del Moro (Valencia, Spain): a study of foraminifers, thecamoebians (Arcellinida) and ostracods, Hist Biol 34(8):1448–1457. https://doi.org/10.1080/08912963.2022.2034807

Haile-Selassie Y, Howell C (2009) Carnivora. In: Haile-Selassie Y, WoldeGabriel G (eds) *Ardipithecus kadabba*: Late Miocene Evidence from the Middle Awash, Ethiopia. University of California Press, Berkeley, pp 237–276

Hendey QB (1974) The late Cenozoic Carnivora of the Southwestern Cape Province. Ann S Afr Mus 63:1–369

Hendey QB (1978) Late Tertiary Hyaenidae from Langebaanweg, South Africa, and their relevance to the phylogeny of the family. Ann S Afr Mus 76(7):265–297

Hensel RF (1862) Über die Reste einiger Säugetierarten von Pikermi in der Münchener Sammlung. Monatsber Akad Wiss 27:560–569

Howell FC (1987) Preliminary observations on Carnivora from the Sahabi Formation. In: Boaz NT, El-Arnauti A, Gaziry AW, de Heinzelin J, Boaz DD (eds) Neogene Paleontology and Geology of Sahabi. Liss, New York, pp 153–181

Howell FC, Petter G (1980) The *Pachycrocuta* and *Hyaena* lineages (Plio-Pleistocene and extant species of the Hyaenidae). Their relationships with Miocene ictitheres: *Palhyaena* and *Hyaenictitherium*. Geobios 13(4):579–623. https://doi.org/10.1016/S0016-6995(80)80004-0

Howell FC, Petter G (1985) Comparative observations on some Middle and Upper Miocene hyaenid genera: *Percrocuta* Kretzoi, *Allohyaena* Kretzoi, *Adcrocuta* Kretzoi (Mammalia, Carnivora, Hyaenidae). Geobios 18:419–476. https://doi.org/10.1016/S0016-6995(85)80001-2

Iannucci A (2024) A reappraisal of the lost suids from the Late Miocene of Gravitelli (Sicily, Italy) and paleobiogeographical implications. Palaeoworld 33:469–491. https://doi.org/10.1016/j.palwor.2023.02.001

Iurino DA, Iannucci A, Conti J, Mecozzi B, Sardella R, Strani F (2022) Revised description of the late Miocene *Hyaenictitherium namaquensis* (Carnivora, Hyaenidae) from As Sahabi (North Africa, Libya). Hist Biol 34(8):1373–1380. https://doi.org/10.1080/08912963.2021.2007529

Joeckel R (1998) Unique frontal sinuses in fossil and living Hyaenidae (Mammalis, Carnivora): description and interpretation. J Vertebr Paleontol 18(3):627–639. https://doi.org/10.1080/02724634.1998.10011089

Kargopoulos N, Kampouridis P, Lechner T, Böhme M (2022) Hyaenidae (Carnivora) from the Late Miocene hominid locality of Hammerschmiede (Bavaria, Germany). Hist Biol 34(11): 2249–2258. https://doi.org/10.1080/08912963.2021.2010193

Kargopoulos N, Roussiakis S, Kampouridis P, Koufos G (2023a) Interspecific competition in ictitheres (Carnivora: Hyaenidae) from the Late Miocene of Eurasia. C R Palevol 22(3):33–44. https://doi.org/10.5852/cr-palevol2023v22a3

Kargopoulos N, Kampouridis P, Hartung J, Böhme M (2023b) Hyaenid remains from the Late Miocene of Kutschwan (Shanxi Province, China). Paläont Z 97:653–666. https://doi.org/10.1007/s12542-023-00658-6

Khomenko IP (1914) Meoticheskaya fauna s. Taraklii benderskogo uezda: Fissipedia, Rodentia, Rhinocerotinae, Equinae, Suidae, Proboscidae. Trudy Bessarahskoe Obshchestvo Estestvoispytatelei, Kishinev 5:1–55

Koufos G (1987) *Chasmaporthetes bonisi*, a new hyaenid (Carnivora, Mammalia) from the late Miocene of Macedonia (Greece). Bull Soc Géol Fr 3(8):913–920.

Koufos G (2009) Carnivora. In: Koufos G, Nagel D (eds) The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. Beitr Paläont 31, pp 57–105

Koufos G (2011) The Miocene carnivore assemblage of Greece. Estud Geol 67(2):291–320. https://doi.org/10.3989/egeol.40560.190

Koufos G (2021) The late Miocene middle-sized ictitheres (Mammalia: Hyaenidae) of Greece. Boll Soc Paleontol Ital 60(1):19–48. https://doi.org/10.4435/BSPI.2021.03

Koufos G, Konidaris G (2011) Late Miocene carnivores of the Greco-Iranian Province: Composition, guild structure and palaeoecology. Palaeogeogr Palaeoclimatol Palaeoecol 305:215–226. https://doi.org/10.1016/j.palaeo.2011.03.003

Koufos G, Vasileiadou K (2015) Miocene/Pliocene mammal faunas of southern Balkans: implications for biostratigraphy and palaeoecology. Palaeobiodivers Palaeoenviron 95:285–303. https://doi.org/10.1007/s12549-015-0201-4

Kretzoi M (1938) Die Raubtiere von Gombaszög nebst einer Übersicht der Gesamtfauna. Ann Hist-Nat Mus Nat Hung 31:88–157

Kretzoi M (1952) Die Raubtiere der Hipparionfauna von Polgardi. Ann Inst Geol Pub Hung 40:1–42

Kurtén B (1954) The type collection of *Ictitherium robustum* (Gervais ex Nordmann) and the radiation of the ictitheres. Acta Zool Fennica 86:1–26

Kurtén B (1982) Status of the fossil hyaenids *Ictitherium viverrinum* and *Thalassictis robusta* (Mammalia). Z Geol Wiss 10:1009–1018

Kurtén B, Werdelin L (1988) A review of the genus *Chasmaporthetes* Hay, 1921 (Carnivora, Hyaenidae). J Vertebr Paleontol 8(1):46–66. https://doi.org/10.1080/02724634.1988.10011683

Larivière S, Pasitchniak-Arts M (1996) *Vulpes vulpes*. Mamm Species 537:1–11. https://doi.org/10.2307/3504236

Lydekker R (1877) Notices of new and other Vertebrata from Indian Tertiary and Secondary Rocks. Rec Geol Survey India 10:30–43. https://archive.org/details/recordsgeologicvii/page/n11/mode/2up

Lydekker R (1884) Indian Tertiary and post-Tertiary Vertebrata. Part 6. Siwalik and Narbada Carnivora. Mem Geol Surv India Palaeontol Indica 10:178–363.

Mahmood K, Khan MA (2020) Miocene hyaenids (Hyaenidae; Carnivora) from Siwaliks of Pakistan. Palaeoworld 29(4):761–768. https://doi.org/10.1016/j.palwor.2019.11.003

Mansino S, Ruiz-Sánchez FJ, Freudenthal M, Montoya P (2014) A new approach to the Late Miocene-Early Pliocene forms of the genus *Apocricetus*. *Apocricetus alberti* (Rodentia, Mammalia) from Venta del Moro (Cabril Basin, Spain). Proc Geol Assoc 125:392–405. https://doi.org/10.1016/j.pgeola.2014.07.002

Mansino S, García-Alix A, Ruiz-Sánchez FJ, Montoya P (2015a) A new *Eliomys* from the late Miocene of Spain, and its implications for the phylogeny of the genus. Acta Palaeontol Pol 60:577–588. https://doi.org/10.4202/app.00014.2013

Mansino S, Ruiz-Sánchez FJ, de Luque L, Montoya P, Gibert L, Morales J, Abella J, Crespo VD, Scott GR (2015b) First early Pliocene micromammal faunas from the Venta del Moro area (Cabriel Basin, Spain): new data on the Messinian dispersal of *Debruijnimys*. J Iber Geol 41:273–293. https://doi.org/10.5209/rev_JIGE.2015.v41.n2.46418

Mansino S, Crespo VD, Montoya P, Ruiz-Sánchez FJ (2017) Muridae from the late Miocene site of Venta del Moro (eastern Spain). Hist Biol 29:677–691. https://doi.org/10.1080/08912963.2016.1232405

Mansino S, Ruiz-Sánchez FJ, Montoya P (2018) Sciuridae (Rodentia, Mammalia) from the Late Miocene of Venta del Moro (Cabriel Basin, Spain): biostratigraphical, phylogenetic and palaeoecological inferences. Hist Biol 30(3):297–304. https://doi.org/10.1080/08912963.2016.1242583

Mech D (1974) *Canis lupus*. Mamm Spec 37:1–6. https://doi.org/10.2307/3503924

Meladze GK (1967) Hipparionovaya fauna Arkneti i Bazaleti. Metsniereba, Tbilisi

Mein P (1990) Updating of MN zones. In: Lindsay EH, Fahlbusch V, Mein P (eds) European Neogene Mammal Chronology. Plenum Press, New York, pp 73–90. https://doi.org/10.1007/978-1-4899-2513-8_6

Mein P (1999) European Miocene mammal biochronology. In: Rössner GE, Heissing K. (eds) The Miocene Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, Munich, pp 25–38

Michaux J (1969) Muridae (Rodentia) du Pliocéne supérieur d'Espagne et du Midi de la France. Palaeovertebrata 3:1–25

Minwer-Barakat R, García-Alix A, Agustí J, Martín-Suárez E, Freudenthal M (2009) The micromammal fauna from Negratín-1 (Guadix Basin, Southern Spain): new evidence of African-Iberian mammal exchanges during the Late Miocene. J Paleontol 83(6):854–879. https://doi.org/10.1666/09-009.1

Minwer-Barakat R, Agustí J, García-Alix A, Martín-Suárez E (2018) The European record of the gerbil *Myocricetodon* (Rodentia, Mammalia) and its bearing on the Messinian salinity crisis. Palaeogeogr Palaeoclimatol Palaeoecol 506:168–182. https://doi.org/10.1016/j.palaeo.2018.06.032

Montoya P, Morales J, Robles F, Abella J, Benavent JV, Marín MD, Ruiz Sánchez FJ (2006) Las nuevas excavaciones (1995–2006) en el yacimiento del Mioceno final de Venta del Moro, Valencia. Estud Geol 62:313–326. https://doi.org/10.3989/egeol.0662128

Montoya P, Morales J, Abella J (2009) *Eucyon debonisi* n. sp., a new Canidae (Mammalia, Carnivora) from the latest Miocene of Venta del Moro (Valencia, Spain). Geodiversitas 31(4):709–722. https://doi.org/10.5252/g2009n4a709

Montoya P, Morales J, Abella J (2011) Musteloidea (Carnivora, Mammalia) from the Late Miocene of Venta del Moro (Valencia, Spain). Estud Geol 67(2):193–206. https://doi.org/10.3989/egeol.40576.183

Morales J (1984) Venta del Moro: su macrofauna de mamíferos y bioestratigrafía continental de Mioceno terminal mediterráneo. Dissertation, Universidad Complutense de Madrid

Morales J, Aguirre E (1976) Carnívoros de Venta del Moro (Valencia). Trab Neógeno-Cuatern 5:31–74

Morales J, Soria D, Aguirre E (1980) Camélido finimioceno en Venta del Moro. Primera cita para Europa Occidental. Estud Geol 36:139–142

Morales J, Pickford M, Soria D (2005) Carnivores from the late Miocene and basal Pliocene of the Tugen Hills, Kenya. Rev Soc Geol Esp 18(1–2):39–61

Morales J, Peláez-Campomanes P, Abella J, Montoya P, Ruiz F, Gibert L, Scott G, Cantalapiedra J, Sanisidro O (2013) The Ventian mammal age (latest Miocene): present state. Span J Palaeontol 28(2):149–160. https://doi.org/10.7203/sjp.28.2.17849

Morales Flores D (2024) Los Hyaenidae de Venta del Moro (Cuenca del Cabriel, Valencia). MSc Thesis, Universitat de Valencia

Nagel D, Koufos G (2009) Carnivore guild structure. In: Koufos G, Nagel D (eds) The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. Beitr Paläontol 31:391–396

Pasitschniak-Arts M (1993) *Ursus arctos*. Mamm Species 439:1–10. https://doi.org/10.2307/3504138

Pesquero MD, Alberdi M., Montoya P (2007) *Hipparion* (Equidae, Mammalia) from Venta del Moro (Valencia Province, Spain). N Jahrb Geol Paläontol 243: 273–297. https://doi.org/10.1127/0077-7749/2007/0243-0273

Pickford M, Morales J (1994) Biostratigraphy and palaeobiogeography of East Africa and the Iberian peninsula. Paleogeogr Paleoclimatol Paleoecol 112:297–322. https://doi.org/10.1016/0031-0182(94)90078-7

Pickford M, Morales J, Soria D (1993) First fossil camels from Europe. Nature 365:701. https://doi.org/10.1038/365701a0

Pickford M, Morales J, Soria D (1995) Fossil camels from the upper Miocene of Europe: implications for biogeography and faunal change. Geobios 28: 641–650. https://doi.org/10.1016/S0016-6995(95)80217-7

Pilgrim GE (1910) Notices on new mammalian genera and species from the Tertiaries of India. Rec Geol Surv India 40:63–71

Pilgrim GE (1931) Catalogue of the Pontian Carnivora of Europe in the Department of Geology. Museum (Natural History), London

Pilgrim GE (1932) The fossil Carnivora of India. Mem Geol Surv India. Palaeontol Indica 18:1–232

Pons Moyà J, Crusafont Pairó M (1978) El *Canis cipio* CRUSAFONT (1950), comparación con los cánidos del Plioceno y Pleistoceno europeo. Acta Geol Hisp 13:133–136

Qiu Z (1985) Restudy of '*Ictitherium hyaenoides*' in the Lagrelius collection. Bull Geol Inst Univ Uppsala n.s. 11:92–112

Qiu Z, Qiu Z (1995) Chronological sequence and subdivision of Chinese Neogene mammalian faunas. Palaeogeog Palaeoclim Palaeoecol 116:41–70. https://doi.org/10.1016/0031-0182(94)00095-P

Robles F (1974) Levante. In: Aguirre E, Morales J (eds) Coloquio Internacional sobre Biostratigrafía Continental del Neógeno Superior y Cuaternario Inferior. Libro-Guía. Madrid, pp 87–133

Robles F, Acuña JD, Gutiérrez G, Nieto M (1983) Lugares de Interés Geológico de la Provincia de València. Diputació Provincial de Valencia, 127 pp.

Rook L (1992) "*Canis*" *monticinensis* sp. nov., a new Canidae (Carnivora, Mammalia) from the late Messinian of Italy. Boll Soc Paleontol Ital 31(1):151–156

Rook L (2009) The wide ranging genus *Eucyon* Tedford & Qiu, 1996 (Mammalia, Carnivora, Canidae, Canini) in the Mio-Pliocene of the Old World. Geodiversitas 31(4):723–741. https://doi.org/10.5252/g2009n4a723

Rook L, Delfino M, Sami M (2015) I vertebrati fossil della Cava del Monticino di Brisighella: una finestra sui popolamenti continentali del Mediterraneo nel Miocene superiore. Mem Istit Ital Speleol 28:79–100

Roussiakis S, Theodorou G (2003) Carnivora from the late Miocene of Kerassia (Northern Euboea, Greece). Deinsea 10:469–497

Salesa MJ, Antón M, Turner A, Alcalá L, Montoya P, Morales J (2010) Systematic revision of the Late Miocene sabre- toothed felid *Paramachaerodus* in Spain. Palaeontology 53(6):1369–1391. https://doi.org/10.1111/j.1475-4983.2010.01013.x

Sardella R (2008) Remarks on the Messinian carnivores (Mammalia) of Italy. Boll Soc Paleontol Ital 47(2):195–202

Schmidt-Kittler N (1995) 7. Carnivora. In: Schmidt-Kittler N (ed) The Vertebrate Locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). Münch Geowiss Abh A 28:75–86

Seguenza L (1902) I vertebrati fossili della provincia di Messina: Parte II. Mammiferi e geologia del piano Pontico. Boll Soc Geol Ital 21:115–172

Semenov Y (1985) *Ictitherium pannonicum* (Carnivora, Viverridae) из мєотических отложений северного причерноморъя. Vestn Zool 1985:23–27

Semenov Y (1989) Ictitheres and morphologically similar hyaenas from the Neogene of the USSR. Dissertation, Naukova Dumka, Kiev

Semenov Y (2001) Stratigraphic distribution of the terrestrial carnivores in the Vallesian and Turolian of Ukraine. Beitr Paläontol 26:139–144

Semenov Y (2008) Taxonomical reappraisal of "ictitheres" (Mammalia, Carnivora) from the Late Miocene of Kenya. C R Palevol 7(8):529–539. https://doi.org/10.1016/j.crpv.2008.09.012

Solounias N (1981) The Turolian fauna from the island of Samos, Greece. Contrib Vertebr Evol 6:1–232

Soria D (1979) Hiénidos fósiles de España. Revisión de la familia Hyaenidae en el Neógeno superior y Pleistoceno inferior. Dissertation, Universidad Complutense de Madrid

Spassov N, Geraads D, Hristova L, Markov G (2019) The late Miocene mammal fauna from Gorna Sushitsa, southwestern Bulgaria, and the early/middle Turolian transition. N Jahrb Geol Paläontol Abh 291(3):317–350. https://doi.org/10.1127/njgpa/2019/0804

Stefen C, Rensberger J (1999) The specialized structure of hyaenid enamel: description and development within the lineage – including percrocutoids. Scanning Microsc 13(2–3):363–380

Stromer EV (1931) Reste Süsswasser und Land bewohnender Wirbeltiere aus den Diamantfeldern Klein-Namaqualandes (Südwestafrika). Sitzungsber math-naturwiss Abt Bayer Akad Wiss Münch 1:17–47

Trouessart EL (1897) Catalogus Mammalium tam Vivientum quam Fossilium. Berolini, R. Friedländer & Sohn, Berlin

Tseng ZJ (2011) Variation and implications of intra-dentition Hunter-Schreger band pattern in fossil hyaenids and canids (Carnivora, Mammalia). J Vertebr Paleontol 31(5):1163–1167. https://doi.org/10.1080/02724634.2011.602161

Tseng ZJ (2012) Connecting Hunter–Schreger Band microstructure to enamel microwear features: New insights from durophagous carnivores. Acta Palaeontol Pol 57(3):473–484. https://doi.org/10.4202/app.2011.0027

Tseng ZJ, Wang X (2007) The first record of the late Miocene *Hyaenictitherium hyaenoide*s Zdansky (Carnivora: Hyaenidae) in Inner Mongolia and an evaluation of the genus. J Vertebr Paleontol 27(3):699–708. https://doi.org/10.1671/0272-4634(2007)27[699:TFROTL]2.0.CO;2

Turner A, Antón M, Werdelin L (2008) Taxonomy and evolutionary patterns in the fossil Hyaenidae of Europe. Geobios 41:677–687. https://doi.org/10.1016/j.geobios.2008.01.001

Valenciano A, Morales J, Govender R (2022) *Eucyon khoikhoi* sp. nov. (Carnivora: Canidae) from Langebaanweg 'E' Quarry (early Pliocene, South Africa): the most complete African Canini from the Mio-Pliocene. Zool J Linn Soc 194(2):366–394. https://doi.org/10.1093/zoolinnean/zlab022

Van Dam JA (1997) The small mammals from the Upper Miocene of the Teruel-Alfambra region (Spain): paleobiology and paleoclimatic reconstructions. Geol Ultraiectina 156:1–204

van der Hoek J, Werdelin L (2024) A hyaena on stilts: comparison of the limb morphology of *Ictitherium ebu* (Mammalia: Hyaenidae) from the Late Miocene of Lothagam, Turkana Basin, Keny with extant Canidae and Hyaenidae. PeerJ 12:e17405. https://doi.org/10.7717/peerj.17405

van der Made J, Morales J (1999) Family Camelidae. In: Rössner GE, Heissig K (eds) The Miocene Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, Munich, pp. 221–224. https://doi.org/10.1016/j.palaeo.2006.03.030

van der Made J, Morales J, Montoya P (2006) Late Miocene turnover in the Spanish mammal record in relation to palaeoclimate and the Messinian Salinity Crisis. Palaeogeogr Palaeoclimatol Palaeoecol 238:228–246. https://doi.org/10.1016/j.palaeo.2006.03.030

van der Made J, Güleç E, Erkman AC (2013) *Microstonyx* (Suidae, Artiodactyla) from the Upper Miocene of Hayranlı-Haliminhanı, Turkey. Turk J Zool 37:106–122. https://doi.org/10.3906/zoo-1202-4

Vangengeim E, Tesakov A (2013) Late Miocene mammal localities of Eastern Europe and Western Asia: Toward biostratigraphic synthesis. In: Wang X, Flynn L, Fortelius M (eds) Fossil Mammals of Asia: Neogene biostratigraphy and chronology. Columbia University Press, New York, pp 521–537. https://doi.org/10.7312/wang15012-023

Villalta Comella JF, Crusafont Pairó M (1943) Los vertebrados del Mioceno continental de la Cuenca Valles-Panades (Provincia de Barcelona). I. Insectivoros. - II. Carnivoros. Bol Inst Geol Minero Esp 65:1–192

Vinuesa V, Madurell-Malapeira J, Werdelin L, Robles J, Obradó P, Alba D (2017) A new skull of *Hyaenictis* Gaudry, 1861 (Carnivora, Hyaenidae) shows incipient adaptations to durophagy. J Mamm Evol 24:207–219. https://doi.org/10.1007/s10914-016-9334-0

Viranta S, Werdelin L (2003) Carnivora. In: Fortelius M, Kappelman J, Sen S, Bernor RL (eds) Geology and Paleontology of the Miocene Sinap Formation, Turkey. Columbia University Press, New York, pp 178–193

Wagner A (1848) Urweltliche Säugethiere-Uberreste aus Griechenland. Abh Bayer Akad Wiss 5:335–378.

Wang X, Tedford RH, Taylor BE (1999) Phylogenetic systematics of the Borophaginae (Carnivora: Canidae). Bull Am Mus Nat Hist 243:1–391.

Wang X-M, Tseng ZJ, Wu W-Y, Ye J, Meng J, Bi S (2020) A new species of *Tungurictis* Colbert, 1939 (Carnivora, Hyaenidae) from the middle Miocene of Junggar Basin, northwestern China and the early divergence of basal hyaenids in East Asia. In: de Bonis

L, Werdelin L (eds) Memorial to Stéphane Peigné – Carnivores (Hyaenodonta and Carnivora) of the Cenozoic. Geodiversitas 42(3):29–45. https://doi.org/10.5252/geodiversitas2020v42a3

Werdelin L (1988a) Studies of fossil hyaenids: the genera *Ictitherium* Roth & Wagner and *Sinictitherium* Kretzoi and a new species of *Ictitherium*. Zool J Linn Soc 93:93–105. https://doi.org/10.1111/j.1096-3642.1988.tb01528.x

Werdelin L (1988b) Studies of fossil hyaenids: the genera *Thalassictis* Gervais ex Nordmann, *Palhyaena* Gervais, *Hyaenictitherium* Kretzoi, *Lycyaena* Hensel and *Palinhyaena* Qiu, Huang & Guo. Zool J Linnean Soc 92:211–265. https://doi.org/10.1111/j.1096-3642.1988.tb01512.x

Werdelin L (1991) Hyaenas: The rise and fall of a carnivore family. Geol Fören Stockh Förh 113(1):95–95. https://doi.org/10.1080/11035899109453840

Werdelin L (1999) Studies of fossil hyaenas: affinities of *Lycyaenops rhomboideae* Kretzoi from Pestlörinc, Hungary. Zool J Linn Soc 126:307–317. https://doi.org/10.1111/j.1096-3642.1999.tb01373.x

Werdelin L (2003) Mio-Pliocene Carnivora from Lothagam, Kenya. In: Leakey MG, Harris JM (eds) Lothagam: The Dawn of Humanity in Eastern Africa. Columbia University Press, New York, pp 261–328. https://doi.org/10.7312/leak11870-013

Werdelin L, Dehghani R (2011) Carnivora. In: Harrison T (ed) Paleontology and Geology of Laetoli: Human Evolution in Context. Volume 2: Fossil Hominins and the Associated Fauna. Springer, Dordrecht, pp. 189–232. https://doi.org/10.1007/978-90-481-9962-4_8

Werdelin L, Kurtén B (1999) *Allohyaena* (Mammalia: Carnivora): giant hyaenid from the Late Miocene of Hungary. Zool J Linnean Soc 126:319–334. https://doi.org/10.1111/j.1096-3642.1999.tb01374.x

Werdelin L, Peigné S (2010) Carnivora. In: Werdelin L, Sanders WJ (eds) Cenozoic Mammals of Africa. University of California Press, Berkeley, pp 609–663. https://doi.org/10.1525/california/9780520257214.001.0001

Werdelin L, Solounias N (1990) Studies of fossil hyaenids: the genus *Adcrocuta* Kretzoi and the interrelationships of some hyaenid taxa. Zool J Linn Soc 98(4):363–386. https://doi.org/10.1111/j.1096-3642.1990.tb01206.x

Werdelin L, Solounias N (1991) The Hyaenidae: taxonomy, systematics and evolution. Fossils Strata 30:1–104. https://doi.org/10.18261/8200374815-1991

Werdelin L, Solounias N (1996) The evolutionary history of hyaenas in Europe and Western Asia during the Miocene. In: Bernor RL, Fahlbusch V, Rietschel S (eds) Later Neogene European Biotic Evolution and Stratigraphic Correlation. Columbia University Press, New York, pp 290–306

Werdelin L, Turner A, Solounias N (1994) Studies of fossil hyaenids: the genera *Hyaenictis* Gaudry and *Chasmaporthetes* Hay, with a reconsideration of the Hyaenidae of Langebaanweg, South Africa. Zool J Linn Soc 111:197–217. https://doi.org/10.1006/zjls.1994.1022

Zdansky O (1924) Jungtertiäre Carnivoren Chinas. Palaeontol Sin 2:1–149. https://doi.org/10.1017/S0016756800106247