A New skull of *Hyaenictis* (Carnivora, Hyaenidae) Shows Incipient Adaptations to Durophagy

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Abstract The European Miocene records a wide diversity of hyaenid ecomorphotypes represented by multiple genera. Among these, *Hyaenictis* is one of the least known. This genus includes four species from the late Miocene and Pliocene of the Old World, but in Europe *Hyaenictis* is only represented by two species, recorded by scarce and fragmentary remains: *Hyaenictis graeca* from Pikermi (MN12; Greece) and *Hyaenictis almerai* from Sant Miquel de Toudell (MN10; Vallès-Penedès Basin, NE Iberia). Here we describe a new skull of *Hyaenictis* aff. *almerai* from the Vallès-Penedès site of Ronda Oest Sabadell Sector D (MN10), representing the most complete European specimen of the genus. In the presence of m2 and virtual lack of m1 metaconid, the described cranium more closely resembles *Hyaenictis* rather than any other medium to large-sized European hyaenid. However, the new skull does not fit well with previously known *Hyaenictis* species, more closely resembling the bone-cracking *Adcrocuta* in the development of premolar accessory cuspids and the possession of relatively broad cheek teeth. These and other features (strong mandibular muscular insertions and enamel microstructure) denote more durophagous adaptations than previously documented in *Hyaenictis* (considered a cursorial/dog-like hyaena), and favor the inclusion of *H.* aff. *almerai* in the transitional bone-cracking hyaenid ecomorphotype.

Introduction

The Genus *Hyaenictis*

Hyaenictis Gaudry, 1861 and its type species, *Hyaenictis graeca* Gaudry, 1861, were erected on the basis of scarce dentognathic remains from the Greek locality of Pikermi (MN12, middle Turolian, late Miocene). The holotype is a juvenile hemimandible with dc, p1 alveolus, dp2–dp4, erupting m1 and m2, and exposed p2-p4 inside their crypts. A few additional dentognathic remains, including two juvenile maxillary fragments, have been further attributed to the same taxon (see also Howell and Petter 1985; Werdelin et al. 1994; Koufos 2011). This species is characterized by a mixture of primitive features (retention of p1 and m2) and several derived traits (such as vestigial m1 metaconid; Gaudry 1861; Howell and Petter 1985; Werdelin et al. 1994). An adult partial hemimandible of this genus was found in 1920 in the Iberian locality of Sant Miquel de Toudell (SMT; formerly spelled 'Taudell'), in the area of Viladecavalls (Vallès-Penedès Basin; MN10, late Vallesian, late Miocene). This specimen was initially attributed to *H. graeca* by Bataller (1921; see also Villalta Comella and Crusafont Pairó 1941, 1943), but later designated as the holotype of another species of the genus, *Hyaenictis almerai* Villalta Comella and Crusafont Pairó, 1948. According to Villalta Comella and Crusafont Pairó (1948), *H. almerai* resembles *H. graeca* in the retention of m2 and the lack of m1 metaconid, but differs from it in several other features (shorter and stouter mandibular corpus, shorter diastema, and apparent lack of p1).

Solounias (1981) synonymized *Adcrocuta* Kretzoi, 1938 with *Hyaenictis* based on similarities in the m1 and the lack of additional remains of *H. graeca* among the vast hyaenid sample from Pikermi. However, this taxonomic opinion was discounted by subsequent authors (Howell and Petter 1985; Werdelin and Solounias 1990, 1991). Werdelin and Solounias (1991) noted that only a few similarities justified the attribution of the hyaenid from Sant Miquel de Toudell to *Hyaenictis*, but tentatively retained this generic assignment, in spite of recognizing that the erection of a new genus might eventually be justified. Later, *Hyaenictis hendeyi* Werdelin, Turner & Solounias, 1994 was erected based on early Pliocene (ca. 5 Ma) material from Langebaanweg in South Africa, previously attributed to *Euryboas* sp. (Hendey 1976, 1978). Some additional middle Miocene to early Pliocene hyaenid remains from elsewhere in Africa have been subsequently attributed to *Hyaenictis*. These specimens are mostly isolated teeth (Ginsburg 1977; Turner 1988; Morales et al. 2005; Werdelin and Peigné 2010). The exception is *Hyaenictis wehaietu* Haile-Selassie & Howell, 2009, from the late Miocene and early Pliocene of the Middle Awash in Ethiopia (5.8–5.2 Ma), which is represented by more abundant material (Haile-Selassie and Howell 2009). Besides its smaller size, this species differs from *H. graeca* by the lack of p1 and m2, and the presence of a well-developed m1 metaconid (Haile-Selassie and Howell 2009). Given the lack of these diagnostic features of the type species of the genus, the inclusion of this species in *Hyaenictis* is questionable (being here referred to as *?Hyaenictis wehaietu*).

Hyaenictis has been classically included in the cursorial hyaenid ecomorphotype (Werdelin and Solounias 1996; Turner et al. 2008), given the lack of the typical durophagous adaptations of *Adcrocuta*. In this paper, we describe a new skull with associated mandible and atlas from the late Vallesian of the Vallès-Penedès Basin that, based on the retention of p1 and m2, as well as the reduced m1 metaconid, is attributed to *Hyaenictis*. This skull, which represents the most complete specimen of *Hyaenictis* known so far from the European Miocene, does not fit well with previously known species of this genus, from which it differs in several morphological and metric features that more closely resemble those of the bone-cracking hyaena *Adcrocuta*. The taxonomic assignment of the described specimen is discussed here, together with its implications for the evolution of durophagous adaptations in hyaenids during the late Miocene.

Age and Geological Background

The described material comes from sector ROS-D within the set of paleontological sites of Ronda Oest Sabadell (ROS), which were discovered between 2009 and 2011 during paleontological surveillance of the construction of a road near the city of Sabadell (Catalonia, Spain; Madurell-Malapeira et al. 2014). From a geological viewpoint, ROS is located within the Vallès-Penedès Basin (Fig. 1), a small and elongated half-gra-

ben oriented parallel to the Mediterranean coastline in the NE Iberian Peninsula and bounded by the Catalan (Prelittoral and Littoral) Coastal Ranges (Cabrera et al. 2004; de Gibert and Casanovas-Vilar 2011). This basin has been intensively sampled for many decades, resulting in a particularly well-known late Aragonian and Vallesian record of terrestrial mammals (Casanovas-Vilar et al. 2011, 2015). Based on biostratigraphic data,
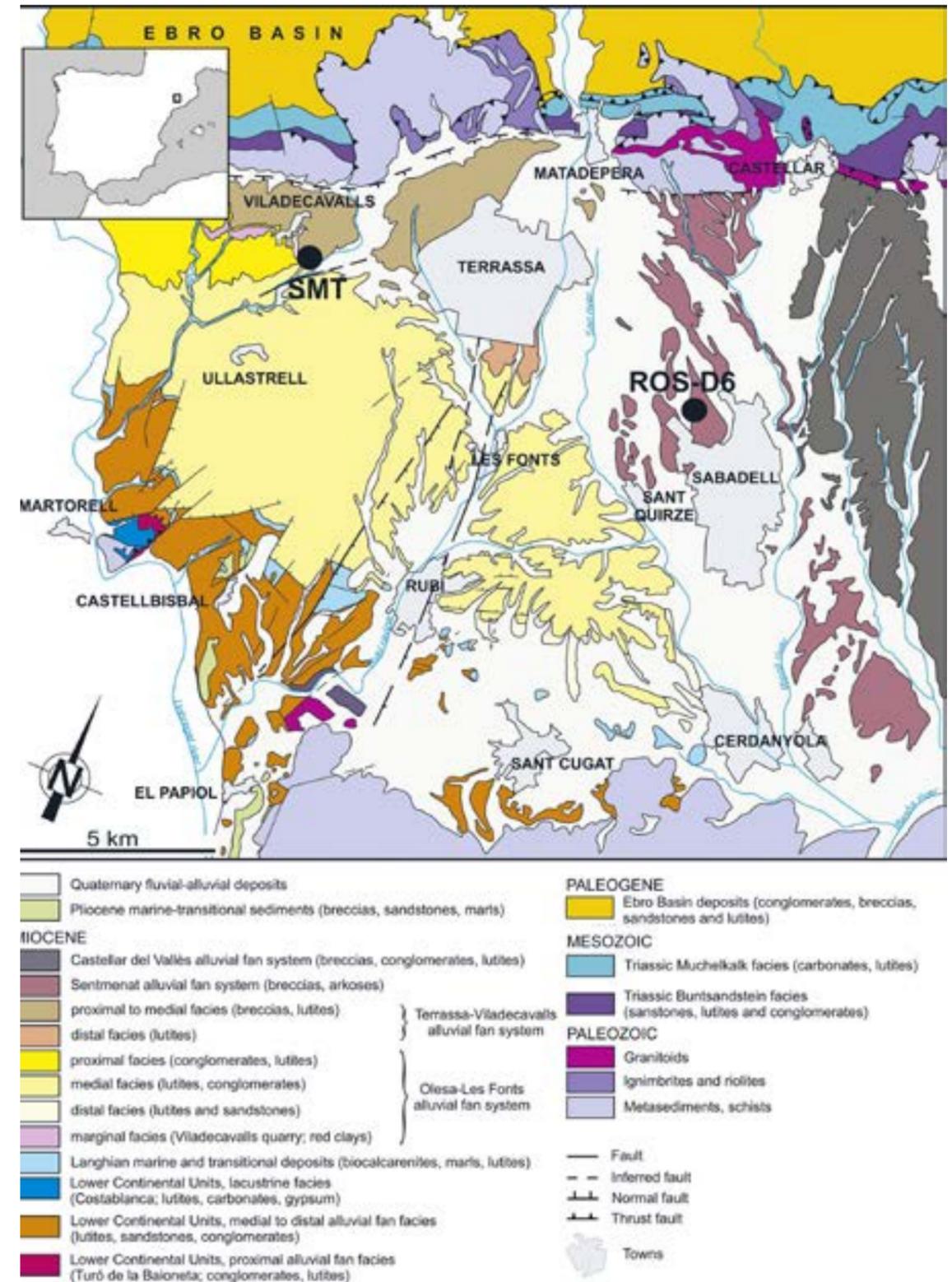

Fig. 1 Detailed geological map of the western (Vallès) sector of the Vallès-Penedès Basin (within the Iberian Peninsula), showing the position of the referred late Vallesian mammal sites (modified after Casanovas-Vilar *et al.*, 2015). Locality acronyms: ROS-D, Ronda Oest Sabadell Sector D; SMT, Sant Miquel de Toudell.

ROS localities cover a time span ranging from the late Vallesian (MN10) to the early Turolian (MN11; Madurell-Malapeira et al. 2014). The remains described here were found stratigraphically 1.5 m below locality ROS-D6, which on the basis of micromammals is correlated to the upper part of MN10 (Madurell-Malapeira et al. 2014; Casanovas-Vilar et al. 2015). More precisely, ROS-D6 is tentatively correlated to the *Rotundomys bressanus* local subzone of the Vallès-Penedès Basin (Casanovas-Vilar et al. 2015), with an estimated age of ca. 9.4–9.1 Ma, although alternatively it might, like SMT, belong to the older *Rotundomys montisrotundi* local subzone, which has an estimated age of 9.6–9.4 Ma (Casanovas-Vilar et al. 2015).

Materials and Methods

Studied Material and Comparative Sample

The hyaenid remains described in this paper are housed in the ICP. The examined fossil comparative sample includes the holotype (MGB16051) of *Hyaenictis almerai* from SMT (MN10), housed in the MCNB; remains of *Adrocuta eximia* Roth and Wagner, 1854 from Torrentet de Traginers (Piera, MN12), housed in the ICP; specimens of *Chasmaporthetes lunensis* (Del Campana, 1914) from La Puebla de Valverde (Teruel, MN17), housed in the MNCN; and topotypic specimens of *Hyaenictis hendeyi* housed in SAM (see institution abbreviations below). Additional data from other Miocene and Pliocene hyaenids included in the comparative sample were taken from the literature (Gaudry 1861; Villalta Comella and Crusafont Pairó 1948; Hendey 1978; Howell and Petter 1985; Qiu 1987; Kurtén and Werdelin 1988; Werdelin 1988, 1999; Koufos 2011; Tseng et al. 2013). They include: *Adcrocuta* (MN10–MN13, Eurasia), including *Adcrocuta eximia*; *Lycyaena* Hensel, 1863 (MN9–MN12, Eurasia and North Africa), including *Lycyaena chaeretis* (Gaudry, 1861), *Lycyaena dubia* Zdansky, 1924, and *Lycyaena crusafonti* Kurtén, 1976; *Chasmaporthetes* (MN12–early Pleistocene, Eurasia, Africa and North America), including *Chasmaporthetes gangsriensis* Tseng, Li and Wang, 2013, *Chasmaporthetes lunensis*, *Chasmaporthetes ossifragus* Hay, 1921, *Chasmaporthetes borissiaki* (Khomenko, 1931), *Chasmaporthetes australis* (Hendey, 1974), and *Chasmaporthetes nitiluda* (Ewer, 1955); *Lycyaenops* Kretzoi, 1938 (MN14–early Pleistocene, Europe and Africa), including *Lycyaenops silberbergi* (Broom in Broom and Schepers, 1946) and *Lycyaenops rhomboideae* Kretzoi, 1938; and *Hyaenictis* (MN10–MN14, Europe and Africa), including *H. graeca*, *H. almerai*, *H. hendeyi* and *?H. wehaietu*. The material of "*Chasmaporthetes*" *bonisi* Koufos, 1987 has been reassigned to *A. eximia* following Werdelin and Solounias (1991). The genera included in the comparative sample have been selected based on their age, geographic distribution and morphological similarities with the ROS-D specimen.

Tooth Enamel Microstructure

Enamel microstructure (Hunter-Shreger Bands, HSB; Stefen 1997; Ferretti 1999, 2007) in the cheek teeth of the described material was described and photographed with a Leica MZ-16 light stereomicroscope with a Leica IC 3D digital camera attached. The resulting images were modified with the HDR (high dynamic range) toning function in Adobe Photoshop CS6 to enhance the contrast of the HSB.

Morphometric Comparisons

Craniomandibular and dental measurements of the studied specimens were taken with digital calipers to the nearest 0.1 mm (see measurement abbreviations below). Dental size and proportions were assessed using bivariate plots of buccolingual breadth (W) vs. mesiodistal length (L) for the lower cheek teeth (p2, p3, p4 and m1). A breadth/length index (BLI) for these teeth was computed as BLI = log (B/L), to assess differences in dental shape among the studied genera. These differences were inspected by means of boxplots and analysis of variance (ANOVA), including pairwise post-hoc comparisons (Bonferroni method), using IBM SPSS Statistics v. 19. A principal component analysis (PCA) based on the BLI of individuals preserving the p2–m1 series was performed with PAST v. 2.15 (Hammer et al. 2001). Note that the PCA (like ANOVA) was run on log-transformed data, so as to minimize the statistical problems associated with the usually non-normal distribution of ratios (although PCA makes no assumptions in this regard, it usually yields better results with normally distributed data; Hammer and Harper 2006). No statistical analyses were undertaken on the basis of the upper dentition, because of the scarcity of sufficiently complete cranial remains for most of the taxa included in the comparative sample (including *Hyaenictis* spp.). *?Hyaenictis wehaietu* was not included in morphometric comparisons (boxplots, ANOVA and PCA), since as noted above this species is unlike to belong to genus *Hyaenictis*.

Abbreviations

Institutional Abbreviations. ICP: Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona (Spain); IPS: acronym of the collections of the ICP (formerly Institut de Paleontologia de Sabadell). MCNB, Museu de Ciències Naturals de Barcelona (Spain); MGB: acronym of the geology collections of the MCNB (including the former Museu de Geologia de Barcelona); MNCN: Museo Nacional de Ciencias Naturales–CSIC, Madrid (Spain); MNHN: Muséum National d'Histoire Naturelle, Paris (France); SAM: Iziko South African Museum, Cape Town (South Africa).

Locality Abbreviations. PIK: Pikermi; PQ-L: Pelletal Phosphorite and Quartzose Sand Members undifferentiated, Varswater Formation, "E" Quarry, Langebaanweg; ROS: Ronda Oest Sabadell; SMT: San Miquel de Toudell.

Measurement Abbreviations. B: buccolingual breadth; BLI: breadth/length index; FA: frontal-acrocranion length; LP1–P4: length of the upper premolar series; PA: prosthion-acrocranion length; Hoc: occipital height; PB: prosthion-basion length; L: mesiodistal length; LP4m: mesiodistal length of P4 metastyle; LP4pa: mesiodistal length of fourth upper premolar paracone; LP4pas: mesiodistal length of fourth upper premolar parastyle; Ltm1: mesiodistal length of the m1 talonid; PN: prosthion-nasion length; PF: prosthion-frontal length; PS, prosthion-synsphenion length; PST: prosthion-staphylion length; SB: synsphenion-basion length; SKL: prosthion-occipital condyles length; WC: palatal width at C1; WiP4: palatal width at P4; Woc: width of occipital condyles.

Systematic Paleontology

Order **CARNIVORA** Bowdich, 1821

Suborder **FELIFORMIA** Kretzoi, 1945

Family **HYAENIDAE** Gray, 1821

Subfamily **HYAENINAE** Gray, 1821

Genus *HYAENICTIS* Gaudry, 1861

Type species: Hyaenictis graeca Gaudry, 1861.

Other included species: Hyaenictis almerai Villalta Comella and Crusafont Pairó, 1948; *Hyaenictis hendeyi* Werdelin, Turner and Solounias, 1994; *?Hyaenictis wehaietu* Haile-Selassie and Howell, 2009.

Hyaenictis aff. *almerai*[1] Villalta Comella and Crusafont Pairó, 1948

(Figs. 2, 3, 4A–C)

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[1] For the use of open nomenclature we follow Bengtson (1988).

Holotype: MGB1605, partial right hemimandible from SMT (MN10, Spain).

Original description: "Relatively evolved *Hyaenictis*, having lost the lower P1, diastema very reduced; relatively robust mandible; shortened face, and canine in a more vertical position. Lower M1 without metaconid. Lower P2 long, slightly pointed and with a developed anterior cusp" (Villalta Comella and Crusafont Pairó, 1948, p. 117, our translation from the Spanish original).

Tentatively referred material: IPS62078 from ROS-D, including: a partial cranium with left and right C1-M1; associated left and right hemimandibles with canines, left p3–m1, and right p2–m1 and m2; and associated atlas. See measurements in Table 1.

Description

Cranium The cranium preserves most of the palate, the muzzle and the left side of the neurocranium (including the zygomatic arch), as well as the occipital condyles and the pterygoids (Fig. 2A–C). Most of the basicranium (basisphenoid and basioccipital) and the right side of the braincase (sphenoid complex, caudal end of the frontal, temporal and parietal) are missing (Fig. 2A–C). The nasals are triangular, long and narrow, extending posteriorly until close to the level of the postorbital processes (Fig. 2C). The infraorbital foramen is oval and in lateral view located at the level of P3 (Fig. 2B). The zygomaticomaxillary suture is just above the P4, running from the anterior end of the orbit towards the distal root of P4 (Fig. 2B). The premaxillary-maxillary suture runs from the I3 root towards the mid-point of the nasals without reaching the frontal (Fig. 2C). The nasal fossa is wide and oval. The palate is wide at the level of P4 and narrows mesialwards to the canines (Fig. 2A). There is a slight postcanine constriction (Fig. 2C). The transverse palatine suture reaches the distal end of M1 (Fig. 2A). The palatine fissures are present at the level of the canine and are oval in shape (Fig. 2A). On the basicranium, the retroarticular processes are transversely wide and robust (Fig. 2A).

Mandible The two hemimandibles are almost complete, except for a small fragment of the right coronoid process and the distal-most part of the left angular process (Fig. 2I–N). The corpus is straight and slender, and has a single mental foramen below the p2 at about corpus midheight (Fig. 2I,L). The ramus is low, with a rounded coronoid process slightly expanded backwards and a condylar process that is located at about the same level as the occlusal plane (Fig. 2I,J,L,M). The masseteric fossa is deep and extends anteriorly until the level of m2 (Fig. 2I,L). The angular process is well developed and protrudes posteriorly beyond the condylar process (Fig. 2L,M).

Dentition The dentition is quite worn, with dentine exposure at the tips of the main and most of the accessory cusps. The upper dentition is more complete on the left side, where the I3–M1 series is preserved, whereas on the right side the canine is broken, the P1 is missing, and the P4 and M1 are detached (Fig. 2A,D–F,R–T). The two I3s and the left canine are very worn. The P1 is buccolingually wider than mesiodistally long and displays a distal cingulum. The P2 has a blunt crest running from the protocone to the mesiolingual margin and a small distal accessory cusp just mesial to the distal cingulid. The P3 has two accessory cusps: the mesial one is rather small, located very close to the protocone and on the lingual half of the crown; the distal accessory cusp is broad but low, and located just mesial to the small cingulum present on the distal crown margin. The two P4 (Fig. 2A,D-F) are quite worn, so that only a few occlusal characters can be observed, including the presence of a well-developed protocone and of a parastyle that is mesiodistally shorter than the paracone. The M1 is present but similarly worn, and displays a subrectangular occlusal contour with no visible cusp features (Fig. 2A, R–T).

Most of the lower dentition is preserved, except for the incisors, the p1s, and the left p2 and m2 (Fig 2I–Q). The lower canines, like their upper counterparts, are quite worn. The diastema between the canine and p2 is moderately short and displays, closer to the p2, an alveolus for a single-rooted p1. All the remaining premolars are longer than wide but moderately stout, with a subrectangular (rather than oval) occlusal outline. The p2 has a small distal accessory cusp, which is separated from the protoconid and from the distal cingulid by small
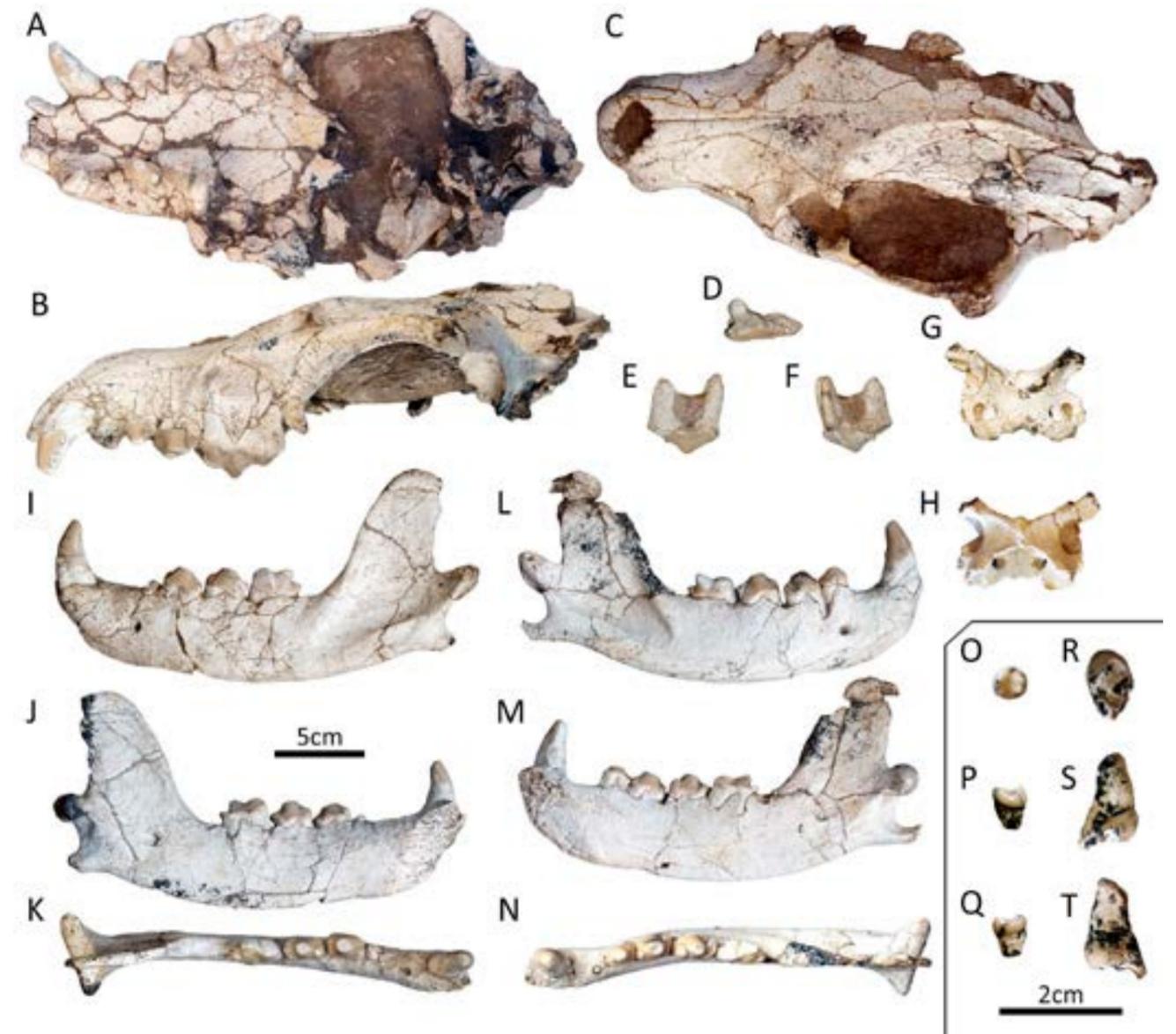

Fig. 2 *Hyaenictis* aff. *almerai* IPS62078 from ROS-D. **a–c**, cranium, in ventral (**a**), left lateral (**b**) and dorsal (**c**) views. **d–f**, right P4, in occlusal (**d**), labial (**e**) and lingual (**f**) views. **g–h**, atlas, in dorsal (**g**) and ventral (**h**) views. **i–k**, left hemimandible, in labial (**i**), lingual (**j**) and occlusal (**k**) views. **l–n**, right hemimandible, in labial (**l**), lingual (**m**) and occlusal (**n**) views. **o–q**, right m2 in occlusal (**o**), lingual (**p**) and labial (**q**) views. **r–t**, right M1 in occlusal (**r**), distal (**s**) and mesial (**t**) views. **o–t** are depicted at a different scale.

notches. The p3 and p4 have better developed protoconids and two accessory cusps, the mesial one located towards the lingual side of the crown, and the distal one situated on the marked distal cingulid (more buccally on p3 and more centrally on p4). The m1 paraconid and protoconid are too worn to observe their morphology, but it can be ascertained that the metaconid, located distolingually from the protoconid, is only slightly developed and not completely isolated from the former cusp. The m1 talonid is much lower and shorter than the trigonid, and displays three main cuspids, of which the hypoconid is larger than the entoconid and hypoconulid. The m2 (Fig. 2O-Q) has a round occlusal outline, a single trigonid cuspid (the mesially located paraconid) and two smaller talonid cuspids (entoconid and hypoconid) that are more distally situated.

With regard to tooth enamel microstructure, HSB are observable in all the lower and upper cheek teeth (at least on the bottom crown portion, and also, when preserved, in the middle of the crown wall, since the apical parts of the crowns are in all instances worn away). These bands clearly show a zig-zag pattern (Fig. 3) like that in extant bone-cracking hyaenids (Ferretti 1999; Tseng 2011, 2012) on the middle crown portions and, to some extent, on their bottom portion (although closer to the cervix the HSB pattern progressively becomes acute-angled undulating).
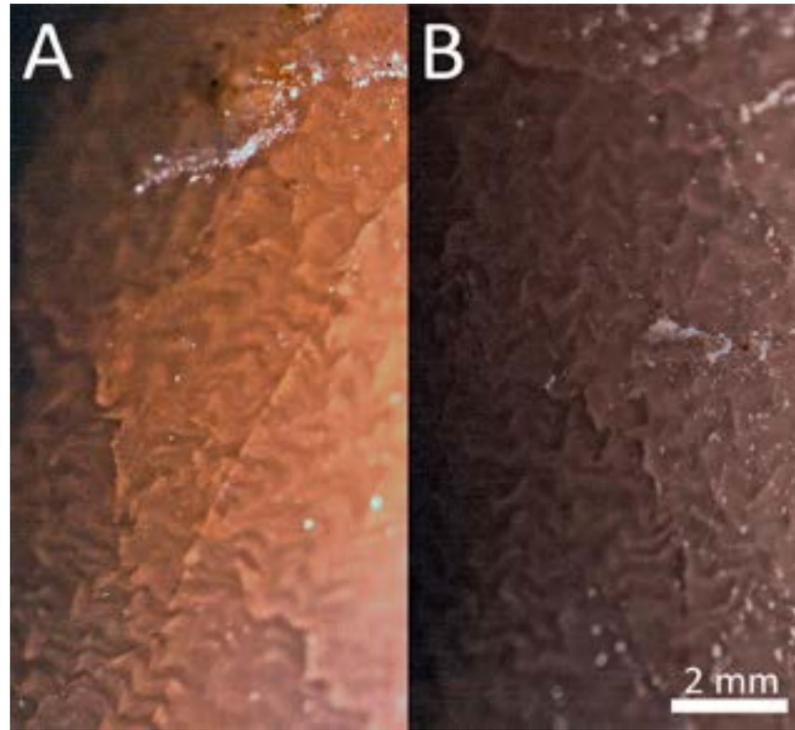
Fig. 3 Photographs of the HSB pattern on the outer enamel surface of the bottom crown portion of P3 (**a**) and the middle crown portion of p3 (**b**) in *Hyaenictis* aff. *almerai* IPS62078 from ROS-D. Apical is towards the top of the image. Note that closer to the crown base of the P3 (**a**), the zig-zag pattern progressively becomes acute-angled undulating.

Atlas The atlas (Fig. 2G, H) is nearly complete, with only the wings broken. The vertebral arch is slender and medially displays a small craniodorsal protuberance. The lateral vertebral foramen and the transverse foramen are distinct (close to each other but not confluent), being anteriorly situated just below the alar notch, which is not very marked. The vertebral body is quite narrow and has a pointed protuberance on its caudal margin. The cranial articular fovea is wide and slightly expanded cranially on its dorsal portion.

Results

Morphological Comparisons with other Miocene Hyaenids

Comparisons with other hyaenid genera

Overall, the dentition of IPS62078 is more slender (it displays relatively narrower premolars) than *Adcrocuta eximia* (see Werdelin and Solounias 1990, 1991; Turner et al. 2008). IPS62078 further differs from *A. eximia* in the larger P4 protocone, the presence of a p3 mesial accessory cusp, the longer and tricuspid m1 talonid (instead of bicuspid, as *Adcrocuta* lacks the hypoconulid), and the retention of m2.

The dentition of the described species also does not resemble that of *Chasmaporthetes*, which is characterized by more slender and trenchant premolars with well-developed distal accessory cusps, as well as several more derived features that are absent in *Hyaenictis* spp. (Turner et al. 2008). Thus, IPS62078 differs from *Chasmaporthetes* (see Kurtén and Werdelin 1988; Werdelin and Solounias 1991; Werdelin and Turner 1996; Antón et al. 2006; Tseng et al. 2013) in the presence of p1, the relatively broader cheek teeth, the less developed accessory cusps in the premolars, the mesial and distal accessory cusps of the premolars aligned with the main cusp (instead of lingually tilted), the presence of metaconid (even if vestigial), the tricuspid m1 talonid (*Chasmaporthetes* lacks the hypoconulid and sometimes the hypoconid), and the presence of m2.

Compared to *Lycyaena*, the dentition of IPS62078 is larger, somewhat stouter (i.e., it displays relatively broader cheek teeth), and is further characterized by smaller and more indistinct premolar accessory cusps

(Werdelin 1988; Werdelin and Solounias 1991). The specimen further differs from *Lycyaena* (see Werdelin 1988; Werdelin and Solounias 1991; Werdelin and Peigné 2010) in the occlusal morphology of the m1 (with a reduced instead of well-developed metaconid, and a shorter talonid with less developed cuspids), the presence of m2, and the deeper and stouter mandibular corpus.

In terms of mandibular robusticity and relative breadth of the lower premolars, IPS62078 resembles *Lycyaenops*, in spite of numerous differences in the occlusal morphology of the lower dentition (see Kretzoi 1938; Werdelin and Solounias 1991; Werdelin 1999; Werdelin and Peigné 2010). Thus, the described specimen mainly differs from *Lycyaenops* in the presence of p1, the better developed p3 accessory cusps, the less developed p4 distal accessory cusp, the presence of an m1 metaconid (even if reduced), and the longer and tricuspid (instead of bicuspid) m1 talonid.

With regard to tooth enamel microstructure, although the top portion of the cheek teeth crowns in IPS62078 are worn away, their preserved middle and bottom portions allow one to ascertain that, on the outer enamel surface, the HSB clearly display a zig-zag pattern (except closest to the cervix; Fig. 3). In this regard, the condition of the described specimen is most similar to *Chasmaporthetes*, in which the zig-zag pattern (unlike in extant and extinct fully-developed bone-cracking hyaenids, such as *Adcrocuta*) generally does not reach the base of the crown (Tseng 2012). In contrast, the condition of IPS62078 is much more similar to bone-cracking taxa than to that displayed by *Lycyaena*, which does not display a zig-zag pattern of HSB at any crown level (Tseng 2012).

Comparisons with other Hyaenictis species

The dentition of IPS62078 more closely resembles that of other species of *Hyaenictis*, except ?*H. wehaietu* from the late Miocene and early Pliocene of Ethiopia, which is smaller, lacks the p1 and m2, and further displays a well-developed and isolated m1 metaconid (Haile-Selassie and Howell 2009). In particular, IPS62078 resembles the other three species of *Hyaenictis* in the possession of a long and slender mandible with m2, the weak development of the mesial accessory cusp in the lower premolars, the short m1 without a well-developed metaconid, and the presence of more than a single cuspid in the m1 talonid (Werdelin et al. 1994).

Compared to the type species of the genus, *H. graeca* (Fig. 4J, K; Gaudry 1861; Howell and Petter 1985; Werdelin and Solounias 1990, 1991; Werdelin et al. 1994), IPS62078 (Fig. 4A–C) displays a similarly robust mandibular corpus that is only slightly curved on its inferior margin behind the m1 (although comparisons are hindered by the juvenile status of the holotype mandible of *H. graeca*). Both specimens also resemble one another in the retention of p1 and m2, as well as in the m1 occlusal morphology (characterized by a greatly reduced metaconid and a tricuspid talonid with a large hypoconid). However, IPS62078 differs from *H. graeca* in several features, namely the relatively broader lower premolars, the lower p2 protocone, the more restricted and simpler distal cingulids in the premolars, the p3 mesial accessory cusp p3 aligned with the protoconid (instead of lingually tilted), and the smaller distal accessory cusp but larger distal crest in the p4.

Specimen IPS62078 differs even more clearly from *H. hendeyi* (Fig. 4D–F) from the earliest Pliocene of South Africa (Hendey 1974, 1978; Werdelin et al. 1994; Werdelin and Peigné 2010) in the relatively broader lower cheek teeth with a subrectangular (instead of elliptic) occlusal outline, the retention of the p1, the p2 with a lower protoconid and a smaller and more indistinct distal accessory cusp, and the tricuspid m1 talonid (instead of bicuspid, as *H. hendeyi* lacks the hypoconulid).

Differences are less marked when IPS62078 is compared with the holotype of *H. almerai* (Fig. 4G–I), from the similarly-aged Vallès-Penedès locality of SMT (Villalta Comella and Crusafont Pairó 1948; Werdelin and Solounias 1991; Werdelin et al. 1994), whose lower cheek teeth are somewhat more elongated (relatively narrower), but which nevertheless display a less oval occlusal outline than in *H. graeca* and *H. hendeyi* (thus more closely resembling IPS62078). Although the latter specimen resembles *H. almerai* (as well as *H. graeca* and *H. hendeyi*) in the retention of m2, it differs from *H. almerai* (and more closely resembles *H. graeca*) in the longer mandibular diastema and the presence of a p1 alveolus. Given the very small available sample sizes for European *Hyaenictis*, it cannot be discounted that the presence/absence of p1 was variable, as in some
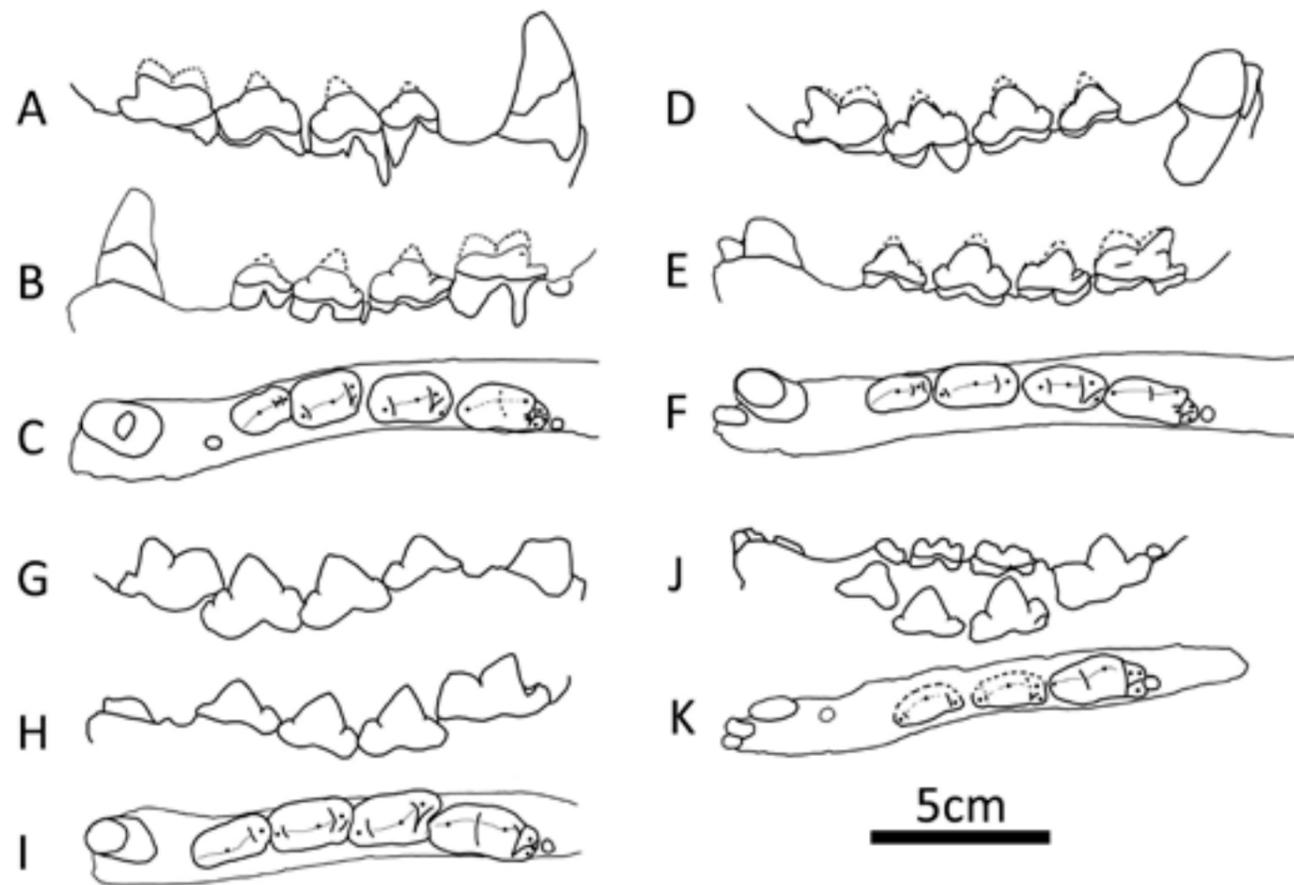
Fig. 4 Schematic drawings of the right postcanine toothrow of the ROS-D specimen and three species of *Hyaenictis*. **a–c**, *Hyaenictis* aff. *almerai* (IPS62070), in labial (**a**), lingual (**b**) and occlusal (**c**) views. **d–f**, *Hyaenictis hendeyi* (based on PQ-L21792 and the holotype PQ-L21000), in labial (**d**), lingual (**e**) and occlusal (**f**) views. **g–i**, *Hyaenictis almerai* (holotype, MGB16051), in labial (**g**), lingual (**h**) and occlusal (**i**) views. **j–k**, *Hyaenictis graeca* (holotype, MNHN-PIK-3002), in lingual (**j**) and occlusal (**k**) views. In the occlusal views, crests and cingulids are represented by thin lines, cuspids are denoted by black dots, and discontinuous lines represent inferred morphology (covered, missing and worn areas).

other hyaenids (e.g., *Lycyaena*; Werdelin 1988; Werdelin and Solounias 1991; Werdelin and Peigné 2010). In addition, in *H. hendeyi* the p1 is absent (Werdelin et al. 1994) suggesting that the presence of this tooth is variable in the genus as a whole. Nevertheless, IPS62078 specimen further differs from *H. almerai* in several other occlusal features, including the smaller distal accessory cusp surrounded by a low distal cingulid in the p2, the mesial accessory cusps of the p3 and p4 aligned with the protoconid (instead of lingually tilted), and the more developed distal cingulid in the p4.

Morphometric Comparisons

Comparisons of dental size for the lower cheek teeth are reported by means of bivariate plots of buccolingual breadth (B) vs. mesiodistal length (L) in Fig. 5, whereas dental proportions are assessed by means of boxplots (Fig. 6) and ANOVA comparisons of log-transformed breadth/length index (BLI). Among the analyzed genera (*Adcrocuta*, *Chasmaporthetes*, *Lycyaena* and *Hyaenictis* for p2–m1, and *Lycyaenops* for p2–p3), there are significant differences ($p<0.001$) in dental proportions for all the analyzed lower cheek teeth ($F=107.22$ for p2, $F=79.16$ for p3, $F=64.68$ for p4, and $F=6.68$ for m1). Among other differences (see below), the bone-cracking *Adcrocuta* differs from the remaining genera (except for *Lycyaenops*) by displaying in all instances significantly broader premolars, with $p<0.001$ (see also Figs. 5A–C, 6A–C). In the case of the lower carnassial, there are no significant differences between *Hyaenictis* and *Adcrocuta*, which tend to display broader m1 than *Chasmaporthetes* and *Lycyaena* (although differences between *Hyaenictis* and *Chasmaporthetes* are not significant at $p<0.05$; see also Figs. 5D, 6D). The lower carnassial is thus the least useful cheek
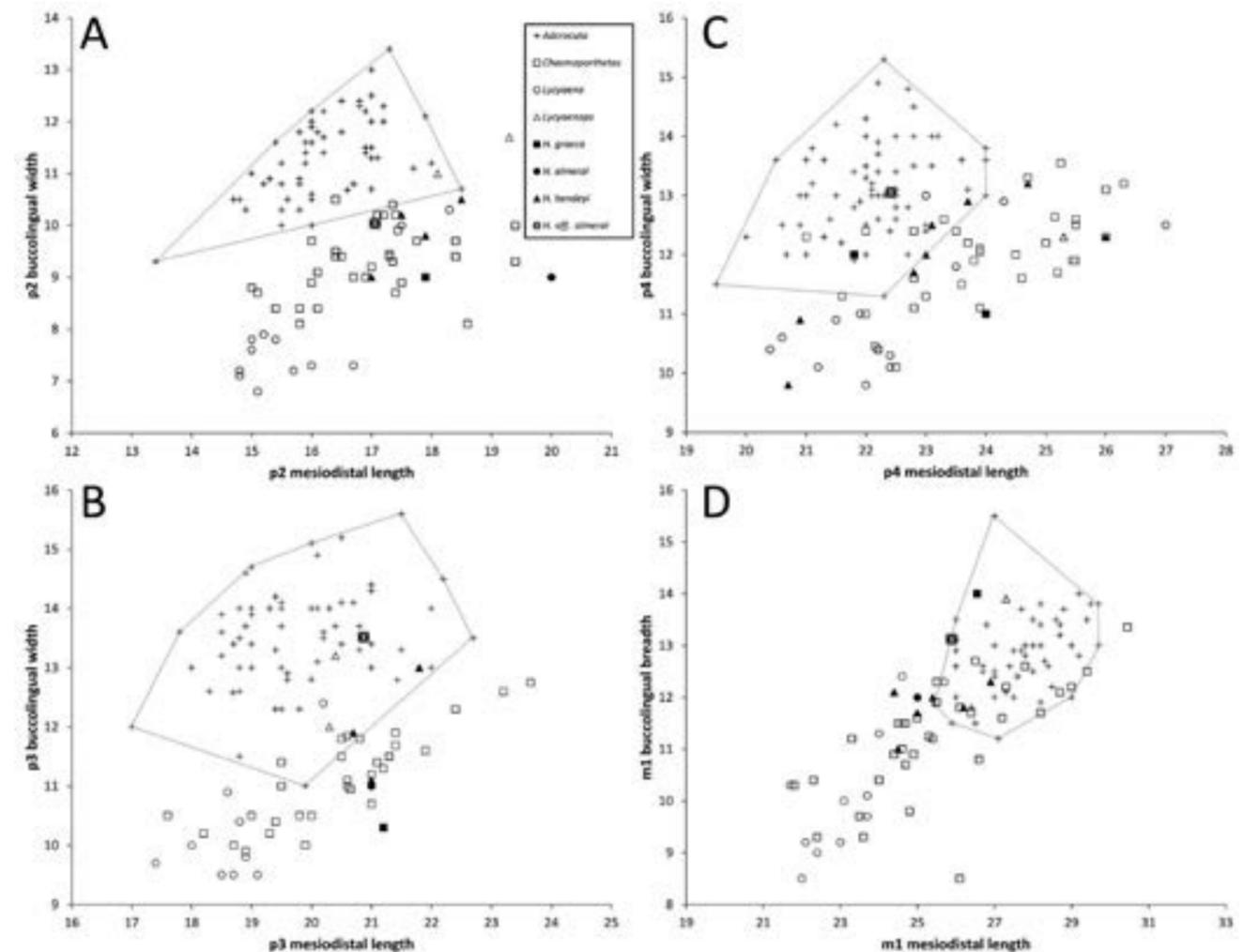

Fig. 5 Bivariate plots of buccolingual breadth vs. mesiodistal length in the cheek teeth of *Hyanictis* aff. *almerai*, compared with those of other selected Miocene hyaenids. **a**, p2. **b**, p3. **c**, p4. **d**, m1. Convex hulls encompass the range of variation in our sample of the bone-cracking *Acrocuta*.
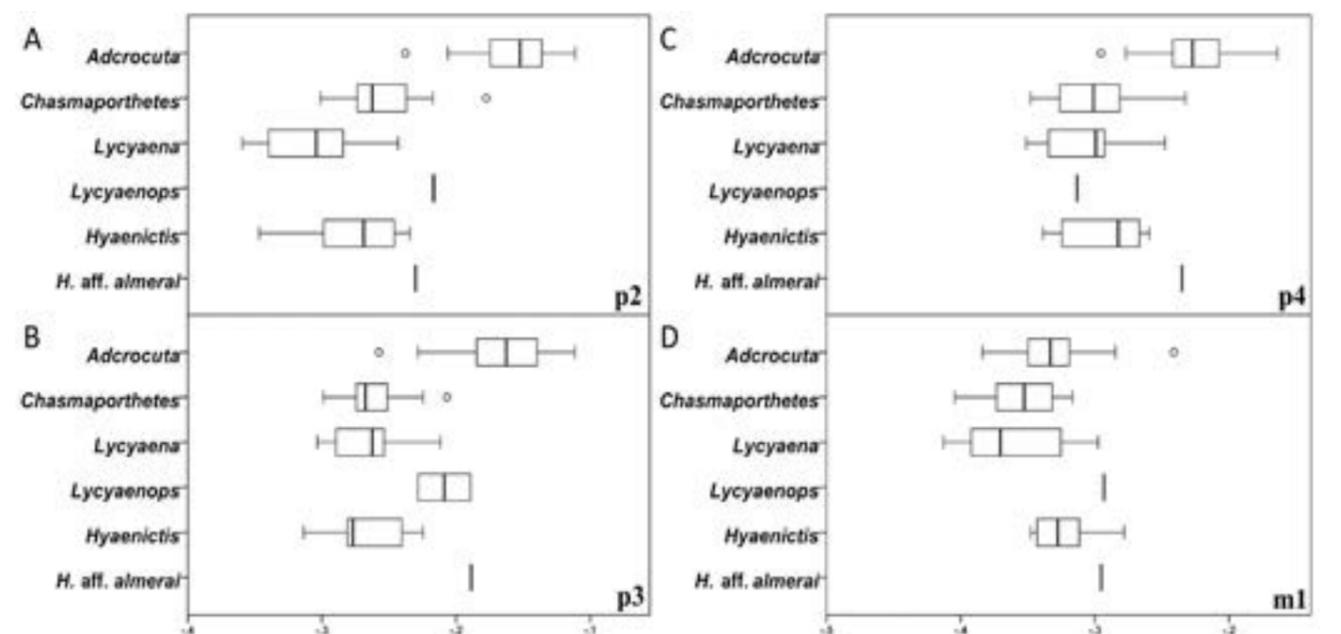

Fig. 6 Boxplots of breadth/length index (BLI) in the cheek teeth of *Hyaenictis* aff. *almerai*, compared with those of other selected Miocene hyaenids. **a**, p2. **b**, p3. **c**, p4. **d**, m1.

IPS62078 falls close to (but outside) the convex hull depicting the variability of *Adcrocuta*, overlapping with the latter in the PC1 and with *Hyaenictis* (which more closely resembles *Chasmaporthetes* and *Lycyaena*) in the PC2. The investigated bone-cracking and cursorial hyaenids mostly differ in PC1, which explains most of the variance (85%) and is largely driven by the buccolingual breadth of the premolars (mostly p2, but also p3 and p4). For this component, IPS62078 overlaps with *Adcrocuta* and falls far from the remaining *Hyaenictis* species and other cursorial hyaenids, as a result of the relatively broader p3 and p4 (which more closely resemble the condition of *Adcrocuta*). The PC2 explains 7% of variance and is mostly positively driven by the breadth of the m1 and, to a lesser extent, the p4. On this axis, which segregates *Hyaenictis* spp. from both the cursorial hyaenids and *Adcrocuta* (with only minimal overlap), IPS62078 only overlaps with the former. Overall, the results of the PCA highlight that IPS62078 clearly differs from the analyzed cursorial hyaenids other than *Hyaenictis*, although it does not comfortably fit into the latter or *Adcrocuta*. Given that only three specimens of European *Hyaenictis* are available, it is not possible to confidently discount that their variability in dental proportions can be accommodated within a single genus. However, IPS62078 is clearly in this regard much more similar to (albeit less extreme than) the bone-cracking condition of *Adcrocuta*.

Discussion

Taxonomic Attribution

The skull with mandible from ROS-D described in this paper (IPS62078) differs from the bone-cracking Miocene hyena *Adcrocuta* in several features, such as the presence of m2, the smaller premolar accessory cusps, the larger P4 protocone, the reduced m1 metaconid, and the tricuspid and longer m1 talonid. The former further differs from cursorial Miocene hyenas, such as *Chasmaporthetes*, *Lycyaena* and *Lycyaenops* in several occlusal features, namely: the presence of m2, the presence of p1 and the tricuspid m1 talonid (only compared
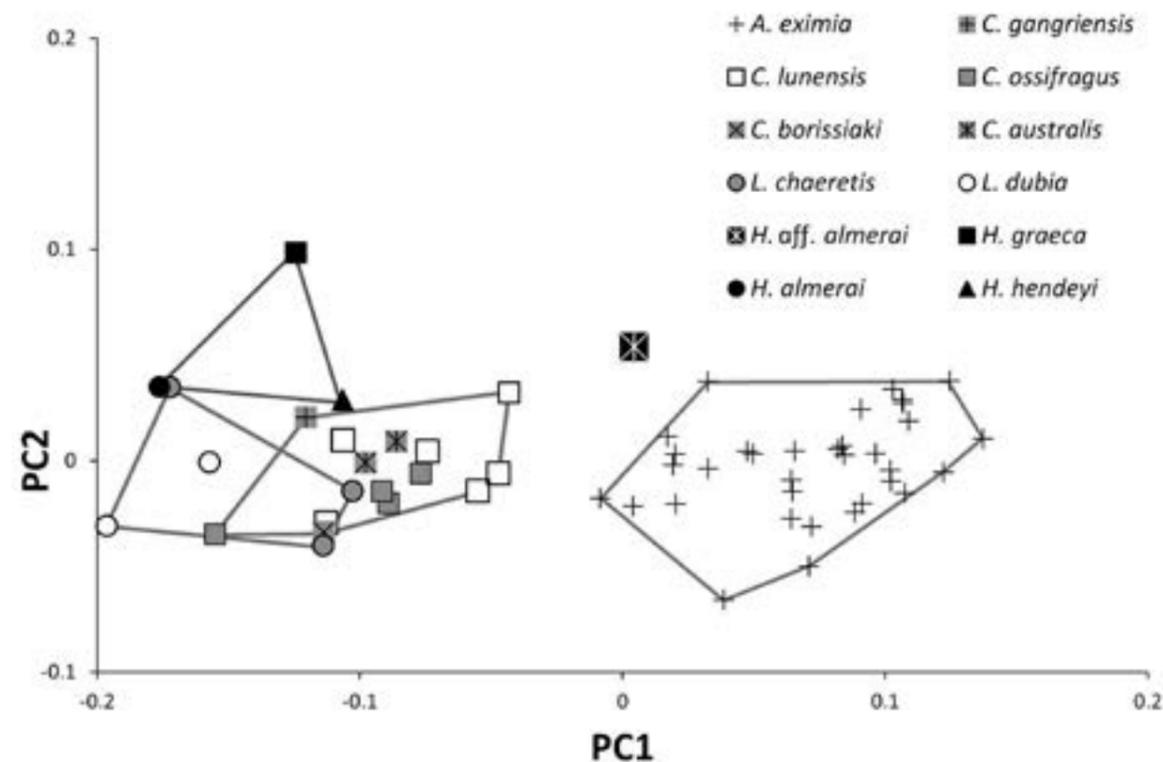
to *Chasmaporthetes* and *Lycyaenops*), the shorter m1 talonid with smaller cuspids (compared to *Lycyaena*), the reduced m1 metaconid (instead of well-developed, as in *Lycyaena*, or entirely absent, as in *Chasmaporthetes* and *Lycyaenops*), the smaller premolar accessory cusps (compared to *Chasmaporthetes* and *Lycyaena*, and to *Lycyaenops* in the case of the p4), and the lingually placed premolar accessory cusps (compared to *Chasmaporthetes*).

In the above-mentioned features and other characters, the described specimen from ROS-D (IPS62078) more closely resembles species of *Hyaenictis* other than ?*H. wehaietu*, and especially the Miocene European species *H. graeca* and *H. almerai*. Similarities include the presence of m2, the weakly developed anterior accessory cusps of the premolars, the P4 metastyle larger than the paracone, and the mesiodistally short m1 (with absent or greatly reduced metaconid, and a bicuspid or tricuspid talonid). In the retention of p1, IPS62078 more closely resembles *H. graeca*, although we do not consider this feature to be taxonomically relevant, since the small available samples preclude to ascertain whether this feature might have been variable in European *Hyaenictis*. In fact, the described species does not comfortably fit into any of these species, from which it differs in the stouter (relatively broader) lower premolars (especially p3 and p4), resulting in dental proportions that are intermediate between those of previously known *Hyaenictis* (plus other cursorial hyaenids such as *Chasmaportethes*) and those of the bone-cracking *Adcrocuta*. IPS62078 further differs from other species of *Hyaenictis* (especially *H. graeca* and *H. hendeyi*) in some details of dental morphology, such as the more rectangular (less elliptical) occlusal outline of the premolars, the presence of a distal cingulid (behind the distal accessory cusp) in p2, and the lingually tilted mesial accessory cusps of the premolars (instead of aligned with the protoconid).

The above-mentioned differences preclude attribution of the described specimen to any of the previously known species of *Hyaenictis*. However, given that only a single individual is available from ROS-D and that the samples for both *H. graeca* and *H. almerai* are also very small, the possibility cannot be conclusively discounted that the above-mentioned differences in dental proportions and minor occlusal details merely reflect intraspecific variation. Specimen IPS62078 from ROS-D and the holotype of *H. almerai* have a similar geographic provenance and are roughly coeval (the former is no more than 0.5 million years younger, probably less). Taken all this evidence together, we choose to attribute IPS62078 to *Hyaenictis* aff. *almerai*. This assignment recognizes the closer morphological similarities with *H. almerai* and further takes into account the similar and age and geographical provenance, while at the same time it does not discount the possibility that IPS62078 represents a previously unknown species. Additional specimens from the late Miocene of the Vallès-Penedès Basin and elsewhere would be required to further ascertain the taxonomic allocation of European specimens currently attributed to *Hyaenictis* spp.

Implications for Feeding Behavior

European *Hyaenictis* have generally been included in the hyaenid ecomorphotype 4 (cursorial meat- and bone-eating hyenas, including among others *Chasmaporthetes* and *Lycyaena*), instead of ecomorphotype 5 (transitional bone-cracking hyenas, like *Belbus* Werdelin and Solounias, 1991 and *Metahyaena* Viranta and Werdelin, 2003) or 6 (fully-developed bone-cracking hyenas such as *Adcrocuta*; Werdelin 1996; Werdelin and Solounias 1996; Turner et al. 2008). However, some previous studies have favored some degree of durophagy in cursorial Miocene hyaenids such as *Chasmaporthetes*, in spite of noting their lesser bone-cracking abilities compared to fully developed bone-crackers (Kurtén and Werdelin 1988; Werdelin et al. 1994; Ferretti 1999; Antón et al. 2006). This was further confirmed by a finite elements analysis of the skull of *Chasmaporthetes* (Tseng et al. 2011), according to which this taxon would have been able to the resist the masticatory stresses generated by a bone-cracking diet (although less efficiently than *Crocuta*). In agreement with this, Tseng (2011, 2012) further showed that *Chasmaporthetes* displays a zig-zap pattern of HSB on the outer enamel surface of at least the top and middle crown portions of the premolars, and even on the bottom portion of p4, as is characteristic of all the cheek teeth of extant durophagous hyaenids and some extinct bone-cracking hyaenas (such as *Adcrocuta*, *Pliocrocuta* Kretzoi, 1938 and *Pachycrocuta* Kretzoi, 1938; Stefen 1997; Ferretti 1999, 2007; Stefen 1999; Stefen and Rensberger 1999; Tseng 2011, 2012; Vinuesa et al. 2014). While enamel microstructure is quite plastic from an evolutionary perspective (Tseng 2012), morphological changes in

Fig. 7 Bivariate plot of the two first axes (PC2 vs. PC1) of the principal components analysis based on breadth/length index of the lower cheek teeth of *Hyaenictis* aff. *almerai*, compared with those of other selected Miocene hyaenids. The variability of each genus is denoted by convex hulls. Discontinuous lines denote questionable genus ascription.

Legend:
+ A. eximia
☒ C. gangriensis
□ C. lunensis
▨ C. ossifragus
✶ C. borissiaki
✶ C. australis
◉ L. chaeretis
○ L. dubia
⊠ H. aff. almerai
■ H. graeca
● H. almerai
▲ H. hendeyi

craniodental features most clearly evidence that some Miocene cursorial hyaenids such as *Chasmaporthetes* were, to some extent, already adapted to (albeit not specialized for) bone-cracking (Tseng et al. 2011). Based on the development of the zig-zag pattern of the HSB of IPS62078, *Hyaenictis* aff. *almerai* would have been at least as durophagous as *Chasmaporthetes*, although less so than *Adcrocuta*, which is entirely comparable to extant bone-cracking hyaenids and in some respects more derived than they are.

Furthermore, the premolar proportions of *Hyaenictis* aff. *almerai* from specimen IPS62078 (especially those of p3 and p4) are intermediate between those of *Chasmaporthetes* and previously known *Hyaenictis* spp., on the one hand, and those of *Adcrocuta*, on the other. This is shown not only by the breadth/length proportions of p3 and p4 separately, but also a multivariate analysis that takes into account all the lower cheek teeth (except p1) simultaneously. Our results therefore suggest for IPS62078 from ROS-D a higher commitment to durophagy than in other hyaenids customarily included in ecomorphotype 4 (including other *Hyaenictis*), thus being best qualified as a transitional bone-cracking hyena (ecomorphotype 5). This is further supported by other features of the described specimen, such as the deep masseteric fossa and the large insertions for the pterygoids, which are shown (although to a greater extent) by extant bone-cracking hyaenas as well as *Adcrocuta* (Werdelin and Solounias 1991, 1996; Turner et al. 2008). Unfortunately, the small available samples of European *Hyaenictis* preclude discerning whether IPS62078 differs from the latter in displaying greater durophagous adaptations (as it seems), or whether European *Hyaenictis* as a whole were somewhat intermediate between cursorial hyaenids such as *Chasmaporthetes* and fully-developed bone-crackers like *Adcrocuta*. In any case, the presence of some durophagous adaptations in the studied material, coupled with the fully-developed bone-cracking adaptations of the roughly coeval *Adcrocuta eximia* (which is first recorded in the MN10 of Ravin de la Pluie, Greece; Bonis and Koufos 1981; Turner et al. 2008), support the contention that the early evolution of the bone-cracking ecomorphotype (the most common among extant hyaenids) in Europe was not related to competition with canids of the genus *Eucyon*, which did not disperse from America into Eurasia until the Turolian (MN12; Sotnikova and Rook 2010).

Another interesting possibility raised by the present study derives from the fact that the earliest *Hyaenictis* (such as the one described here) and the earliest *Lycyaena* (i.e., *L. crusafonti*) are the most potentially durophagous species of their respective lineages (Kurtén 1976; Werdelin 1988; Werdelin and Solounias 1991; Werdelin et al. 1994). Therefore, it is possible that the earliest members of lineages within the *Chasmaporthetes* clade were more durophagous than later representatives of these lineages. This may imply that some degree of durophagy first evolved earlier than customarily assumed, in some (currently unknown) representative of the hyaenictitheres, and that reduction of durophagy subsequently evolved in parallel along several lineages.

Summary and Conclusions

Here we describe a nearly complete skull with associated mandible and atlas of a medium-sized hyaenid from the late Miocene (MN10) of ROS-D (Vallès-Penedès Basin, NE Iberian Peninsula). Compared to other late Miocene hyaenids from Europe, the described specimen (IPS62078) most closely resembles the European species of *Hyaenictis* in several features, such as the retention of m2 and the reduced m1 metaconid. The described remains represent the most complete specimen recovered so far of European *Hyaenictis*, previously recorded from fragmentary remains attributed to *H. almerai* (MN10 of the same basin) and *H. graeca* (MN12 of Greece). In spite of the similar chronology and geographic provenance to *H. almerai*, specimen IPS62078 from ROS-D is only tentatively assigned to this taxon (*Hyaenictis* aff. *almerai*). This is because the described specimen does not fit well into any of the previously known species of *Hyaenictis*, from which it differs by displaying cheek tooth proportions (in particular, relatively broader premolars) and other occlusal and mandibular features more similar to *Adcrocuta*, the earliest European hyaena with fully developed bone-cracking adaptations. Coupled with tooth enamel microstructure, this indicates a greater degree of durophagy in *H.* aff. *almerai* than previously recognized for *Hyaenictis*, seemingly intermediate between cursorial (ecomorphotype 4) and fully bone-cracking (ecomorphotype 6) hyaenids. This suggests that, during the Vallesian, bone-cracking adaptations evolved in parallel among several Eurasian hyaenid taxa due to selection pressures unrelated to competition with canids, which did not disperse from America into the Old Word until much later.

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	PA	SKL	PB	SB	PS	FA	PN	PF	PST	LP1–P4	Woc	WiP4	WC	Hoc
Skull	287.0	—	—	—	—	148.0	125.9	139.1	141.5	93.1	—	57.9	36.3	—

	LC1	W C1	LP1	W P1	LP2	W P2	LP3	W P3	LP4	W P4	LP4pas	LP4pa	LP4m	L M1	W M1
Cranium (left)	18.8	5.8	8.9	7.0	19.7	11.1	25.7	14.2	37.2	20.5	—	—	—	6.2	10.3
Cranium (right)	—	—	—	—	20.3	11.9	26.0	15.4	37.8	20.9	—	—	—	6.7	10.4

	L c1	W c1	L p1	W p1	L p2	W p2	L p3	W p3	L p4	W p4	L m1	W m1	L tm1	L m2	W m2
Mandible (left)	18.7	13.2	5.3	4.6	—	—	21.23	13.6	22.7	13.3	25.92	13.14	5.12	—	—
Mandible (right)	18.7	13.2	5.3	4.6	17.1	10.0	20.5	13.4	22.3	13.3	25.9	13.1	5.2	5.5	5.8

Table 1 Measurements (in mm) of *Hyaenictis* aff. *almerai* (IPS62078) from ROS-D. For measurement abbreviations, see the Materials and methods.

	PC1	PC2	PC3	PC4
Eigenvalue	0.009281	0.000764	0.000520	0.000367
% variance	84.89	6.99	4.76	3.36
BLI p2 loading	0.651	-0.270	0.708	0.048
BLI p3 loading	0.598	-0.186	-0.649	0.432
BLI p4 loading	0.460	0.462	-0.197	-0.732
BLI m1 loading	0.090	0.824	0.196	0.524

Table 2. Results of the principal components analysis based on breadth/length index (BLI) of the lower cheek teeth (p2 to m1) of *Hyaenictis* aff. *almerai* (IPS62078), compared with individuals of other selected Miocene hyaenid genera (*Hyaenictis*, *Adcrocuta*, *Chasmaporthetes*, and *Lycyaena*). For each principal component (PC), the loadings on each original variable are reported.