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# The giant short-faced hyaena from Dmanisi: taxonomy and palaeobiology

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*KEYWORDS* - Pachycrocuta brevirostris*, Carnivora, Palaeoanthropological site, Eurasia, Africa, Early Pleistocene, late Villafranchian.*

*ABSTRACT - Abundant, complete and well-preserved specimens attributed to several carnivorans were recovered from the Calabrian palaeoanthropological site of Dmanisi, Georgia (ca. 1.8 Ma). Herein, we describe the hyaenid remains unearthed from this locality, comparing them with other similar forms from coeval sites from Eurasia. The main objective of this contribution is to test the possible co-occurrence of two hyaena species in Dmanisi, as has been reported by previous authors. Our analyses show that the whole Dmanisi sample corresponds to a single taxon of large and stout size, the giant short-faced hyaena* Pachycrocuta brevirostris *(Gervais, 1850). Furthermore, we discuss the taphonomic implications of this species in the accumulation of fossil assemblages during the Early Pleistocene in Eurasia and, based on the dental anatomy, the palaeobiology of this hyaenid, suggesting different feeding behaviours for juvenile and adult individuals in the exploitation of fat and meat.*

## INTRODUCTION

The unearthed late Lower Pleistocene fossil record of the palaeoanthropological site of Dmanisi (Mashavera River valley, the Lesser Caucasus, Georgia), dated to 1.85-1.78 Ma (Ferring et al., 2011), attests to one of the best, well-preserved European Lower Pleistocene large mammal assemblages, with abundant and complete skeletal remains. The exceptional significance of the mammal record from this locality has recently been highlighted by the publication of the molecular phylogeny of *Stephanorhinus etruscus* (Falconer, 1868) (Cappellini et al., 2019). The Dmanisi site records the presence of twenty-seven species of large vertebrates: one ostrich, *Pachystruthio dmanisiensis* (Burchak-Abramovich & Vekua, 1990), and twenty-six large mammal taxa, representing a combination of species evolving in Europe during the early-middle Villafranchian, such as the elephant *Mammuthus meridionalis* (Nesti, 1825) and the ursid *Ursus etruscus* Cuvier, 1823. The latter species are found in association with taxa that originated in Asia, such as the bovids *Bison* (*Eobison*) *georgicus* (Burchak-Abramovich & Vekua, 1994) and *Gallogoral meneghinii sickenbergii* Kostopoulos, 1996, the deer *Praemegaceros obscurus* (Azzaroli, 1953), the horse *Equus stenonis* Cocchi, 1867, and the rhinoceros *S. etruscus*, as well carnivores, including *Xenocyon lycaonoides* (Kretzoi, 1938) and *Canis borjgali* Bartolini-Lucenti et al., 2020. The faunal assemblage is finally characterised by the occurrence of taxa with African origin, including *Homo erectus* (Dubois, 1894) or *Megantereon whitei* (Broom, 1937), which dispersed into Europe at the beginning of the late Villafranchian (Martínez-Navarro & Palmqvist, 1995, 1996; Vekua, 1995; Lordkipanidze et al., 2007; Palmqvist et al., 2007; Martínez-Navarro, 2010; Rook & Martínez-Navarro, 2010) (see also tab. 1 in Bartolini-Lucenti et al., 2022a).

Most of the carnivorans characterising the Dmanisi guild (Bartolini-Lucenti et al., 2022b) are putatively effective pursuit or ambush predators; this is especially the case for the five species of felids – *Homotherium latidens* (Owen, 1846), *Megantereon whitei*, *Panthera onca georgica* Hemmer et al., 2010, *Acinonyx pardinensis* (Croizet & Jobert, 1828) and *Lynx issiodorensis* (Croizet & Jobert, 1828) – which are able to cut and eat the soft parts of the carcasses, leaving several skeletal parts of the prey they hunt, which are rich in fat (including the bone marrow content and the brain). This scenario is the same for the large canids, *Xenocyon lycaonoides* and *Canis borjgali*, which are good social hunters (see Bartolini-Lucenti et al., 2021). Conversely, the ursid *U. etruscus* is a hunter but is mainly omnivorous, eating plant food items (fruits, roots, etc.), and fishes, and sometimes operating as a scavenger, but it is not a bone cracker (Medin et al., 2019). The small carnivores are mostly adapted for eating small vertebrate prey or a wide variety of food items. For these reasons, these small carnivorans would not compete with the large carnivores for the large ungulate carcasses. Finally, the

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occurrence in this carnivore guild of the abundant remains of a large bone-cracking hyaenid is notable (Vekua, 1995; Lordkipanidze et al., 2007).

In the past, two different species of hyaena have been listed at Dmanisi (Vekua, 1995; Lordkipanidze et al., 2007), the medium-sized *Pliocrocuta perrieri* (Croizet & Jobert, 1828), reported as *Pachycrocuta perrieri*, and the large-sized and stout hyaena *Pachycrocuta* sp. The attribution of fossil remains to the genus *Pliocrocuta* was based on the dP4 morphology of D1129 (a specimen better attributable to *Pachycrocuta*; see Results section), and on D167, a right maxilla fragment with P3 and the alveolus of P4, not figured at that time, which is in fact not a hyaenid, but rather a large feline (details in Supplementary Online Material [SOM] 1: Fig. S1). The attribution to *Pachycrocuta* was based on a distal humerus (D341), two third metatarsals (one right and one left, respectively D650 and D1024), and a left fifth metatarsal (D603). Since those descriptions, new specimens have been recovered from the site; consequently, we felt the need to clarify the taxonomy of the hyaenid of Dmanisi considering its relevance for the taphonomy of the site (Tappen et al., 2022) and its role in the Dmanisi carnivores guild (Bartolini-Lucenti et al., 2022b). Thus, in this paper, we describe and analyse the new findings in a comparative study within the Eurasian *Pliocrocuta perrieri* and *Pachycrocuta brevirostris* fossil record.

The hyaena species identification at Dmanisi has noteworthy taphonomic implications, since both taxa correspond to bone-cracking hyaenas but with radically different inferred behaviours. On the one hand, and despite the abundance of *Pl. perrieri* in middle Villafranchian European sites (ca. 2.5-2.0 Ma), no significant accumulation made by this species has been documented (e.g., Saint-Vallier [Viret, 1954], Senèze [Argant, 2024; Delson et al., 2024; Fernández-Jalvo et al., 2024], Villarroya [De Villalta-Comella, 1952] or la Puebla de Valverde [Kurtén & Crusafont-Pairó, 1977]). On the other hand, *P. brevirostris* is one of the most frequently recorded carnivoran species of the late Villafranchian and Epivillafranchian Eurasian taphocoenoses. Thanks to its habit of transporting and accumulating carcasses to its dens, this species is considered one of the major causes of site formation in this timespan (e.g., Mazza et al., 2004; Mazza, 2006; Palmqvist et al., 2011).

## MATERIALS AND METHODS

### *Comparative sample*

This study is based on the comparative anatomical analysis of the hyaenid material from Dmanisi and other Pleistocene samples from Europe, Asia and Africa. The Dmanisi fossil collection is housed at the S. Janashia Museum of Georgia, Georgian National Museum (Tbilisi). The comparative fossil materials of late Villafranchian and Epivillafranchian from Eurasia are housed at AUT, ICP, IGF, MAEG, MCPV, MdC, MPM, MPRM, NMB, NNHC-HUJ and UCBL FSL (see abbreviations below). These comparative fossil samples include: 1) specimens of *Pachycrocuta brevirostris* (Gervais, 1850) (see Alba et al., 2013) from the Iberian sites of Orce (Venta Micena, Fuente Nueva 3, Barranco León), Incarcal Complex, Cueva Victoria and Vallparadís Section; the French sites of Sainzelles and Vallonnet; the Italian sites of Olivola, Pirro Nord, and Upper Valdarno Basin; the Greek sites of Libakkos, Tsiotra Vrisi and Apollonia 1 (Koufos & Kostopoulos, 1997; Koufos, 2018, 2024); the German site of Untermassfeld (Turner, 2001; Iannucci et al., 2022); and the Chinese site of Zhoukoudian 1 (Pei, 1934); 2) specimens of *Pliocrocuta perrieri* from the Iberian sites of La Puebla de Valverde and Villarroya (Vinuesa et al., 2014) and the French sites of Saint-Vallier (Viret, 1954) and Senèze (Argant, 2024), and 3) specimens of *Crocuta crocuta* Erxleben, 1777 from the Israeli site of 'Ubeidiya (Ballesio, 1986; Martínez-Navarro et al., 2009).

### *Metric procedures and morphometric analyses*

For linear measurements, we used the standardised measurements proposed by von den Driesch (1976) and Werdelin & Solounias (1991). The measurements were made directly on the samples using a digital calliper to the nearest 0.1 mm. To characterise the deciduous dentition, we calculated the width on length ratios of the deciduous premolars (dp) of Dmanisi (specimens D153, D1062, D2668, D3212, D3917, D4353, D5551, D6655, D6656, D6660; see the Results section for the detailed list of specimens and their descriptions). We compared these values to those of *Pliocrocuta* and *Pachycrocuta* from different localities across Europe. Measurements of the dp of the comparative samples were taken personally by the authors (e.g., *Pl. perrieri* from St. Vallier for the specimens housed in MdC, NMB, UCBL FSL; *P. brevirostris* from Cueva Victoria for the specimens housed in the MAC and IMEDEA; from Upper Valdarno for the specimens housed in IGF; from Vallonnet for the specimens housed in MPRM; and from Venta Micena for the specimens housed in MAEG) or, in some instances, taken from literature (Gerakarou-1 from Koufos, 1992; Untermassfeld from Turner, 2001; Iannucci et al., 2022). We also measured the height of the juvenile mandibles distally to the dp3 and to the dp4 and their breadth under the interalveolar space between dp3 and dp4. For this purpose, we measured specimens in which the permanent dentition had not yet erupted. We plotted the ratios as violin plots to assess the variance in morphometries of the deciduous teeth in the considered hyaenids and used biplots for the mandibular measures.

To characterise the adult specimens, we performed two Principal Component Analyses: the first one used five log-transformed variables of the upper carnassial (i.e., its mesiodistal length, its maximum buccolingual width, its width at the carnassial blade; the mesiodistal length of the P4 paracone; and the mesiodistal length of the metastyle). As a sample, we used the single P4 (D2286) and compared it to *P. brevirostris* and *Pl. perrieri* to ascertain its most probable attribution. The data on the fossil taxa were taken from Lewis & Werdelin (2022).

Our second analysis was a between-group Principal Component Analyses (bgPCA) on selected dentognathic variables, conducted as an attempt to discriminate between different taxa while taking into consideration several dentognathic parameters. We used species as a priori grouping factors; the ones considered here include *Crocuta crocuta*, *Crocuta spelaea* Goldfuss, 1823, *Hyaena hyaena* (Linnaeus, 1758), *P. brevirostris*, *Parahyaena* *brunnea* (Thundberg, 1820), and *Pl. perrieri.* In particular, we considered six measurements on the adult lower cheek dentition and a mandibular one. These measurements were: the mesiodistal length and buccolingual width of the p3, p4 and m1 and the height of the mandible distally to the p3. The log-transformed measurements were used to perform the bgPCA. We used the RStudio software (v. RStudio 2024.12.1+563 "Kousa Dogwood" Release 27771613951643d8987af2b2fb0c752081a3a853, 2025-02-02; RStudio Team, 2024) in the R environment (v. 4.3.2, R Core Team, 2024) to perform our analyses and produce graphs. The bgPCA was performed using the *groupPCA()* ("*Morpho*" package v. 2.12; Schlager, 2017) on the comparative extant and fossil samples; the results for the adult specimen from Dmanisi were plotted a posteriori to check their affinity to any of the a priori groups (i.e., the hyaenid species). We did this by centring the observations on the preliminary dataset and then projecting the centred new observations into the bgPCA space by calculating the dot product of each centred observation with the bgPCA loadings. This was done row-by-row using the *apply()* function ("*base*" v. 4.3.2, R Core Team, 2024) to ensure compatibility with the matrix format of the loadings. The plots were obtained using the *ggplot()* ("*ggplot2*" package v.3.4.0; Wickham et al., 2016).

### *Details of HSB acquisition*

The pictures of the dental microstructures on the Dmanisi specimens were acquired using a stereomicroscope (OLYMPUS BX43) from the Palaeoanthropology and Palaeobiology Research Institute, Georgian National Museum (Tbilisi). Pictures were taken at different levels of magnification (1.6×, 2.5×, 4×) using the native software of the microscope. Comparative specimens from IGF were photographed using a digital microscope (Hirox RX-100) from the DSTUNIFI. To highlight the Hunter-Schreger bands, we used a lateral source of light with an approximate incident angle of 45° (following the methodology described by Ferretti, 2007).

### *Anatomical and measurement abbreviations*

BMdp34: breadth of the mandible corpus measured at the level of the interalveolar space between dp3 and dp4; d: deciduous; dp: deciduous premolar; HMp3: height of the mandibular corpus measured distally to the p3 (in adults); HMdp3: height of the mandibular corpus measured distally to the dp3 (in juveniles); HMdp4: height of the mandibular corpus measured distally to the dp4 (in juveniles); L: mesiodistal length; LCR: upper cheek toothrow mesiodistal length (P1-M2); Lm: mesiodistal length of the P4 metastyle; LMR: upper molar row mesiodistal length (M1-M2); Lp: mesiodistal length of the P4 paracone; LPR: upper premolar row mesiodistal length (P1-P4); tdm1: talonid of m1; trm1: trigonid of m1; W: buccolingual width; Wa: buccolingual width of the P4 at the level of the protocone; Wbl: buccolingual width of the P4 at the level of carnassial blade.

### *Institutional abbreviations*

D: catalogue number of the Dmanisi collections of the S. Janashia Museum of Georgia, Georgian National Museum (Tbilisi); AUT: Department of Earth Sciences, Aristotle University of Thessaloniki (Thessaloniki, Greece); DSTUNIFI: Dipartimento di Scienze della Terra, Università di Firenze (Florence, Italy); ICP: Institut Català de Paleontologia Miquel Crusafont (Sabadell, Spain); IGF: Museo di Storia Naturale, Sezione Geologia e Paleontologia, Università di Firenze (Italy); IMEDEA: Institut Mediterrani d'Estudis Avançats (Esporles, Mallorca, Spain); MAEG: Museo Arqueológico y Etnológico (Granada, Spain); MAC: Museo Arqueológico de Cartagena (Cartagena, Spain); MCPV: Musée Croizatier (Puy-en-Velay, France); MdC: Musée des Confluences (Lyon, France); MPM: Museo Paleontologico di Montevarchi (Montevarchi, Arezzo, Italy); MPRM: Musée de Préhistoire Régionale (Menton, France); NMB: Naturhistorisches Museum Basel (Basel, Switzerland); NNHC-HUJ: National Natural History Collections, Institute of Earth Sciences, The Hebrew University of Jerusalem (Jerusalem, Israel); UCBL FSL: Department of Geology, University of Claude Bernard Lyon-1 (Lyon, France).

### *Generic abbreviations disambiguation*

*C.*: *Crocuta*; *H*: *Hyaena*; *P.*: *Pachycrocuta*; *Pa.*: *Parahyaena*; *Pl.*: *Pliocrocuta.*

### *Data availability*

Decidual dentition ratios, juvenile mandibular parameters and variables of the upper P4 are provided in SOM 4. The remaining set of data analysed and generated during the current study are available from the corresponding authors on reasonable request.

## RESULTS

### *Referred specimens*

Dentognathic specimens (Figs 1 and 2; Tab. 1) - D4240, premaxilla with right and left I1-I3; D6652, right I3; D79, right C1; D3619, left C1; D6962, left P1; D3209, left P2; D6658, right P3; D2286, left P4; D3996, right dC; D6661, left dC; D6653, right dC; D74, left dP2; D3209, mesial fragment of right dP3 with mesial root; D2430, left i3; D4384, right incomplete dp4; D153, right hemimandible with alveolus of incisors and c, dp2-dp4, and germinal m1; D3917, left hemimandible with dp2-dp4 and germinal m1; D2668, left hemimandible with roots of dp2, complete dp3, germinal p4, and alveolus of m1; D5551a, left hemimandible corpus with dp2-dp4, germinal adult premolars and m1 inside corpus; D6650, right hemimandible with c alveolus, distal root of p2, and p3-m1; D6651, right corpus fragment with p3-p4; D2365, right di2; D3908, right di3; D3619, left dc; D3726, left dc; D6656, left dp3; D4353, left dp4; D3212, right dp4 fragment; D1062, right dp4; D1129, right dp4; D6660, left broken dp4; D6655, left dp4; D1647, left i2; D2420, left i3; D6659, left i3; D7043, right m1.

Postcranial specimens (Figs 3 and 4; Tab. 2) - D3646, one thoracic and five lumbar vertebrae in anatomical connection; D341, distal fragment of right humerus; D1882, distal fragment of right humerus; D3757, distal end of juvenile humerus; D4688, complete right radius; D4687, partial left ulna; D2952, shaft of right femur; D5337, distal end of right tibia; D5225, right calcaneus;

D4020, right talus; D3834, right pelvis fragment with acetabulum and ilium; D6645, right III mtc; D6646, right V mtc; D2493, proximal phalanx; D6647, proximal phalanx; D4483, partial proximal phalanx; D6648, medial phalanx; D3749, distal phalanx; D6649, distal phalanx.

### *Description of the dentognathic specimens*

Adult upper dentition - I3 is caniniform and considerably larger than I1-I2. The upper canines D79 and D3619 have a lingually oriented conical cusp. Upper premolars are represented in the sample by only a left P2 (D3209), a right P3 (D6658) and a left P4 (D2286). The P2 displays a low crown, with a buccolingually stout protocone with a small cingular projection and large distal accessory cusp. The P3 has similar morphology to the P2, but the protocone is higher in buccal view and there is no evidence of a mesial cingular projection. The P4 shows a well-developed protocone perpendicularly oriented with respect to the three other P4 cusps. The metastyle appears mesiodistally enlarged with respect to the paracone being curved buccally (Fig. 1d).

Deciduous upper dentition - The upper canines D3996 and D96653 have a typical low crown. The deciduous premolars are represented by a dP2 (D74) and a mesial fragment of dP3 (D3209). The dP2 has a protocone with a mesial robust cingulum with mesial and mesiobuccal tubercles. Distally, a distal tubercle is also visible with reduced cingulum. The dP3 (D3629) preserves the mesial root with the protocone and the mesial accessory cusp.

Adult lower dentition - The lower incisors are only represented by a left i3 (D2430). It has a conical shape in buccal view, with a laterally developed tubercle. No p2 is present in the sample. The other preserved lower premolars (D6650 and D6651; Fig. 1e) are characterised by their buccolingual robustness. This is marked in the p3, which possesses a high protoconid and a developed distal cingulid with a tubercle in the distobuccal region. The p4 possesses a protruding protoconid, lower than in p3, and mesial and distal accessory cuspids with mesiolingual and distobuccal tubercles (Fig. 1e). The m1 displays a developed paraconid and mesiodistally shorter protoconid without metaconid. The talonid is mesiodistally short, with only two reduced cuspids: the hypoconid and the entoconid. The latter buccal one is more protruding than the hypoconid, as clearly visible in D6650 (Fig. 1e; Tab. 1).

Deciduous lower dentition - The lower incisors are characterised by their reduced size. The lower canines are also smaller compared to the upper ones, which, in turn, are buccolingually flattened. The lower premolars possess protoconids with sharp and high cuspids. The dp2 and dp3 both have a main central cuspid, the protoconid (Fig. 2a-b). The dp2 has no mesial cingulid, whereas the distal one possesses a tubercle. The dp3 is mesiodistally larger than the dp2 and it has developed mesial and distal cingulids. Both these cingulids have evident tubercles (Fig. 2). The dp4 has a typical trigonid with a mesiodistally longer paraconid, as opposed to the higher protoconid. It shows a practically non-existent metaconid on the distolingual surface of the protoconid and a small talonid with a developed distal cingulid (Fig. 2).

### *Description of the postcranial specimens*

The record of unearthed hyaena postcranial specimens from Dmanisi is not very abundant. The entire sample consists of a few vertebrae, incomplete long bones and autopodial specimens (see Tab. 2). The distal right humerus fragment D341 shows a lateromedially stout distal epiphysis with a proximodistally large medial epicondyle

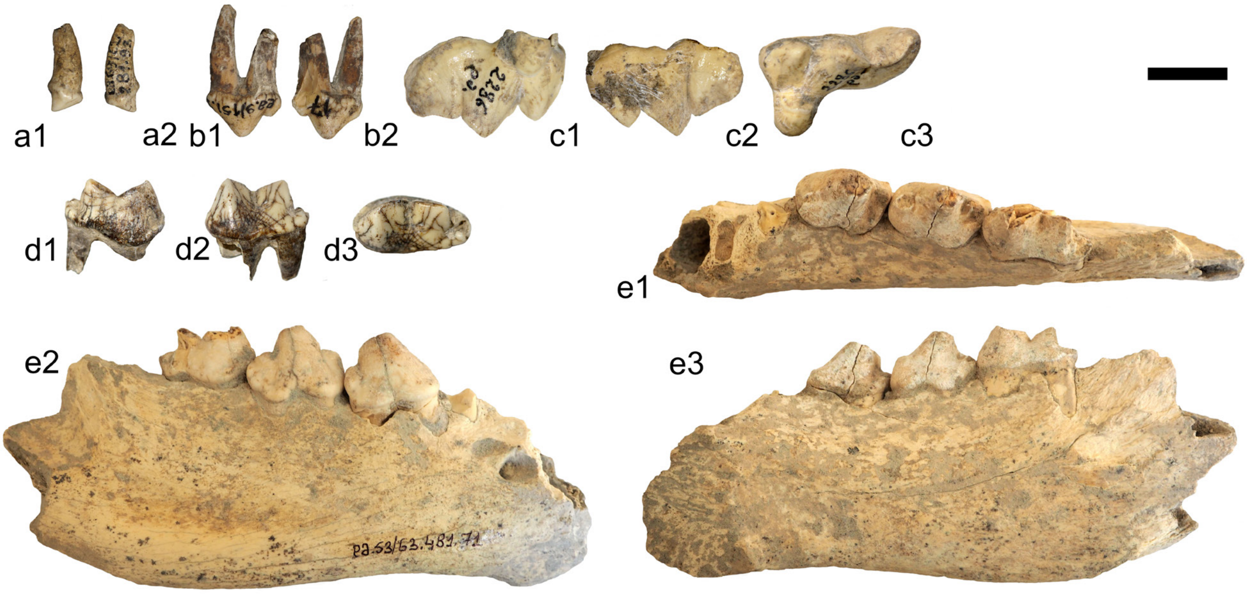


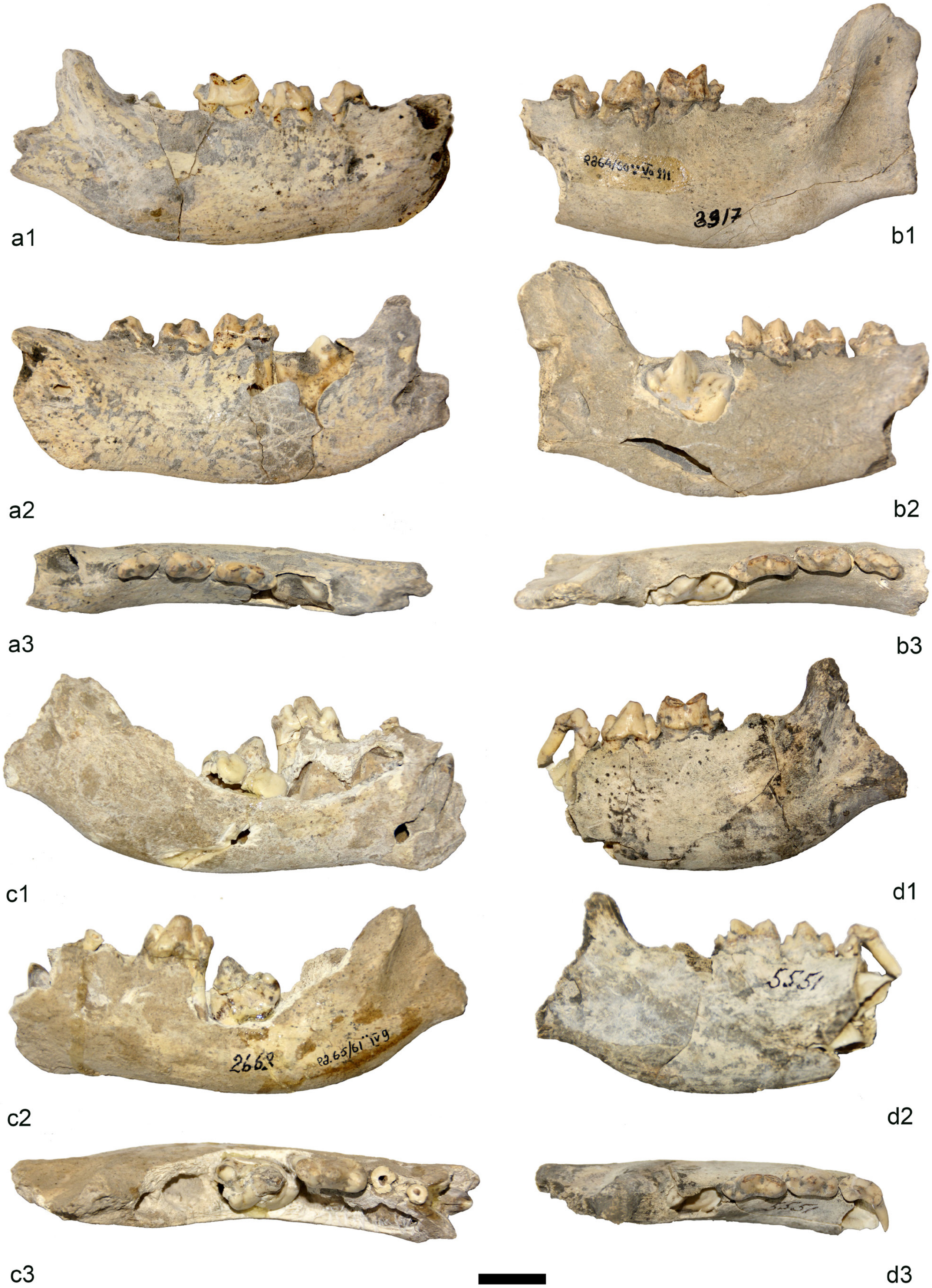
Fig. 1 (color online) - Adult dentognathic remains of *Pachycrocuta brevirostris* from Dmanisi. a) D6962, left P1 in buccal (a1) and lingual (a2) views. b) D3209, left P2 in buccal (b1) and lingual (b2) views. c) D2286, left P4 in buccal (c1), lingual (c2) and occlusal (c3) views. d) D7043, right m1 in buccal (d1), lingual (d2), and occlusal (d3) views. e) D6650, right hemimandible with c alveolus, distal root of p2, and p3-m1 in occlusal (e1), buccal (e2), and lingual (e3) views. Scale bar represents 2 cm.

| Record nº | I1L | I1W | I2L | I2W | I3L | I3W | C1L | C1W | P2L | P2W | P3L | P3W | P4L | P4W |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| D2286 l. | | | | | | | | | | | | | 39.4 | 24.1 |
| D4240 r. | 6.4 | 8.4 | 8.4 | 12.2 | 18.4 | | | | | | | | | |
| D4240 l. | 6.3 | 8.8 | 8.8 | 12.1 | 17.5 | 18.4 | | | | | | | | |
| D3209 l. | | | | | | | | | 18.1 | 12.3 | | | | |
| D6658 r. | | | | | | | | | | | 21.9 | 16.6 | | |
| D6652 r. | | | | | 18.7 | 15 | | | | | | | | |
| | dI1L | dI1W | dI2L | dI2W | dI3L | dI3W | dC1L | dC1W | dP2L | dP2W | dP3L | dP3W | dP4L | dP4W |
| D74 l. | | | | | | | | | 19.8 | 11.4 | | | | |
| D3209 r. | | | | | | | | | | | | 8.3 | | |
| D6653 (?) r. | | | | | | | | 6.1 | | | | | | |
| D3996 r. | | | | | | | 9.7 | 6.1 | | | | | | |
| | i2L | i2W | i3L | i3W | c1L | c1W | p2L | p2W | p3L | p3W | p4L | p4W | m1L | m1W |
| D6659l. | | | 11.7 | 9.7 | | | | | | | | | | |
| D7043 r. | | | | | | | | | | | | | 28.0 | 13.9 |
| D1647 l. | 8.4 | 9.4 | | | | | | | | | | | | |
| D2420 l. | | | 9.5 | 12.5 | | | | | | | | | | |
| D2430 l. | | | 9.5 | 14.3 | | | | | | | | | | |
| D6651 r. | | | | | | | | | 24.1 | 18.9 | 25.9 | 17.8 | | |
| D6650 r. | | | | | | | | | 25.3 | 16.7 | 27 | 17.2 | 28.6 | 14.1 |
| | di2L | di2W | di3L | di3W | dc1L | dc1W | dp2L | dp2W | dp3L | dp3W | dp4L | dp4W | Ld | Wd |
| D153 r. | | | | | | | 14.1 | 7.8 | 16.7 | 8.3 | 20 | 7.6 | 51.2 | 20.1 |
| D3917 l. | | | | | | | 13.8 | 6.3 | 17.1 | 7.8 | 20.5 | 7.8 | | 19.1 |
| D2668 l. | | | | | | | | | 19.6 | 9.4 | | | | 21 |
| D5551 l. | | | | | | | 14 | 7.7 | 17.2 | 8 | 19.7 | 7.9 | 50 | 19.5 |
| D4353 l. | | | | | | | | | | | 21.7 | 7.7 | | |
| D6660 l. | | | | | | | | | | | | 8.3 | | |
| D3212 r. | | | | | | | | | | | 20.4 | | | |
| D1062 r. | | | | | | | | | | | 19.8 | 8 | | |
| D6656 l. | | | | | | | | | 16.6 | 7.1 | | | | |
| D6655 l. | | | | | | | | | | | | 7.6 | | |
| D3619 l. | | | | | 9.5 | 6.7 | | | | | | | | |
| D2365 r. | 5.1 | 6.1 | | | | | | | | | | | | |
| D3726 l. | | | | | 5.8 | 8.6 | | | | | | | | |
| D3908 r. | | | 6.4 | 6.9 | | | | | | | | | | |
| D1129 r. | | | | | | | | | | 19.9 | 7.5 | | | |

Tab. 1 - Dental measurements of *Pachycrocuta brevirostris* from Dmanisi. Abbreviations: L, mesiodistal length; W, buccolingual width; Ld, mesiodistal length of dp2-dp4 series; Wd, buccolingual width of the corpus at dp3.

compared with the lateral one. The cranial coronoid fossa has a triangular outline and is deep (Fig. 3a). On the palmar side, the olecranon fossa is wide and deep. A right radius (D4688) is the only complete long bone preserved in the sample and displays the characteristic anteroposterior curvature and a sub-ovoidal proximal epiphysis outline (Fig. 3d). In the distal epiphysis, the styloid process of the radius is well developed and projected distally. A partial left ulna (D4687), missing the proximal and distal ends, is rather stout. It shows a feeble craniopalmar curvature (Fig. 3e). The body of the complete right astragalus (D4020) is mediolaterally stout and characterised by two large ridges. The head is developed in line with the body, unlike the case in other carnivorans, where it is laterally projected. The neck is not so compressed, but rather mediolaterally robust. The sinus is diagonally oriented from proximolateral to distomedial. The lateral calcaneal facet is less developed mediolaterally in comparison to the medial one (Fig. 3c). The right calcaneus (D5225; Fig. 3b) is proximodistally short and stout, with a well-developed and protruding coracoid process.

D3646 includes six vertebrae in anatomical connection (Fig. 4), probably corresponding to T16 and L1-L5 (Fig. 4). The putative last dorsal vertebra (T16) lacks several parts, including the mid-part of the centrum, where the costal facets are placed. Nevertheless, the general shape


a1
b1
3917
a2
b2
a3
b3
c1
d1
c2
2662
d2
5551
c3
d3

| Humerus | Record nº | | | DMLDt | DMLDa | DAPM | DAPD | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | D341 r. | | | 69.5 | 49.2 | 49.4 | 42.5 | | | |
| | D1882 r. | | | 67 | 48.8 | 50.1 | 41.7 | | | |
| Radius | | L | DMLD | DAPP | DMLM | DMLD | DMLDm | DMLDa | DAPDm | DAPDa |
| | D4688 r. | 248 | 32.9 | 22.4 | 22.9 | 16 | 44.4 | 38.3 | 29.5 | 23.1 |
| Ulna | | L (pres.) | DAPPa | DAPPmin | DMLPa | DMLM | MAPM | | | |
| | D4678 l. | 240 | 53.1 | 32.3 | 37.8 | 22 | 24.9 | | | |
| Metacarpals | | L | DMLP | DAPP | DMLM | DAPM | DMLD | DAPD | | |
| | D6645 3rd r. | 67.6 | 14.1 | 22.4 | 12.8 | 11.5 | 15.1 | 15.6 | | |
| | D6646 5th Mt r. | 54.1 | 17.7 | 15 | 9.2 | 8.5 | 13.2 | 12.9 | | |
| Femur | | L (pres.) | DMLD | DAPD | | | | | | |
| | D2952r | 205 | 21.4 | 20.3 | | | | | | |
| Tibia | | DMLD | DAPD | | | | | | | |
| | D5337r | 39.7 | 27.5 | | | | | | | |
| Calcaneum | | L | DMLM | DAPM | DAPD | DMLD | | | | |
| | D5225r | 70 | 29.8 | 30.5 | 23.7 | 19.9 | | | | |
| Talus | | Lm | DMLP | DMLD | DAPm | DAPD | | | | |
| | D4020r | 41.8 | 30.7 | 24.7 | 34.6 | 24 | | | | |
| Phalanges | | L | DMLP | DAPP | DMLM | DAPM | DMLD | DAPD | | |
| | D2493 prox. | 35.6 | 14.3 | 13.1 | 9.7 | 8.5 | 13.1 | 9.1 | | |
| | D4483 prox. | 29.6 | 14.6 | 11.2 | 9 | 8.3 | | 7.2 | | |
| | D6647 prox. | 34.4 | 17.4 | 13.3 | 11.3 | 9.6 | 11.9 | 8.5 | | |
| | D6648 med. | 20.5 | 11.6 | 9.8 | 9 | 6.4 | 9.5 | 6.9 | | |

Tab. 2 - Measurements of postcranial specimens of *Pachycrocuta brevirostris* from Dmanisi. Abbreviations: L, proximodistal length; DML, mediolateral proximal diameter; DAPP, anteroposterior proximal diameter; DMLM, mediolateral mid-shaft diameter; DAPM, anteroposterior mid-shaft diameter; DMLD, mediolateral distal diameter; DAPD, anteroposterior distal diameter; m, maximum; a, articular.

is reminiscent of a lumbar vertebra of the genus *Crocuta*. The lumbar vertebrae (L1-L5) show craniocaudally long centra, as in extant hyaenas, but a spinous process that is very long and robust craniocaudally as compared with the extant genus *Crocuta.* The transverse processes are more horizontally placed and craniocaudally robust than in the genus *Crocuta*, where they are more inclined ventrally and slender.

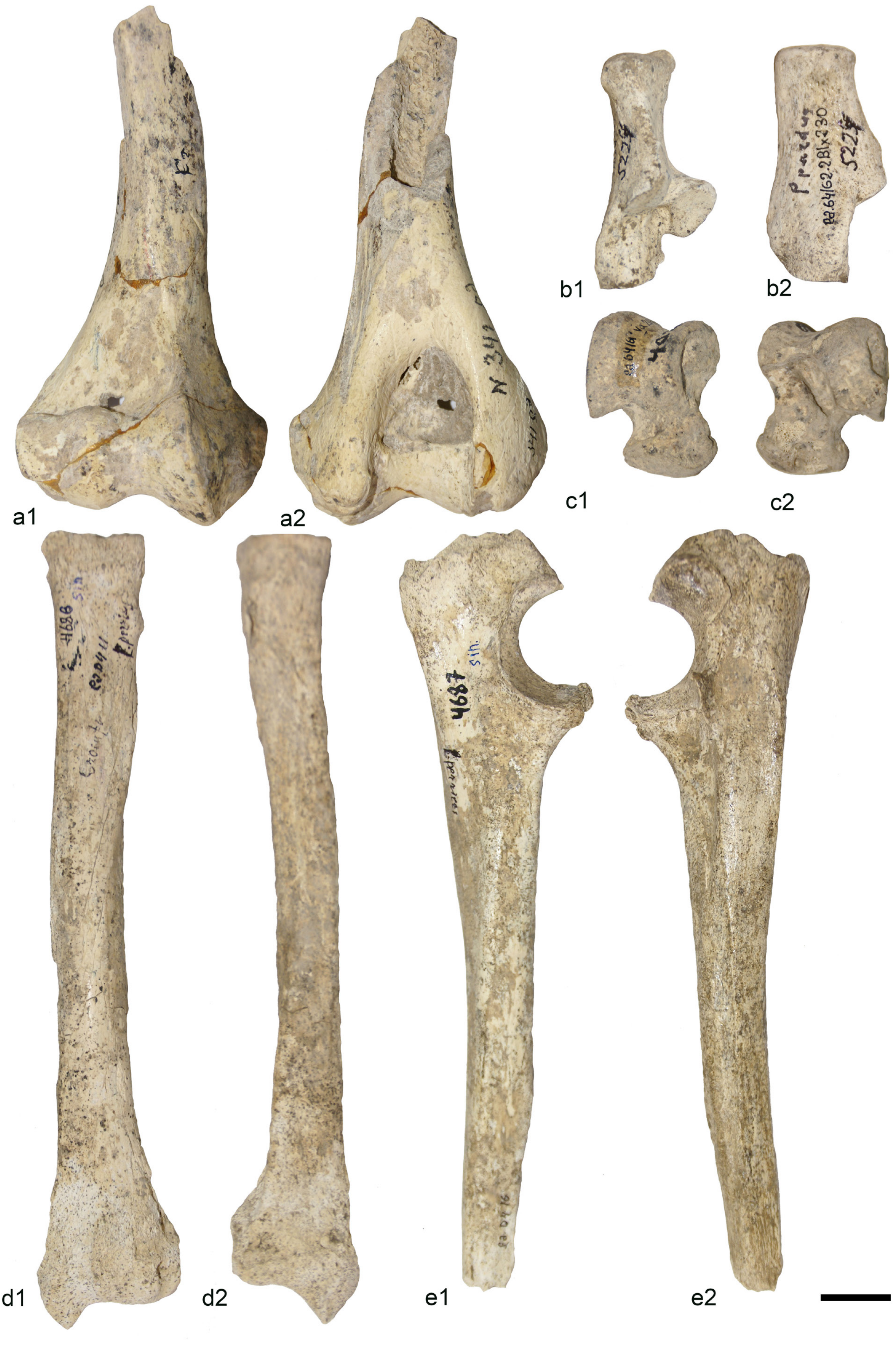
### *Enamel microstructure of teeth*

Figure 5 shows the enamel microstructure of the studied specimens from Dmanisi, observed using stereomicroscopy, in both adult and juvenile specimens (D153 at mid-level of the crown of the dp4; Fig. 5b) also in comparison to *Pachycrocuta* from Upper Valdarno (Fig. 5c-d). Figure 5a shows that the adult specimens from Dmanisi are characterised by Hunter-Schreger bands (HSB) with a clear zig-zag pattern (see the detailed picture and the schematic graphic representation in the bottom left corner of Fig. 5a2). This morphology is comparable to that of *Pachycrocuta* from Upper Valdarno (Fig. 5c, detailed picture and graphic scheme). Conversely, the juvenile individuals (e.g., Fig. 5b) have smoothed and undulated HSB on the deciduous lower fourth premolar (see the detailed picture and the schematic graphic representation in the bottom left corner of Fig. 5b2), which exhibits an undulating pattern. This morphology recalls the one of juvenile *Pachycrocuta* in the Upper Valdarno (Fig. 5d, detailed picture and graphic scheme).

### *Morphological comparisons*

As already mentioned, previous studies considered the Dmanisi hyaena sample as representative of two different coexisting species *Pachycrocuta* sp. and *Pliocrocuta perrieri* (Vekua, 1995; Lordkipanidze et al., 2007). From a general point of view, very few differences separate *P. brevirostris* and *Pl. perrieri* in terms of dental morphology. Furthermore, most of the differences could be attributed to intraspecific variation (Fig. 6). Both species are characterised in their lower dental morphology (the most abundant at Dmanisi) by buccolingually stout premolars, especially the p3 and the p4, with strong distal accessory

Fig. 2 (color online) - Juvenile dentognathic remains of *Pachycrocuta brevirostris* from Dmanisi. a) D153, right hemimandible with alveolus of incisors, c, dp2-dp4, and germinal m1 in buccal (a1), lingual (a2) and occlusal (a3) views. b) D3917, left hemimandible with dp2-dp4, and germinal m1 in buccal (b1), lingual (b2), and occlusal (b3) views. c) D2668, left hemimandible with dp3-dp4 in lingual (c1), buccal (c2), and occlusal (c3) views. d) D5551, left hemimandible with dp2-dp4, and germinal m1 in buccal (d1), lingual (d2), and occlusal (d3) views. Scale bar represents 2 cm.


a1
a2
b1
b2
c1
c2
d1
d2
e1
e2

cuspulids. The latter morphology is a clear bone-cracking adaptation; consenquently, both species are included in the Ecomorphotype 6 of bone-cracking hyaenas (Werdelin & Solounias, 1991; Turner et al., 2008). The lower m1 also displays a stout buccolingual morphology with a mesiodistally longer paraconid than protoconid and a talonid with one or two cuspids (Werdelin & Solounias, 1991; Turner et al., 2008; Madurell-Malapeira et al., 2015; Liu et al., 2021). Additionally, the m1 of *Pliocrocuta* can display a lingually-placed metaconid, as in several Chinese samples (Fig. 6) or it may only display it in very low frequency, as in Saint Vallier, Montopoli, Layna, Villarroya and La Puebla de Valverde (Viret, 1954; Qiu, 1987; J.M.-M. unpublished data). In fact, as reported by Howell & Petter (1980), the m1 metaconid is only present in the 49% of the largest known sample of *Pl. perrieri* (Odessa catacombs). On the other hand, *Pachycrocuta* never displays it (Madurell-Malapeira & Vinuesa, 2016).

Most of the dental sample from Dmanisi consists of deciduous teeth. Even in this sample, however, very few differences are evident between *Pliocrocuta* and *Pachycrocuta*, especially in the dP3. In *Pliocrocuta* the mesial root is separated from the main tooth axis and shows a small cusp on it, whereas in *Pachycrocuta* the mesial root is situated just below the main tooth axis and has no internal cusp, showing a more carnivorous feeding adaptation, as clearly observed at the sites of Venta Micena (Spain) and Vallonnet (France) (Martínez-Navarro, 1991; Moullé & Tréguier, 2006; Fig. 7). The dp4 of *Pliocrocuta* generally has a short talonid and no metaconid (Qiu, 1987; Fig. 7); rarely, it displays a mesiodistally elongated talonid or a metaconid (Qiu, 1987). In contrast to this morphology, dp4 in most of the *Pachycrocuta* specimens bears a mesiodistally short talonid without metaconid (Fig. 7; Viret, 1954; Howell & Petter, 1980; Qiu, 1987; Argant, 2004).

Therefore, the only remarkable differences between the above-mentioned species are related to the stoutness of the adult dentition and especially in the morphology of the mandibular corpus. In *Pachycrocuta*, the corpus is much stouter and higher at the p4-m1 in buccal view than in *Pliocrocuta* (Fig. 6). This character is also remarkable in juvenile specimens of *Pachycrocuta* compared with those of *Pliocrocuta* (Fig. 7). Additionally, the profile of the mandibular symphysis in *Pachycrocuta* is more vertical than in *Pliocrocuta*, also as a consequence of the overall robustness of the corpus (Figs 6 and 7).

To sum up, the mandibular remains within the Dmanisi sample are differentially characterised by possessing a high and stouter corpus with a vertical symphysis, m1 without metaconid and dp4 with a short talonid and vestigial or absent metaconid (Figs 1-2, 6-7). The former characteristics are sufficient to include all the studied specimens in the hypodigm of *Pachycrocuta brevirostris* (Figs 1 and 2).

Regarding the postcranial specimens: unfortunately, only a few complete bones of *Pachycrocuta* or *Pliocrocuta* have been unearthed and published (Viret, 1954; Kurtén & Crusafont-Pairó, 1977; Turner & Antón, 1996; Argant, 2004; Palmqvist et al., 2011). Probably the only exception is the excellent record of *Pachycrocuta* bones from Zhoukoudian 1, sketchily described and figured by Pei (1934). The only common elements in different associations of the former species are complete or partial humeri, specifically specimens collected from La Puebla de Valverde and Upper Valdarno (*Pl. perrieri*) and Incarcal Complex (*P. brevirostris*) (Fig. 8; Ficcarelli & Torre, 1970; Kurtén & Crusafont, 1977). As seen in Fig. 8, the morphological similarities among all specimens are evident, apart from the largest and stoutest overall morphology of the humerus of *P. brevirostris* (Fig. 8a-d), also exemplified in the morphology and deep muscular insertions, or in the deep morphology of the coronoid fossa (Fig. 8), shared by the Zhoukoudian-1 specimens (Pei, 1934: p. 209, pl. XXI). Finally, the medial epicondyle also seems more developed and protruding in *P. brevirostris* than in *Pl. perrieri* (Fig. 8).

The only radius figured by Pei (1934) shares many features with the Dmanisi specimen (D4688), especially for the remarkable limited distal development of the radial styloid process. The left partial ulna (D4687) lacks the olecranon tuberosity; however, the anconeal process is poorly developed, as in the Zhoukoudian-1 specimens (Pei, 1934: p. 209, pl. XXI).

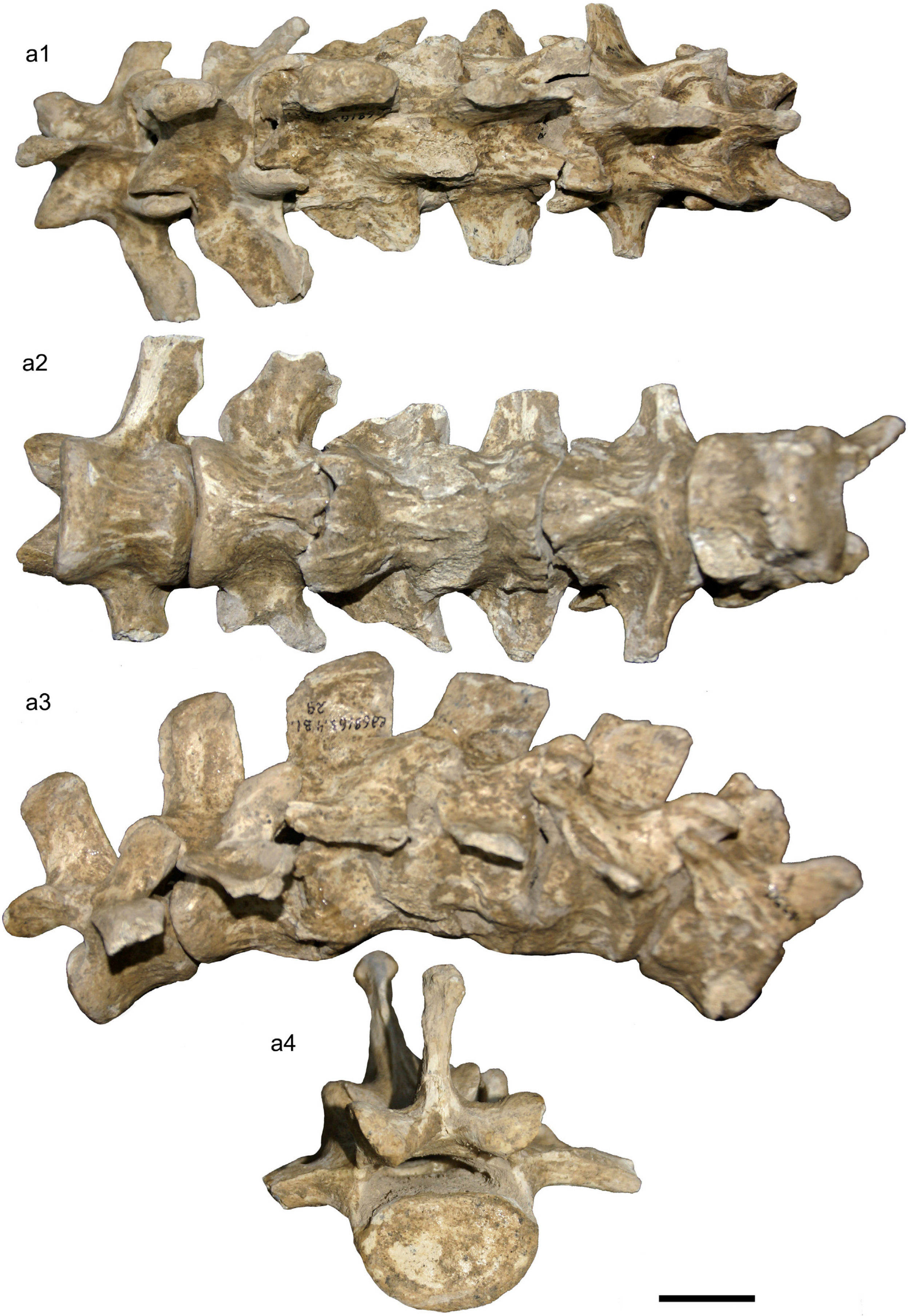
Several other postcranial bones attributed to *P. brevirostris* unearthed from Dmanisi (astragalus, calcaneus or metapodial bones) are not figured and described in detail by Pei (1934) and are unknown from other sites where *P. brevirostris* is recorded, thus preventing a direct comparison with the material studied here.

### *Biometric comparisons*

Most of the dentognathic elements recovered from Dmanisi belong to the lower dentition, both adult and deciduous. Previous authors who have analysed the differences in size and morphology between the Villafranchian hyenas *Pl. perrieri* and *P. brevirostris* have concluded that, despite few morphological differences, the two species mainly differ in the larger overall dimensions of the latter, both in dentognathic and postcranial variables (Howell & Petter, 1980; Qiu, 1987; Werdelin & Solounias, 1991; Turner, 2001; Turner et al., 2008).

Considering the numerous juvenile individuals recovered in the Dmanisi sample, and the past confusion of their taxonomic attribution, we performed some morphometric comparisons between the considered specimens and juvenile specimens of both *Pliocrocuta* and *Pachycrocuta*. Figure 9 reports violin plots of the ratios between width and length in the deciduous dentition of the three taxa, showing how poorly informative the measurements of the non-permanent teeth are as classification parameters. On the contrary, mandibular parameters are more discriminant, as shown in Fig. 10. In both biplots, *Pliocrocuta* and *Pachycrocuta* are clearly

Fig. 3 (color online) - Postcranial remains of *Pachycrocuta brevirostris* from Dmanisi. a) D341, distal fragment of right humerus in anterior (a1), and posterior (a2) views. b) D5225, right calcaneus in anterior (b1), and lateral (b2) views. c) D4020, right talus in anterior (c1) and posterior (c2) views. d) D4688, complete right radius in anterior (d1), and posterior (d2) views. e) D4687, partial left ulna in medial (e1), and lateral (e2) views. Scale bar represents 2 cm.


a1
a2
a3
a4

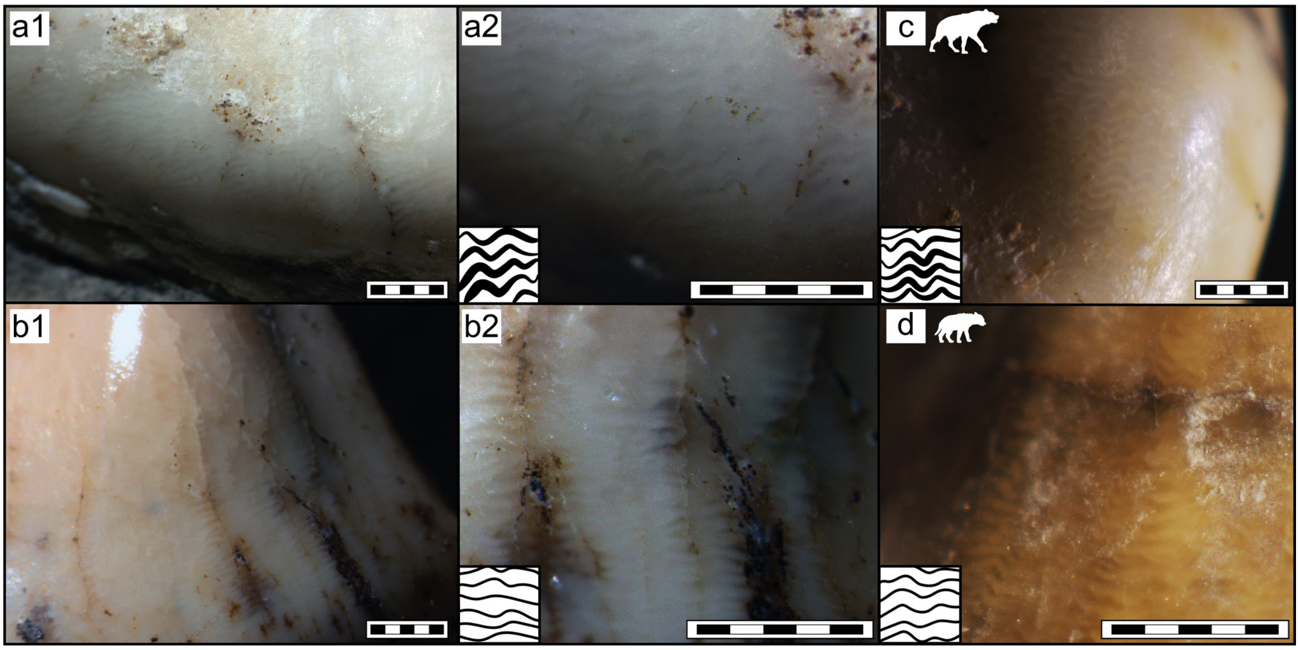


Fig. 5 (color online) - Hunter-Schreger bands in adult and juvenile *Pachycrocuta brevirostris* from Dmanisi, Pirro Nord and Upper Valdarno. a1-2) D6650 first lower molar. b1-2) D3917 fourth decidual lower premolar. c) DSTUNIFI specimen without number of an adult *Pachycrocuta brevirostris* from Pirro Nord. d) IGF 847 fourth decidual lower premolar of *P. brevirostris* from Upper Valdarno.

separated from one another, with no overlapping. In these evident dichotomous distributions, juvenile hyaenas from Dmanisi lie close to and sometimes overlap the specimens of *Pachycrocuta*, far from the variability of *Pl. perrieri*.

On the adult specimens, we performed a PCA on P4 measurements to take into consideration as many variables as possible. The results are shown in Fig. 11. The PC1 explains the 81.22% of the variability and is positively influenced by all the variables used, especially the mesiodistal length of the tooth and of the metastyle (see SOM 2). Along this axis, a clear distinction is evident between *Pliocrocuta* and *Pachycrocuta*, with the former occupying the negative values of this axis whereas the specimens of the latter are all clustered on the positive side of the PC1. D2286 lies close to *Pachycrocuta* specimens. The PC2 explains the 11.90% of the variability and is mainly positively influenced by the maximum width (with the protocone) and the width at the carnassial blade; the axis is negatively influenced by the lengths of the paracone and of the metastyle (see SOM 2). Along this axis is a wider range of variability of all the considered taxa as *Pachycrocuta* and *Pliocrocuta*'s ranges overlap.

Considering the scatterplot of PC1-PC2, we noted how close D2286 is to the variance of *Pachycrocuta*. On adult dentognathic specimens, we performed a bgPCA analysis on log-transformed dentognathic variables of the permanent lower dentition and the height of the mandibular corpus at p3 on fossil species *P. brevirostris*, *Pl. perrieri* and *C. spelaea* and the extant ones (i.e., *C. crocuta, Pa. brunnea* and *H. hyaena*). The species were used as an a priori grouping factor and the Dmanisi adult mandible (D6650) was plotted a posteriori on the resulting distribution (see material and methods for more information). The results are displayed in Fig. 12. The bgPC1 accounts for the 90.11% of the variance, and bgPC2 for the 8.72% of the total variance (see SOM 3). The bgPC1 is negatively influenced by all the variables and especially by the height of the mandible distal to the p3 and the width of the p3 and p4. The bgPC2 is positively influenced by the length of the carnassial and the width of the p3, and negatively by the height of the mandible at p3 and width of the p4 (see SOM 3). Clearly, in both bgPC1 and bgPC2, there is a general separation between the species and lineages. For instance, the different species of the genus *Crocuta* are close, but not overlapped together. Moreover, they are markedly distant from the other taxa (*Hyaena*, *Parahyaena*, *Pliocrocuta* and *Pachycrocuta*) on the positive end of the bgPC2. The other considered taxa are located on the negative values of bgPC2.

Along bgPC1, three distinct groups can be identified: the first is composed of *P. brevirostris*, occupying the left side of the plot, on the negative side of bgPC1. The second, the central one, includes the species of *Crocuta*, *Pl. perrieri* and *Pa. brunnea*. The last is that of *H. hyaena* at the positive end of bgPC1. As briefly expressed before, even along bgPC2, a certain degree of separation occurs between taxa, although in only two groups here and less clearly compared to that of bgPC1. *Crocuta spelaea* and *C. crocuta* occupy the higher (i.e., more positive) values of the axis. The other taxa all have negative values for bgPC2, apart from two specimens of *P. brevirostris*. The most complete specimen from Dmanisi, D6650, falls

◄

Fig. 4 (color online) - D3646 six vertebrae (T16+L1-L5) of *Pachycrocuta brevirostris* in anatomical connection. Dorsal (a1), ventral (a2), lateral (a3) and caudal (a4) views of L5. Scale bar represents 3 cm.

within the variability of *P. brevirostris* (within both bgPC1 and bgPC2), as evident from Fig. 12. This confirms the morphological data regarding the plausible ascription of the sample from Dmanisi to the large-sized short-faced hyaena.

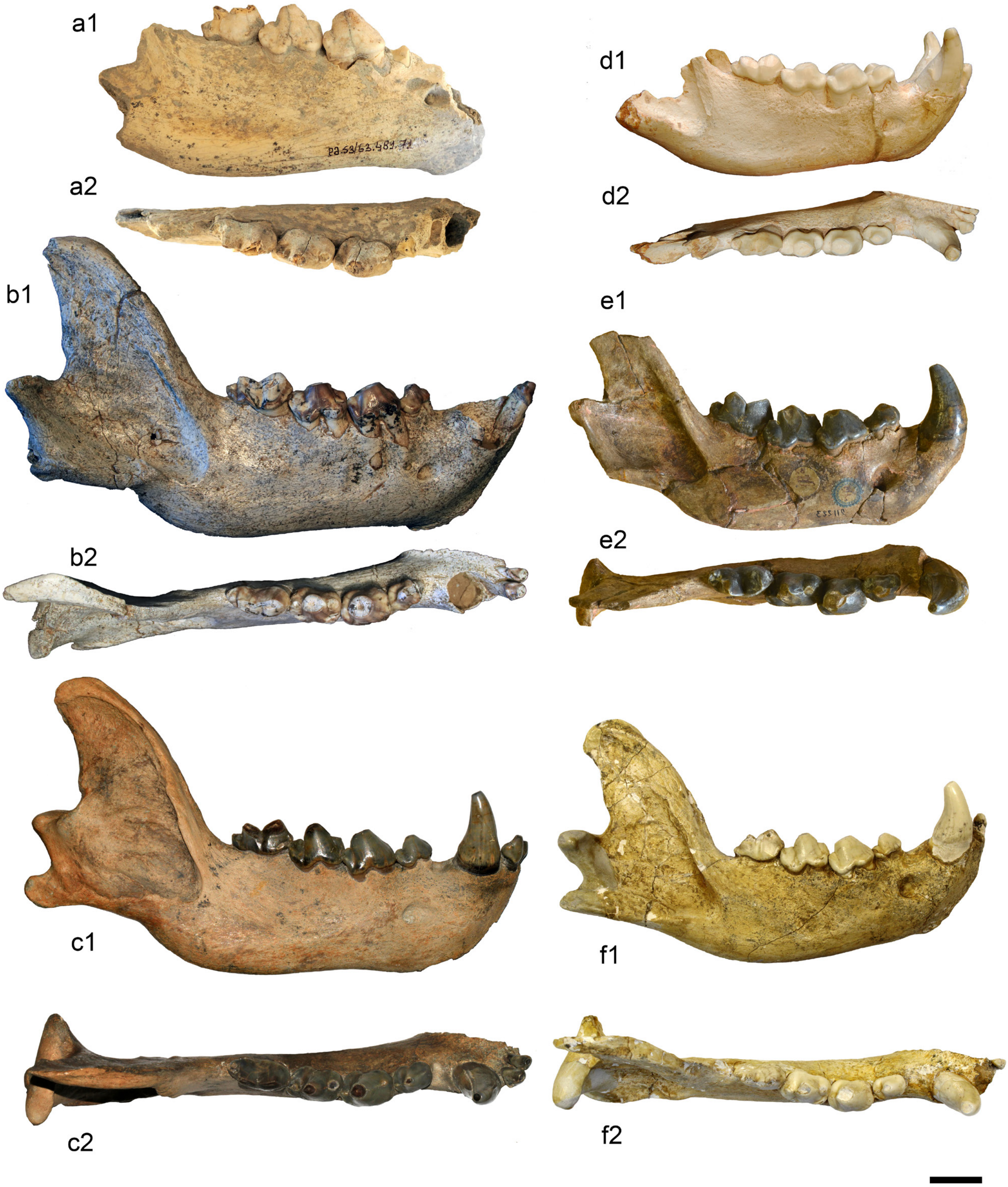


Fig. 6 (color online) - Dentognathic remains of *Pachycrocuta brevirostris* and *Pliocrocuta perrieri* from several European sites. a) D6650, right hemimandible of *Pachycrocuta brevirostris* from Dmanisi with c alveolus, distal root of p2, and p3-m1 in buccal (a1) and occlusal (a2) views. b) EVT25416, right corpus of *Pachycrocuta brevirostris* from Vallparadís Section layer EVT12 with p2-m1 in buccal (b1) and occlusal (b2) views. c) NMB Va.1714, right corpus of *Pachycrocuta brevirostris* from Upper Valdarno with c1-m1 in buccal (c1) and occlusal (c2) views. d) IPS27307, mandible of *Pliocrocuta perrieri* from La Puebla de Valverde (reversed) with i1-m1 in buccal (d1) and occlusal (d2) views. e) UCBL FSL211233 right hemimandible of *Pliocrocuta perrieri* (holotype) from Perrier with c1-m1 in buccal (e1) and occlusal (e2) views. f) ML20.161768 right hemimandible of *Pliocrocuta perrieri* from Saint Vallier with i3-m1 in buccal (f1) and occlusal (f2) views. Scale bar represents 2 cm.

Further interesting elements can be pointed out. The position of *P. brevirostris* is influenced by its large size and robustness (e.g., in the mandible corpus). The fact that the extant *Parahyaena brunnea* and fossil *Pliocrocuta perrieri* fall close to one another – or rather that the variability of our sample of *Pa. brunnea* is close to and partially overlapping with the hull of *Pliocrocuta perrieri* (Fig. 12) – is related to their comparable scavenger-

Fig. 7 (color online) - Mandibular juvenile remains of European Pleistocene hyaenas. a) Right juvenile hemimandible of *Pachycrocuta brevirostris* from Dmanisi (D153) in buccal (a1) and occlusal (a2) views. b) Left juvenile hemimandible of *Pachycrocuta brevirostris* from Dmanisi (reversed, D3917) in buccal (b1) and occlusal (b2) views. c) Right juvenile hemimandible of *Pachycrocuta brevirostris* from Dmanisi (D5551) in buccal (c1) and occlusal (c2) views. d) Right juvenile hemimandible of *Pachycrocuta brevirostris* from Upper Valdarno (IGF 847) in buccal (d1) and occlusal (d2) views. e) Right juvenile hemimandible of *Pachycrocuta brevirostris* from Upper Valdarno (IGF 848) in buccal (e1) and occlusal (e2) views. f) Left juvenile hemimandible of *Pliocrocuta perrieri* from Saint Vallier (reversed, FSL496220) in buccal (f1) and occlusal (f2) views. Scale bar represents 2 cm.

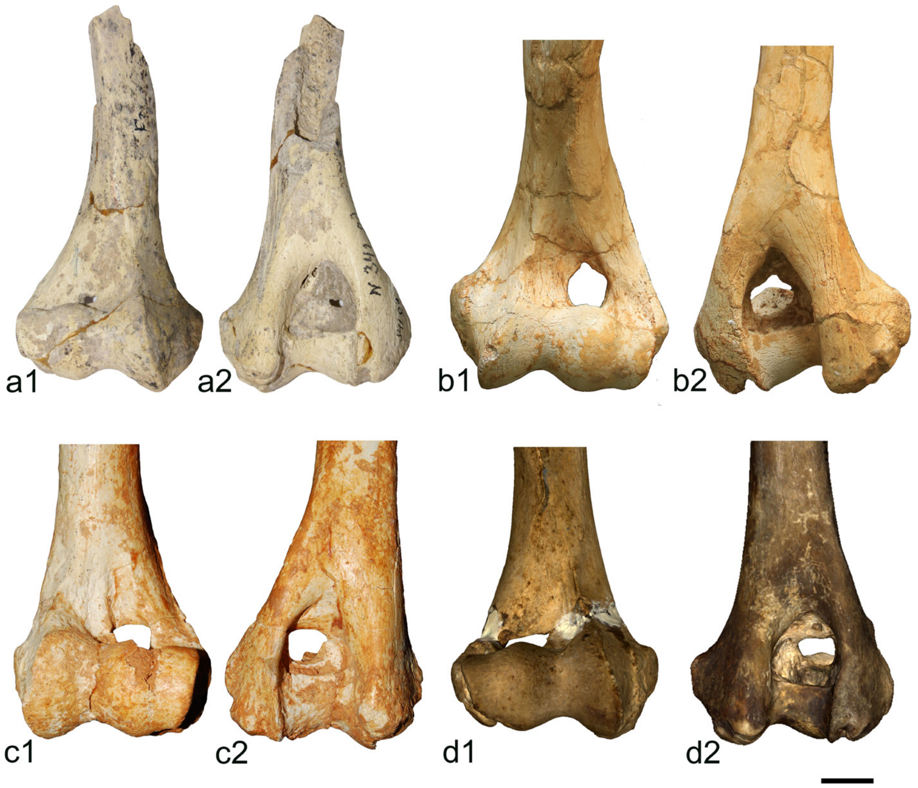


Fig. 8 (color online) - Humeri of *Pachycrocuta brevirostris* and *Pliocrocuta perrieri* from several European sites. a) D341, distal fragment of right humerus of *Pachycrocuta brevirostris* from Dmanisi in anterior (a1) and posterior (a2) views. b) IN-I-305, left humerus of *Pachycrocuta brevirostris* from Incarcal-I in anterior (b1) and posterior (b2) views. c) IPS27344, left humerus of *Pliocrocuta perrieri* from La Puebla de Valverde in anterior (c1) and posterior (c2) views. d) IGF 12473, right humerus of *Pliocrocuta perrieri* from Upper Valdarno in anterior (d1) and posterior (d2) views. Scale bar represents 2 cm.

opportunistic hunting strategy with a strong adaptation to consume bones regularly in the diet. *Crocuta* spp. are separated from the other hyenids by their comparatively shallower mandible and elongated m1 typical of more dedicated carnivorous predators. The Dmanisi specimens, with stout mandibles and large teeth, are consistent with the variability of *P. brevirostris*.

The biometrical measurements of the postcranial remains recovered from Dmanisi, especially the humerus and radius, also fit perfectly with the proportions previously published for *P. brevirostris* (Pei, 1934; Turner & Antón, 1996; Palmqvist et al., 2011). The length of the right radius (D4688) is 248 mm and fits in the lower range of the variability reported by Pei (1934) based on 22 specimens (range from 243 to 265 mm). Thus, D4688 fits within the lower range for *P. brevirostris* (from 243-266 mm) as we previously stated (Pei, 1934; Turner & Antón, 1996; Palmqvist et al., 2011). As evident also in Fig. 8, the Dmanisi postcranial specimens are not as large as the Zhoukoudian-1 and Incarcal-I, which are really large-sized specimens.

## DISCUSSION

### *Background of the origin of the Pleistocene bone-cracking hyaenas*

*Pachycrocuta*, *Pliocrocuta* and *Crocuta*, together with *Parahyaena* and *Hyaena*, are the genera fully adapted to bone-cracking behaviour (Ecomorphotype 6 of Werdelin & Solounias, 1991, 1996; Turner et al., 2008), recorded in the Pleistocene of Eurasia and Africa. Their adaptations allow them to feed on the marrow of the bones of their prey and do not imply a strictly scavenger lifestyle, as exemplified by the extant *Crocuta*, which actually hunts most of its prey (i.e., Mills, 1990). Although several authors defend the idea that *Pliocrocuta* and *Pachycrocuta* are synonyms (e.g., Vekua, 1995; Pérez-Claros, 2024, and references therein), we deem that enough anatomical data differentiate these genera of hyaenids, as exposed in this study.

*Pachycrocuta*, *Pliocrocuta* and *Crocuta* were probably ecologically vicars, occupying a similar ecological niche in the Pleistocene palaeobiocoenoses in Asia (*Pachycrocuta*), Europe (*Pliocrocuta*) and Africa (*Crocuta*). *Pliocrocuta* seems to be a European taxon because its earliest record is in Lower Pliocene sites, such as Serrat d'en Vaquer, Perpignan, France (Turner et al., 2008). *Crocuta* has a clear African origin, being recorded since 4.0 Ma in Africa (Werdelin & Peigné, 2010). The origin of *Pachycrocuta* is more doubtful. The earliest records of *Pachycrocuta* are more or less coeval in Asia and Africa, around 4.0-3.5 Ma (Werdelin, 1999; Werdelin & Peigné, 2010; Liu et al., 2021). According to Werdelin (1999), *Pachycrocuta* supposedly originated in Asia and later dispersed into Africa. In the African continent the genus is recorded until 2.5 Ma in East Africa, while it persists until 1.3 Ma in South Africa, with the species *P. bellax* (Ewer, 1954)

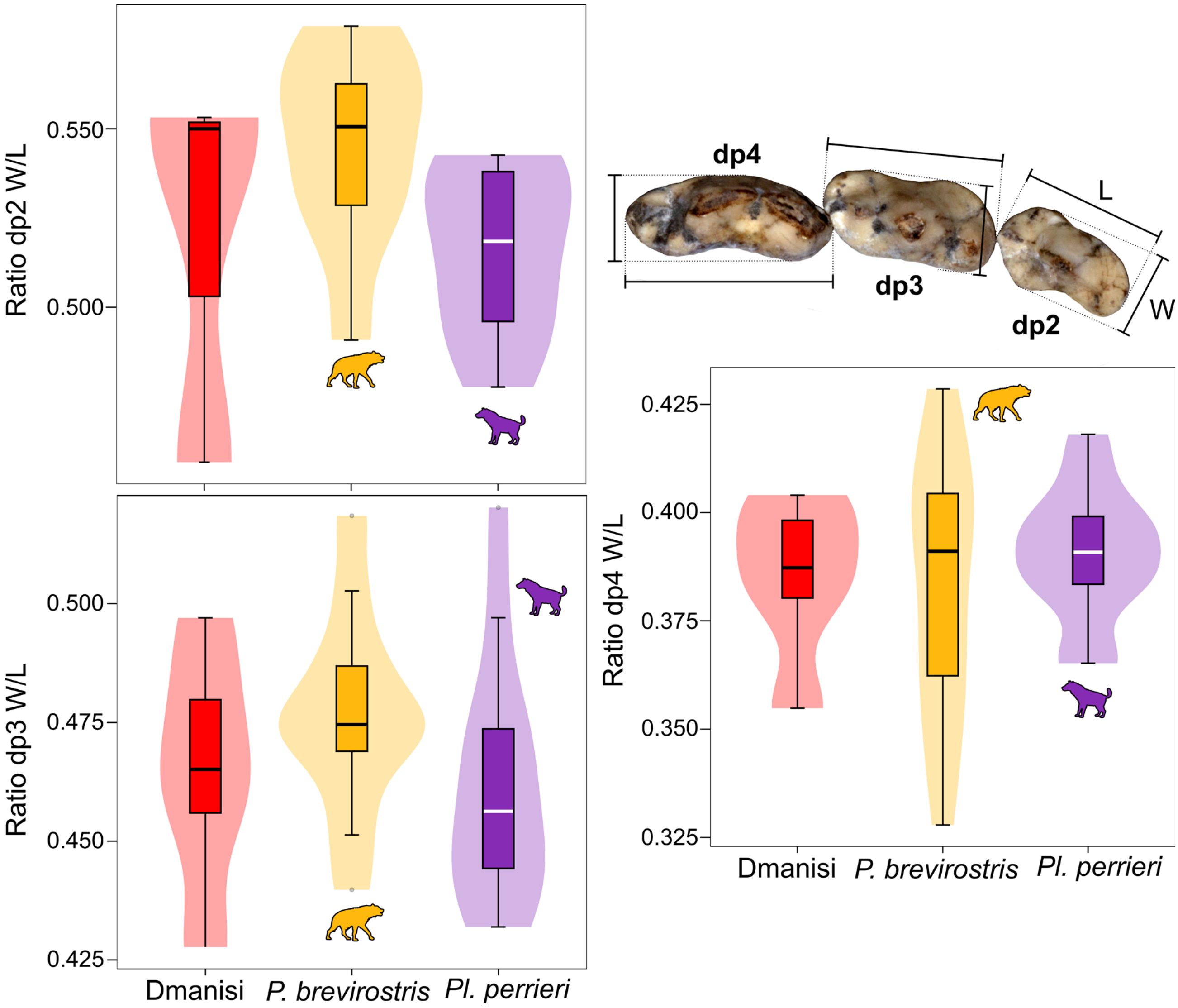


Fig. 9 (color online) - Violin plots of the width/length ratios of the deciduous premolars of juvenile Early Pleistocene hyaenids *Pliocrocuta* (from Gerakarou-1 and St. Vallier), *Pachycrocuta* (from Cueva Victoria, Gerakarou-1, Untermassfeld, Upper Valdarno, Vallonnet, Venta Micena) and Dmanisi. The picture shows the measurements used in the plots. Note the general overlapping of all the taxa in all the variables.

(Werdelin & Peigné, 2010). This evolutionary hypothesis was also supported by Liu et al. (2021), who revised the lineages of this large-sized bone-cracking hyaena based on the excellent cranial material from Chinese sites. Following the indication of Werdelin (1999) and their own evidence, these authors suggest that the dispersal of this form into Europe at ca. 2.0 Ma originated from an Asian stock. This also seems to find confirmation if we consider that, at that time, *Pachycrocuta brevirostris* was restricted to South Africa. On the other hand, Martínez-Navarro (2010), and Palmqvist et al. (2011), based on the African Late Pliocene and Early Pleistocene record of *Pachycrocuta*, supported an African origin for this species. In any case, *Pachycrocuta* is recorded since the base of the late Villafranchian in Europe, in sites such as the Upper Valdarno (ca. 2.00-1.8 Ma; Rook et al., 2013; Madurell-Malapeira et al., 2024) until the latest Lower Pleistocene layer EVT7 of Vallparadís Section (ca. 0.86 Ma; Madurell-Malapeira et al., 2010, 2017, 2024) and survived in Asia until the Middle Pleistocene (Pei, 1934; Jiangzuo et al., 2022).

### *The "*Pachycrocuta brevirostris *event" and the beginning of the late Villafranchian*

The middle-to-late Villafranchian faunal turnover was traditionally described in Europe as the "*Wolf event*" (Azzaroli, 1977, 1983; Rook & Torre, 1996) based on the arrival of three large canids (*Xenocyon falconeri* Forsyth Major, 1877, *Canis etruscus* Forsyth Major, 1877, and *Canis arnensis* Del Campana, 1913) on the continent. Torre et al. (1992) were the first to propose the fortunate definition of a "*Pachycrocuta brevirostris* dispersal event". This expression was later reused by later authors, such as Palombo et al. (2008) and particularly Martínez-Navarro (2010), the latter of which frequently cited as the work that replaced the Azzaroli's "*Wolf event*" (see also the discussion of Iannucci et al., 2023 and Spassov, 2024). This interpretation is based on the increasing evidence of the diachronic nature of the "*Wolf event*" (Lacombat et al., 2006; Sotnikova & Rook, 2010; Bartolini-Lucenti & Spassov, 2022; Marciszak et al., 2023; Spassov, 2024, and references therein) and, particularly, upon consideration of the radical impact of this large hyaenid as a biological agent of accumulation and modification of late Villafranchian and Epivillafranchian European fossil assemblages, since its arrival in Europe at the base of the late Villafranchian, ca. 2.0-1.8 Ma (Madurell-Malapeira et al., 2024).

### *The Dmanisi sample in the framework of the Old World record and the* Pachycrocuta *origin and dispersal*

Our morphological and morphometric comparisons, both on juvenile and adult specimens, clearly indicate the better attribution of the hyaenid from Dmanisi to *Pachycrocuta*, while discouraging the previous interpretation to the earlier and more primitive form *Pl. perrieri* (as advocated by Vekua, 1995; Agustí & Lordkipanidze, 2011). Vekua reported the occurrence of *Pl. perrieri* on the basis of two specimens: 1) a dp4 (D1129: Tab. 1; Fig. S1), which fits perfectly with the morphology and measurements of *P. brevirostris* from European sites and the rest of the Dmanisi sample (Figs 2, 7, 9); and 2) a maxillary fragment with the P3 and the alveolus of the P4 (D167: Fig. S1). This specimen differs greatly from the morphology of hyaenids, as the P3 has a buccolingually compressed and short occlusal morphology, a high and sharp protocone, and possesses a distinctive disto-basal portion of the crown with a small distal accessory cusp (Fig. S1). On the contrary, hyaenas have buccolingually larger morphology, oval in occlusal shape, with a stout and enlarged P3 protocone (e.g., fig. 2 in Madurell-Malapeira et al., 2024). Thus, the maxillary fragment should be correctly attributed to a mid-sized felid on the basis of the P3 morphology.

Indeed, the size of the deciduous dentition (often used as discriminating parameter) has, in the present study, proven to be rather variable both in *Pachycrocuta* and *Pliocrocuta* (Fig. 9). It should be noted that Vekua (1995) did not mention comparisons with *P. brevirostris* and instead performed metric comparisons only with *Pl. perrieri*. The uninformative comparative sample confused, rather than strengthened, Vekua's conclusions. Even the morphological argument of the absence (or rare presence) of the metaconid on the dp4 (Vekua, 1995) seems to represent a shared characteristic between *Pachycrocuta* and *Pliocrocuta* (see Viret, 1954; Martínez-Navarro, 1991; Moullé & Tréguier, 2006) rather than a diagnostic feature of *Pl. perrieri*.

Characteristics that are apparently more robust diagnostically are found in mandibular parameters, as shown in Fig. 10. The use of these features on samples from known sites (where only *Pachycrocuta* or *Pliocrocuta* were recorded) allows discrimination between

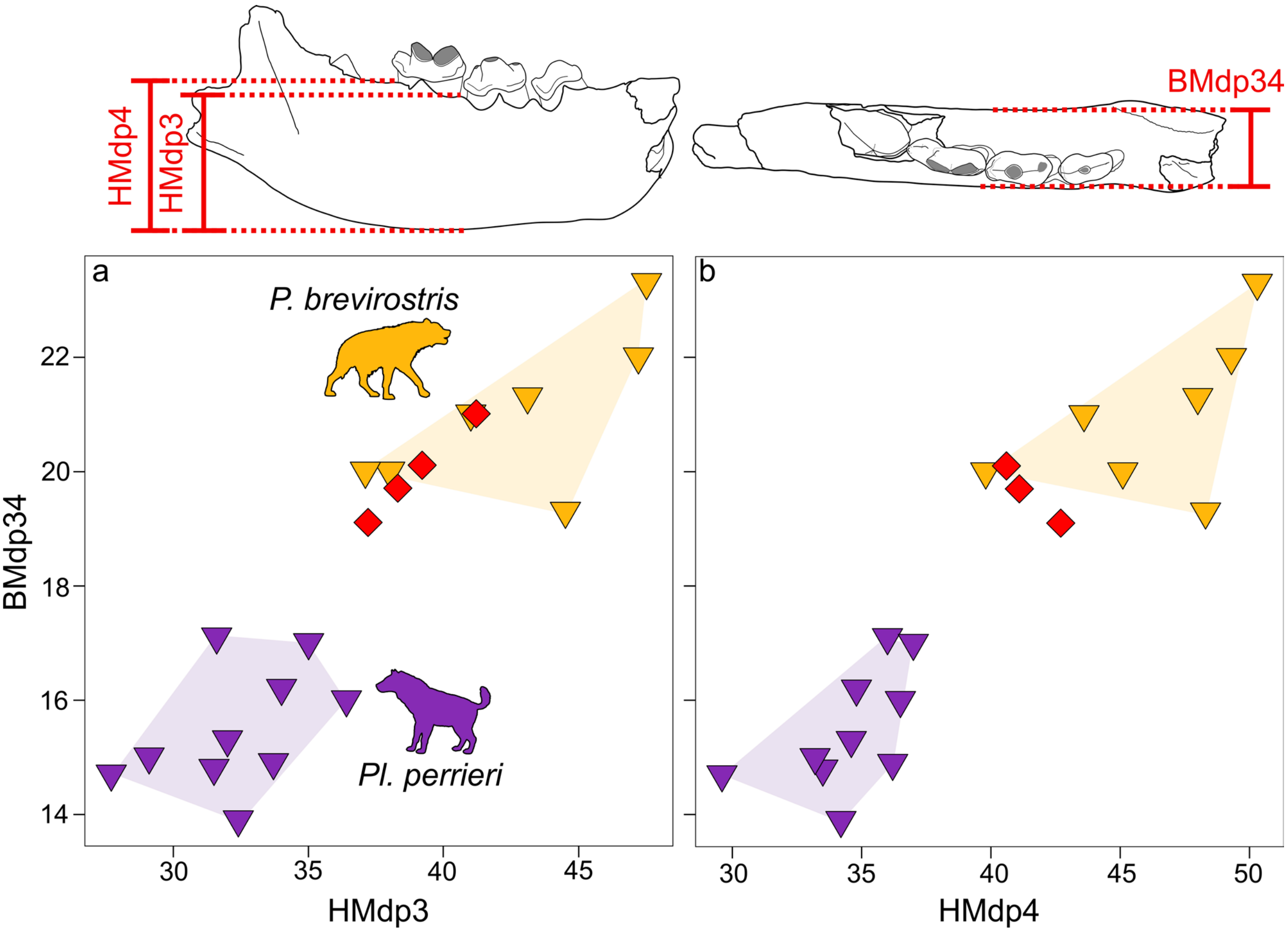


Fig. 10 (color online) - Plots of the height of the mandible measured distally to the dp3 (HMdp3) (a) and to the dp4 (HMdp4) (b) opposed to the breadth of the mandible at the interalveolar space between dp3-dp4 (BMdp34) in *Pliocrocuta* (from St. Vallier), *Pachycrocuta* (from Untermassfeld, Upper Valdarno, Vallonnet) and Dmanisi. Clear separation between *Pliocrocuta* and *Pachycrocuta* suggests the diagnostic value of these parameters.

juvenile mandibles of one or the other taxon. In our case, the mandibles from Dmanisi clearly and markedly grouped with *Pachycrocuta*, leaving very little doubt regarding their taxonomic attribution. The same unambiguous results emerge from the analyses of adult specimens (Figs 11 and 12), where the P4 (D2286) and the adult mandible (D6650) lie close to or even enclosed within the variability of *P. brevirostris* and lie far from *Pl. perrieri* or other taxa.

Several authors have reported the coexistence of both *P. brevirostris* and *Pl. perrieri* in the same site (Koufos, 1992; Konidaris & Kostopolous, 2024). In their revision of Early-Middle Pleistocene hyaenid occurrences, Iannucci et al. (2021) mentioned this coexistence in Fonelas P-1 (Southern Iberian Peninsula) and Gerakarou (Greece). In the former site, Arribas & Garrido (2008) attributed a dp3 (FP1 2001-0089) to *Pachycrocuta brevirostris*, among other fragmented decidual teeth (Arribas & Garrido, 2008: fig. 1, p. 205). The morphology of this dp3 contrasts with the ascribed taxon for the lingual inclination of the mesial and distal accessory cuspulids. The mesial accessory cuspulid is rather small. This morphology is closer to *Pl. perrieri* (e.g., cf. Viret, 1954; Moullé & Tréguier, 2006), as the mesial accessory cuspulid in *P. brevirostris* is well-developed and the two accessory cuspulids are in the same line with the protoconid (cf. Moullé & Tréguier, 2006). Thus, the ascription of the tooth from Fonelas P1 to *Pachycrocuta* is rather dubious and should be taken with care. The mention of *P. brevirostris* in Gerakarou is similar to the case of Fonelas P1; Koufos (1992) described the adult dentognathic material of *Pl. perrieri* and decided to ascribe eight deciduous and dentognathic fragments to *P. brevirostris*.

We share Koufos' interpretation of the occurrence of *Pl. perrieri* in Gerakarou, as evidenced by the mandible GER-150 (Koufos, 1992: fig. 5.2a-b) characterised by a slender mandibular corpus. Koufos (1992: fig. 6.1-2) also figures two of the eight fragments supposedly attributed to *P. brevirostris* (GER-156 and GER-157). In the fragmentary mandibular corpus with p4-m1 GER-157, the morphology of p4, with buccolingually wide distal part, is characteristic of *Pachycrocuta.* The m1 talonid seems mesiodistally long in way more similar to *Pliocrocuta*, but this morphology could be consequence of a breakage, thus masking or altering the outline of the carnassial at this level. The maxillary fragment GER-156 with DP2-DP3 also shares more similarities with *P. brevirostris* than to *Pl. perrieri.* Specifically, the morphology of the DP2, with a distinctive mesial accessory cuspid and the buccolingually wide distal part, is characteristic of *Pachycrocuta* (Moullé & Tréguier, 2006), as compared with the buccolingually sharp DP2 with reduced mesial accessory cuspid of *Pliocrocuta* (e.g., UCBL FSL495807 from Saint-Vallier; see also Viret, 1954). Nevertheless, despite the morphological and biometrical data seem to indicate the occurrence of the two taxa at Gerakarou, but this affirmation needs to be taken with care. The stratigraphic profile of the Gerakarou site (Koufos & Melentis, 1982; Koufos, 1992) within the Langada basin is formed by deposits 600 m thick. Koufos & Melentis (1982) and Koufos (1992) specified that the fossil site is located in the upper part of the "red beds" sediments of the premygdonian system, a lacustrine and fluvioterrestrial system roughly 100 m thick. This system is composed of dozens of geological layers that are not chronologically restricted (only biochronological data are provided). The stratigraphic provenance of the fossils of hyaenids is not specified by the authors, and their provenance from different geological members/layers (thus with slightly different chronologies) cannot be excluded and must be borne in mind. Moreover, there is also the ecological aspect to consider. Although there are some accounts of living *Hyaena hyaena* – which is phylogenetically close to both *Pliocrocuta* and *Pachycrocuta* – shifting dietary behaviour depending on the presence of the competitor *Crocuta crocuta* (Kruuk, 1976; Mills, 1989), independently from the geographic area observed, the two fossil genera of bone-cracking hyaenas probably displayed the same feeding ecology and perhaps competitively excluded each other, if ever present in the same environment (Johnston & Bronstein, 2019).

In summary, despite the claims of coexistence between *Pliocrocuta* and *Pachycrocuta* in any European site, present data are not sufficiently conclusive or reliable to take them with confidence.

Werdelin & Peigné (2010) improved the original description made by Kretzoi (1938), for the genus *Pachycrocuta*, based on the African samples, characterising it as a very large and stout Hyaenidae with massive premolars (i.e., buccolingually wide); P4 with massive paracone and protocone; p2-p3 lacking mesial accessory cuspulids; m1 mesiodistally short and broad, lacking metaconid and with the talonid possessing only hypoconid. This general description fits well for the Dmanisi specimens described in previous sections, slightly differing only in the m1 talonid morphology.

Although a general consensus exists regarding the monospecific nature of the genus *Pachycrocuta* in its Old World-wide distribution (Turner & Antón, 1996; Palmqvist et al., 2011 and references therein) some authors, especially in the first half of the 20th Century,

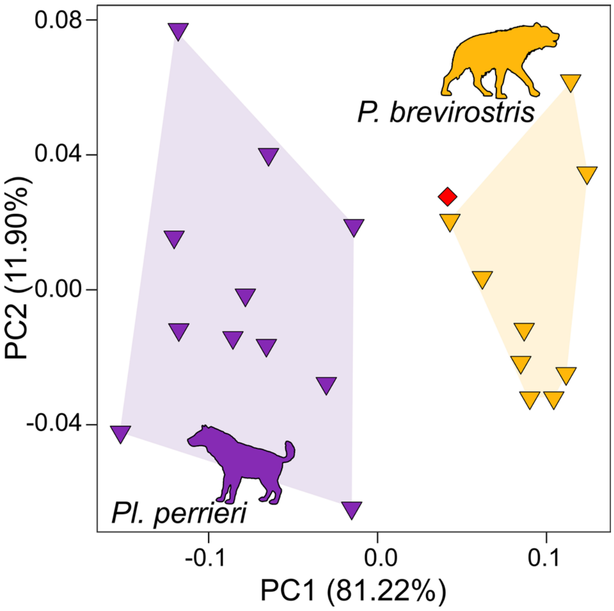


Fig. 11 (color online) - Principal Component Analysis (PCA) performed on log-transformed P4 variables on *Pachycrocuta brevirostris*, *Pliocrocuta perrieri* and the adult P4 from Dmanisi (D2286).

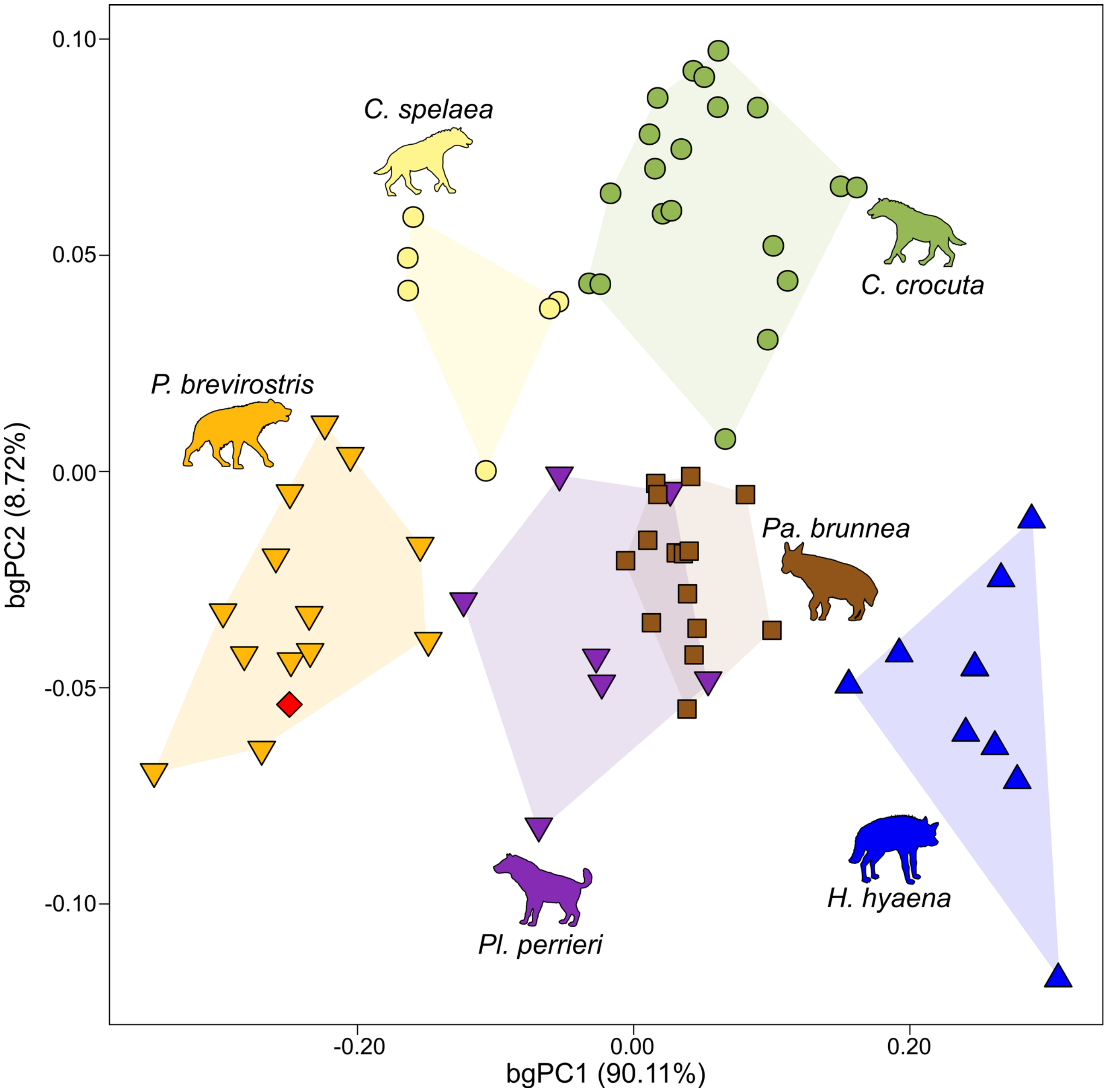


Fig. 12 (color online) - Between-group Principal Component Analysis (bgPCA) performed on log-transformed dentognathic variables on fossil (*Crocuta spelaea*, *Pachycrocuta brevirostris* and *Pliocrocuta perrieri*), extant hyenids (*Crocuta crocuta*, *Hyaena hyaena*, *Parahyaena brunnea*), and the adult specimen from Dmanisi (D6650).

described other taxa that are now generally considered junior subjective synonyms of *P. brevirostris* (Werdelin & Peigné, 2010; Palmqvist et al., 2011). In the Asian continent these include *P. sinensis* (Teilhard de Chardin & Piveteau, 1930), *P. licenti* (Pei, 1934), *P. zdanskyi* (Pei, 1934) and *P. bathygnatha* (Dubois, 1908), while in South Africa, Ewer (1954) named it *P. bellax*. The recent work of Liu et al. (2021) recognises three different chronosubspecies of *P. brevirostris* in China: 1) *Pachycrocuta brevirostris licenti* Pei, 1934, erected on the type material from Nihewan, (middle Villafranchian). This form is characterised by a large M1 and commonly a tricuspid m1 talonid (Pei, 1934; Tong et al., 2023); 2) *Pachycrocuta brevirostris brevirostris* corresponds to the typical European form best exemplified by the Sainzelles skull (Turner & Antón, 1996; Liu et al., 2021), also present in Jinyuan Cave. It displays a reduced P3 mesial accessory cuspid and an m1 with bicuspid talonid with the entoconid larger than the hypoconid in most cases, but also displaying variability in this feature, with occurrence of tricuspid or unicuspid talonids; and 3) *Pachycrocuta brevirostris sinensis* Owen, 1870*,* first proposed based on isolated teeth collected from Sichuan (Owen, 1870). Later, this form was recognised in Zhoukoudian-1 (Pei, 1934), Changzi, Xuzhou and Hexian, among other Middle Pleistocene localities (Liu et al., 2021). It possesses P3 with an extremely reduced or non-existent mesial accessory cusp and m1 talonid with only one cuspid.

In the sample from Dmanisi, only a single specimen, the juvenile hemimandible D3917, bears a complete m1 with preserved a talonid. In D3917, the m1 talonid clearly displays two cuspids, a small buccal hypoconid and a larger, lingually placed, entoconid. These morphological characters are repeated in all the European *Pachycrocuta* samples we analysed (i.e., Vallparadís Section, Incarcal Complex, Cueva Victoria, Venta Micena, Pirro Nord, Upper Valdarno and Vallonnet). Bicuspid or unicuspid m1 talonids may occur, but a bicuspid talonid with small hypoconid and large entoconid is dominant (J.M.-M. unpublished data).

Obviously, analysing all the known samples of *Pachycrocuta* and testing the morphology of the m1 talonid is beyond the scope of this paper; however, it is noteworthy that most of the European samples, including Dmanisi, retain the "intermediate morphotype" described by Liu et al. (2021) as *P. b. brevirostris*. This reinforces the idea of an Asian expansion of *Pachycrocuta* into Europe around 2.2 Ma as a consequence of climate deterioration and the expansion of colder and drier environments to which the subsequent forms of *P. brevirostris* were better adapted (Liu et al., 2021). The former dispersion of Asian species into Europe, diachronous but in a short geological interval, previously reported as the "Wolf event", possibly also includes the pack-hunting canids *Canis borjgali* and *Xenocyon lycaonoides* and certain species of herbivorous animals, as we reported in the introductory section (cfr. Bartolini-Lucenti et al., 2021).

If the Eurasian taxonomic scenario of *Pachycrocuta* is fairly clear, the same cannot be said for the African record of the genus. Traditionally, the South African forms were included in the species *Pachycrocuta bellax*, which Werdelin (1999) synonymised with *P. brevirostris*, although it is of smaller size, and its differentiation from the Eurasian stock most probably started in the Late Pliocene. The record of this African form is fragmentary and scattered in different sites, such as Makapansgat (Randall, 1981), Gladysvale (Mutter et al., 2001) and Kromdraai (the type locality of *P. bellax*), all in South Africa. In fact, the only well-preserved m1 (specimen Ka 55) comes from the latter site (Ewer, 1954). The specimens show a residual metaconid and a tricuspid talonid. The situation in East Africa is not much better, as most of the identified remains correspond to *Pachycrocuta* sp. in sites like South-Turkwel, Laetoli and others (Werdelin, 1999; Werdelin & Lewis, 2000, 2008). The only specifically attributed remains are found in the Nachukui Formation of West Turkana (3.3-2.7 Ma; Werdelin, 1999).

### *Palaeobiology of* Pachycrocuta brevirostris

Turner & Antón (1996) and Palmqvist et al. (2011) described *P. brevirostris* as a typical scavenger hyaena, with stout craniodental proportions and robust postcranial skeletal elements, similar in proportions to the European Cave spotted hyaena (*Crocuta spelaea*), with an average body weight, based on the comparison of the postcranial skeleton of 120 kg, but with some specimens, as those from Zhoukoudian-1 in China close to 190-200 kg (Palmqvist et al., 2011). Furthermore, the structure of its appendicular skeleton is characterised by proportionately shorter distal segments of the fore and hind limbs (especially the tibia), suggesting that this hyaena was less cursorial compared with living hyaenas (Turner & Antón, 1996). Considering its large size and heavily built anatomy, *P. brevirostris* is interpreted as an aggressive and effective scavenger rather than a direct hunter (Turner & Antón, 1996; Palmqvist et al., 2011). It should be noted, though, that most of the former interpretations were based on the only known skeleton of this species (i.e., from Zhoukoudian-1; Pei, 1934).

Studies on the palaeoneurology of the Pleistocene bone-cracking hyaenas by Vinuesa et al. (2015, 2016), based on brain morphology and the relative development of the anterior brain in *Pliocrocuta perrieri*, *Crocuta spelaea* and *Crocuta ultima* (Matsumoto, 1915) revealed that these taxa show less development of the frontal cortex as compared with the extant *C. crocuta*; thus, they more closely resemble the condition of both extant *Hyaena hyaena* and *Parahyaena brunnea.* These results suggest that the more developed anterior brain of extant *C. crocuta* is a derived and recently acquired trait, probably arising in the Late Pleistocene of Africa. Moreover, the evidence suggests that extinct bone-cracking hyaenas (i.e., *Pliocrocuta* and *C. spelaea/ultima*) displayed less-developed social abilities and/or a more restricted adaptability to new environments compared to the former taxa (Vinuesa et al., 2015, 2016). Considering the last working hypothesis, it seems plausible to attribute to *Pachycrocuta brevirostris* limited social abilities or adaptability (i.e., compared to the extant *C. crocuta*) and to suppose that this large-sized species had a similar behaviour to that of *C. spelaea*. These ideas were also supported by previous authors (Turner & Antón, 1996).

### *Interactions between hominins and hyaenas*

Several Lower and Middle Pleistocene sites record the co-existence between hominins and short-faced hyaenas in Europe and Asia. Some examples include the Chinese localities of Zhoukoudian-1 Loc. 1; Gongwangling in Lantian; Hexian in Anhui Province and Yunxian in Hebei (Liu et al., 2021 and references therein). In Europe, examples include sites like Pirro Nord in Italy (Petrucci et al., 2013), Vallonnet in France (Moullé & Tréguier, 2006), or Fuente Nueva 3 and Barranco León in Orce, Spain (Martínez-Navarro et al., 2010; Espigares et al., 2013, 2019, 2023; Toro-Moyano et al., 2013; Palmqvist et al., 2024). Additionally, sites such as Venta Micena or Zhoukoudian-1 show evidence of distinctive patterns of accumulation and selective consumption of large mammal carcasses made by this bone-cracking hyaena (Palmqvist et al., 2011, 2024 and references therein; Espigares et al., 2013, 2023). In all the sites in which *P. brevirostris* and hominins co-exist, this carnivore plays a major role in the accumulation of bones, suggesting that hominins had a limited role among the factors contributing to the site's formation (Espigares et al., 2013 and references therein).

The scenario in sites where the record of *Pl. perrieri* is abundant seems radically different. First, the studied middle Villafranchian sites where this species is abundant, such as Saint-Vallier, Villarroya, or Puebla de Valverde (Viret, 1954; Kurtén & Crusafont-Pairó, 1977; J.M.-M. unpublished data), no selective accumulations and patterns of consumption made by *Pl. perrieri*, despite the abundance of juvenile specimens in several sites (e.g., Villarroya or La Puebla de Valverde), therefore suggesting a hyaena den (Valli, 2004; J. M.-M. unpublished data). Today, hyaena dens and general areas used to rear the cubs are located in small caves or spaces under jutting rocks (Mills, 1990). Similar denning behaviour could be hypothesised for the fossil species. The abundance of young individuals in cave or karstic contexts is plausible, considering the high rate of death of cubs in dens. Lastly, at present, no site is known in which *Pl. perrieri* and hominins co-existed.

The record of *P. brevirostris* in Dmanisi is characterised by the occurrence of abundant juvenile specimens (as at Vallonnet, Cueva Victoria, Vallparadís Section EVT12, and Venta Micena), suggesting an accumulation related to a high carnivore activity and a probable hyaena den (Palmqvist et al., 2011; Coil et al., 2020; Tappen et al., 2022). In fact, the depositional formation of the Dmanisi major fossil layers (namely B1, see Lordkipanidze et al., 2007; Ferring et al., 2011; Tappen et al., 2022) can be considered a pseudokarst (Coil et al., 2020). As in other sites in which *Pachycrocuta* and hominins co-existed, the sample from Dmanisi exhibits a high density of bones with surface modifications made by carnivores and a small number of stone tools. This is normally related to the fact that carnivores played a preponderant role in the site formation (Coil et al., 2020; Tappen et al., 2022). As suggested above, the scenario in Dmanisi thus saw carnivores as active accumulators, similarly to the situation in the other sites where *Pachycrocuta* is recorded. At the same time, it contrasts with assemblages associated with *Pliocrocuta*. All considered, the structure and the taphonomic evidence reinforce our taxonomic conclusions based on the anatomy of the studied remains.

Therefore, another explanation needs to be proposed to account for the number of juveniles of *P. brevirostris.* This might be related to the feeding behaviour of this hyaenid, as evident from the abundance of juvenile-subadult individuals (i.e., specimen D153; Fig. 2), with deciduous dentition showing a large size with stoutly built mandibles despite the sharp and slender dentition. These young *P. brevirostris* could not exploit bone marrow as the adults were able to do because of their durophagous dentition. Instead, the sharp and thin dentition allowed the young hyaenas to feed mainly on the meat of the carcasses, similarly to felids. Indeed, although *P. brevirostris* cubs may also have consumed a small portion of bone, this intake would have come from carnivoran bones and not from the thick-walled long bone of the herbivores. This behaviour is documented in other Lower Pleistocene accumulations made by *P. brevirostris* (e.g., Poggio Rosso; see Mazza et al., 2004) and it seems to be frequent in the extant *Parahyaena brunnea* when rearing cubs (Brain, 1981). Furthermore, a similar relation/behaviour was suggested for *P. brevirostris* and *C. borjgali* by Tappen et al. (2022) in their recent taphonomy analysis. Carnivoran bones are thinner-walled and less rich in marrow and fat, so cubs would still need to eat a lot of meat to reach the large size of individuals able to join the adults of the group in hunting and to support them in kleptoparasitic activities and prey defence. Indeed, the reduced bone cracking capabilities of hyaena juveniles compared to those of the adults must have led *P. brevirostris* individuals to specialise in the exploitation of different parts of a carcass: the meat for the juveniles and the marrow and fat for the adults.

These later affirmations were corroborated by the different HSB pattern seen in the juveniles and adults of Dmanisi (Fig. 5). The adults of *P. brevirostris* display a clear zig-zag HSB outline, which made the enamel more resistant to stresses on the teeth as consequences of bone-eating behaviour (as well known in the literature: Stefen & Rensberger, 1999; Ferretti, 2007; Tseng, 2012). On the other hand, the deciduous dentition of *Pachycrocuta* shows a different and more undulating outline, which more closely resembles that of other carnivorans (Stefen & Rensberger, 1999). This pattern is normally present in hypercarnivorous or mesocarnivorous taxa (inter alios Ferretti, 2007; Novelli et al., 2008; Tseng, 2011, 2012).

Curiously, a parallelism can be made to the possible behaviour of the early *Homo erectus* of Dmanisi, which was one of the main competitors of the large-sized hyaena. As with *P. brevirostris*, specimens of *H. erectus* were adapted to be scavengers, but they were only able to eat fresh carrion, because, as upstart carnivores, they were not physiologically prepared to digest rotten meat, as most carnivores do. Therefore, humans needed quick access to the carcasses, before any other large carnivore. Otherwise, they could not eat any part of the carcasses. In this specialisation, humans also broke the bones of the carrion with the help of the large oldowan tools they used as hammers. Once the bones were cut open, *H. erectus* took the marrow and the brain from the carcasses. However, in this case, these materials were most probably used to feed the elderly people, as probably is the case of the old individual recorded by the toothless cranium and mandible (D3444/D3900; Lordkipanidze et al., 2005), as well as possibly juveniles with incipient deciduous teeth. In all likelihood, only human individuals with adult and erupted deciduous teeth were able to eat meat. Humans also took advantage of scavenging and eating the carcasses of large mammals, but they were using fat to feed babies, young children and aged individuals, leaving the meat for older children and adults.

## CONCLUSIONS

The site of Dmanisi offers the opportunity to study one of the best preserved and diverse records of Lower Pleistocene large fossil carnivores of Eurasia. In previous publications, the unearthed specimens of Hyaenidae were referred to as two different taxa. Here, we review and redescribe the hyaenid sample of Dmanisi, concluding that all the recovered specimens can be accommodated in one species, *Pachycrocuta brevirostris*. The stout overall morphology and large dimensions of the Dmanisi sample allow its differentiation from other species, such as *Pliocrocuta perrieri*. The morphological traits observed in the studied sample fit with the available European record of the late Villafranchian and Epivillafranchian *P. brevirostris* while differing from some Asian middle Villafranchian and derived Middle Pleistocene forms. The scarce *Pachycrocuta* African record does not enable us to perform an in-depth comparison of our samples with African specimens, especially those from South African sites.

Concerning palaeobiological and/or taphonomic inferences, the data from Dmanisi, where carnivores play a major role in an accumulation dominated by juvenile hyaena specimens in a pseudokarstic scenario, seem more similar to other studied and well known *Pachycrocuta* accumulations than to assemblages associated with *Pliocrocuta*. Additionally, the abundant record of juvenile specimens of *P. brevirostris* at Dmanisi can be further interpreted as related to the eating behaviour of this species. The large size of the hyaena mandibles with preserved deciduous hypercarnivore dentition suggests that they grew very fast as flesh eaters with a diet high in meat proteins and without the ability to break bones and eat the marrow. Bone marrow content was only accessible to adult individuals, which had very robust premolars, capable of breaking the bones. Juvenile and adult *P. brevirostris* individuals accessed different portions of the carcasses: juveniles mostly eating meat, and adults eating meat but also the marrow content inside the bones. This different feeding behaviour in juvenile and adult individuals of *P. brevirostris*, increased their effectiveness in consuming the total carcasses of large mammals (meat, fat and marrow), making this large scavenger the most important competitor for carrion with hominins who, thanks to their technology, were also fighting for the same food.

## SUPPLEMENTARY ONLINE MATERIAL

Supplementary data are available on the BSPI website at: https://www.paleoitalia.it/bollettino-spi/bspi-vol-641/

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## REFERENCES

Agustí J. & Lordkipanidze D. (2011). How "African" was the early human dispersal out of Africa? *Quaternary Science Reviews*, 30: 1338-1342.

Alba D.M., Vinuesa V. & Madurell-Malapeira J. (2013). On the original author and year of description of the extinct hyaenid *Pachycrocuta brevirostris*. *Acta Palaeontologica Polonica*, 60: 573-576.

Argant A. (2004). The Carnivores of the late Pliocene site of Saint-Vallier (Drome, France). *Geobios*, 37: S133-S182.

Argant A. (2024). The Carnivores of Senèze (Haute-Loire). *In* Delson E., Faure M. & Guérin C. (eds), Senèze: life in Central France two million years ago. Paleontology, Geochronology, Stratigraphy and Taphonomy, Springer, Cham: 165-243.

Arribas A. & Garrido G. (2008). Hiénidos [*Pachycrocuta brevirostris* (Aymard, 1846) y *Hyaena brunnea* Thunberg, 1820] del yacimiento de Fonelas P-1 (cuenca de Guadix, Granada). *In* Arribas A. (ed.), Vertebrados del Plioceno Superior Terminal en el Suroeste de Europa: Fonelas P-1 y el Proyecto Fonelas, Instituto Geológico y Minero de España, Madrid: 201-230.

Arribas A., Garrido G., Viseras C., Soria J.M., Pla S., Solano J.G., Garcés M., Beamud E. & Carrión J.S. (2009). A mammalian lost world in Southwest Europe during the late Pliocene. *PLoS ONE*, 4: e7127.

Azzaroli A. (1953). The deer of the Weybourn Crag and Forest Bed of Norfolk. *Bulletin of British Museum (Natural History), Geology*, 2: 1-96.

Azzaroli A. (1977). The Villafranchian stage in Italy and the Plio-Pleistocene boundary. *Giornale di Geologia*, 41: 61-79.

Azzaroli A. (1983). Quaternary mammals and the "End-Villafranchian" dispersal event - A turning point in the history of Eurasia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 44: 117-139.

Ballesio R. (1986). Les Carnivores du gisement Pléistocène d'Oubéidiyeh. *In* Tchernov E. (ed.), Les mammifères du Pléistocène Inférieur, de la Vallée du Jourdain a Oubéidiyeh, Association Paléorient, Paris: 63-92.

Bartolini-Lucenti S. & Spassov N. (2022). Cave canem! The earliest *Canis* (*Xenocyon*) (Canidae, Mammalia) of Europe: taxonomic affinities and paleoecology of the fossil wild dogs. *Quaternary Science Reviews*, 276: 107315.

Bartolini-Lucenti S., Bukhsianidze M., Martínez-Navarro B. & Lordkipanidze D. (2020). The wolf from Dmanisi and augmented reality: review, implications, and opportunities. *Frontiers in Earth Science*, 8: 131.

Bartolini-Lucenti S., Madurell-Malapeira J., Martínez-Navarro B., Palmqvist P., Lordkipanidze D. & Rook L. (2021). The early hunting dog from Dmanisi with comments on the social behaviour in Canidae and hominins. *Scientific Reports*, 11: 13501.

Bartolini-Lucenti S., Cirilli O., Pandolfi L., Bernor R.L., Bukhsianidze M., Carotenuto F., Lordkipanidze D., Tsikaridze N. & Rook L. (2022a). Zoogeographic significance of Dmanisi large mammal assemblage. *Journal of Human Evolution*, 163: 103125.

Bartolini-Lucenti S., Madurell-Malapeira J., Martínez-Navarro B., Cirilli O., Pandolfi L., Rook L., Bushkhianidze M. & Lordkipanidze D. (2022b). A comparative study of the Early Pleistocene carnivore guild from Dmanisi (Georgia). *Journal of Human Evolution*, 162: 103108.

Brain C.K. (1981). The hunters or the hunted?: an introduction to African cave taphonomy. 376 pp. University of Chicago Press, Chicago.

Brisson M.J. (1762). Regnum Animate in classes IX distributum. Sive synopsis methodica. Second edition. 296 pp. Haak, Leiden.

Broom R. (1937). On some new Pleistocene mammals from limestone caves of the Transvaal. *South African Journal of Science*, 33: 750-768.

Burchak-Abramovich N.I. & Vekua A.K. (1990). The fossil ostrich *Struthio dmanisensis* sp. n. from the Lower Pleistocene of Eastern Georgia. *Acta Zoologica Cracoviensia*, 33: 121-132.

Burchak-Abramovich N.I. & Vekua A.K. (1994). Novyj predstavitel pleistocennovych bykov iz vostochnoj Gruzii. *Voprosi Teriologii Paleoteriologija*, 1: 253-261 [in Russian].

Cappellini E., Welker F., Pandolfi L., Ramos-Madrigal J., Samodova D., Rüther P.L., Fotakis A.K., Lyon D., Moreno-Mayar J.V., Bukhsianidze M., Rakownikow Jersie-Christensen R., Mackie M., Ginolhac A., Ferring R., Tappen M., Palkopoulou E., Dickinson M.R., Stafford T.W., Chan Y.L., Götherström A., Nathan S.K.S.S., Heintzman P.D., Kapp J.D., Kirillova I., Moodley Y., Agustí J., Kahlke R.D., Kiladze G., Martínez-Navarro B., Liu S., Sandoval Velasco M., Sinding M.H.S., Kelstrup C.D., Allentoft M.E., Orlando L., Penkman K., Shapiro B., Rook L., Dalén L., Gilbert M.T.P., Olsen J.V., Lordkipanidze D. & Willerslev E. (2019). Early Pleistocene enamel proteome from Dmanisi resolves *Stephanorhinus* phylogeny. *Nature*, 574: 103-107.

Cocchi I. (1867). L'Uomo fossile dell'Italia centrale. *Memorie della Società Italiana di Scienze Naturali*, 2: 1-180.

Coil R., Tappen M., Ferring R., Bukhsianidze M., Nioradze M. & Lordkipanidze D. (2020). Spatial patterning of the archaeological and paleontological assemblage at Dmanisi, Georgia: an analysis of site formation and carnivore-hominin interaction in Block 2. *Journal of Human Evolution*, 143: 102773.

Croizet J.B. & Jobert A. (1828). Recherches sur les ossemens fossiles du département du Puy-de-Dôme. Volume 1. 133 pp. Thibaud Landriot, Clermont Ferrand.

Cuvier G. (1823). Recherches sur les ossemens fossiles, où l'on rétablit les caractères de plusieurs animaux dont les révolutions du globe ont détruit les espéces. Nouvelle edition. Volume 4. 514 pp. G. Dufour et E. d'Ocagne, Paris.

De Villalta-Comella J.F. (1952). Contribución al conocimiento de la fauna de mamíferos fósiles del Plioceno de Villaroya. *Boletin del Instituto Geologico y Minero de España*, 64: 1-204.

Del Campana D. (1913). I cani pliocenici di Toscana. *Palaeontographia Italica*, 19: 189-254.

Delson E., Nomade S., Sen S., Debard E., Pastre J.F., Bahain J.J., Shao Q. & Falguères C. (2024). Geochronology of Senèze: $^{40}$Ar/$^{39}$Ar dating and magnetostratigraphy, with notes on an ESR/U-series dating attempt. *In* Delson E., Faure M. & Guérin C. (eds), Senèze: life in Central France two million years ago. Paleontology, Geochronology, Stratigraphy and Taphonomy, Springer, Cham: 99-122.

Dubois E. (1894). *Pithecanthropus erectus*: Eine menschenähnliche Übergangsform aus Java. 39 pp. Landesdruckerei, Batavia.

Dubois E. (1908). Das Geologische alter der Kendengoder Trinil-fauna. *Tijdschrift van het Koninklijk Nederlandsch Aardrijkskunding Genootschap*, Series 2, 25: 1235-1270.

Espigares M.P., Martínez-Navarro B., Palmqvist P., Ros-Montoya S., Toro I., Agustí J. & Sala R. (2013). *Homo* vs. *Pachycrocuta*: earliest evidence of competition for an elephant carcass between scavengers at Fuente Nueva-3 (Orce, Spain). *Quaternary International*, 295: 113-125.

Espigares M.P., Palmqvist P., Guerra-Merchán A., Ros-Montoya S., García-Aguilar J.M., Rodríguez-Gómez G., Serrano F.J. & Martínez-Navarro B. (2019). The earliest cut marks of Europe: a discussion on hominin subsistence patterns in the Orce sites (Baza basin, SE Spain). *Scientific Reports*, 9: 15408.

Espigares M.P., Palmqvist P., Rodríguez-Ruiz M.D., Ros-Montoya S., Pérez-Ramos A., Rodríguez-Gómez G., Guerra-Merchán A., García-Aguilar J.M., Granados A., Campaña I. & Martínez-Navarro B. (2023). Sharing food with hyenas: a latrine of *Pachycrocuta brevirostris* in the Early Pleistocene assemblage of Fuente Nueva-3 (Orce, Baza Basin, SE Spain). *Archaeological and Anthropological Sciences*, 15: 81.

Erxleben J.C.P. (1777). Systema regni animalis per classes, ordines, genera, species, varietates, cum synonymia et historia animalium: classis I. Mammalia. 752 pp. Imprensis Weigandianis, Lipsiae.

Ewer R.F. (1954). Some adaptive features in the dentition of hyaenas. *Annals and Magazine of Natural History*, 7: 188-194.

Falconer H. (1868). On the European Pliocene and postpliocene species of the genus *Rhinoceros*. *Paleontological Memoires and notes*, 2: 309-403.

Fernández-Jalvo Y., Valli A.M.F., Marín-Monfort M.D. & Pesquero-Fernández M.D. (2024). The Taphonomy of Senèze. *In* Delson E., Faure M. & Guérin C. (eds), Senèze: life in Central France two million years ago. Paleontology, Geochronology, Stratigraphy and Taphonomy, Springer, Cham: 653-681.

Ferretti M.P. (2007). Evolution of bone-cracking adaptations in hyaenids (Mammalia, Carnivora). *Swiss Journal of Geosciences*, 100: 41-52.

Ferring R., Oms O., Agustí J., Berna F., Nioradze M., Shelia T., Tappen M., Vekua A., Zhvania D. & Lordkipanidze D. (2011). Earliest human occupations at Dmanisi (Georgian Caucasus) dated to 1.85-1.78 Ma. *Proceedings of the National Academy of Sciences*, 108: 10432-10436.

Forsyth Major C.I. (1877). Considerazioni sulla fauna dei Mammiferi pliocenici e postpliocenici della Toscana. III. Cani fossili del Val d'Arno superiore e della Valle dell'Era. *Atti della Società Toscana di Scienze Naturali*, Memorie, 3: 207-227.

Gervais P.M. (1850). Zoologie et Paléontologie Françaises Nouvelles recherches sur les animaux vivants et fossiles de la France. Tome I. Contenant l'ènumerération méthodique et descriptive des espèces ainsi que les principes de leur distribution géographique et paléontologique. 271 pp. Arthus Bertrand, Paris.

Goldfuss G.A. (1823). Ueber den Hölenwolf (*Canis spelaeus*). Osteologische Beiträge zur Kenntniss verschiedener Säugetiere der Vorwelt. Acta Physico-Medica Academiea Caesarae Leopoldino-Carolinae *Naturae Curiosorum*, 3: 451-455.

Hemmer H., Kahlke R.D. & Vekua A.K. (2010). *Panthera onca georgica* ssp. nov. from the Early Pleistocene of Dmanisi (Republic of Georgia) and the phylogeography of jaguars (Mammalia, Carnivora, Felidae). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 257: 115-127.

Hendey Q.B. (1974). The late Cenozoic Carnivora of the southwestern Cape Province. *Annals of the South African Museum*, 63: 1-369.

Howell F.C. & 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: 579-623.

Iannucci A., Mecozzi B., Sardella R. & Iurino D.A. (2021). The extinction of the giant hyena *Pachycrocuta brevirostris* and a reappraisal of the Epivillafranchian and Galerian Hyaenidae in Europe: faunal turnover during the Early-Middle Pleistocene transition. *Quaternary Science Reviews*, 272: 107240.

Iannucci A., Mecozzi B., Kahlke R.D. & Sardella R. (2022). New results on Hyaenids from the Early Pleistocene site of Untermassfeld. *In* Kahlke R.D. (ed.), The Pleistocene of Untermassfeld near Meiningen (Thüringen, Germany). Part 5, Monographien. Verlag des Römisch-Germanischen Zentralmuseums, Mainz: 1403-1422.

Iannucci A., Mecozzi B. & Sardella R. (2023). Beware of the "Wolf event" - Remarks on large mammal dispersals in Europe and the late Villafranchian faunal turnover. *Alpine and Mediterranean Quaternary*, 36: 75-90.

Jiangzuo Q., Liu J., Jiang H. & Wang Y. (2022). A huge *Pachycrocuta* from the Middle Pleistocene loess in Luoning County, central China, and the evolution of mandible within *Pliocrocuta-Pachycrocuta* lineage. *Historical Biology*, 1-7.

Johnson C.A. & Bronstein J.L. (2019). Coexistence and competitive exclusion in mutualism. *Ecology*, 100: 1-8.

Konidaris G. & Kostopoulos D. (2024). The Late Pliocene–Middle Pleistocene Large Mammal Faunal Units of Greece. *Quaternary*, 7: 27.

Kostopoulos D. (1996). The Plio-Pleistocene artiodactyls of Macedonia (Greece): systematic, palaeoecology, biochronology, biostratigraphy. 612 pp. Unpublished Ph.D. Thesis, Aristotle University of Thessaloniki, Thessaloniki.

Koufos G.D. (1992). The Pleistocene carnivores of the Mygdonia Basin (Macedonia, Greece). *Annales de Paléontologie*, 78: 205-257.

Koufos G.D. (2018). New material and revision of the Carnivora, Mammalia from the Lower Pleistocene locality Apollonia 1, Greece. *Quaternary*, 1: 6.

Koufos G.D. (2024). Updating the fauna and age of the Neogene-Quaternary large mammal sites of Greece. *Geobios*, 85: 35-57.

Koufos G.D. & Kostopoulos D.S. (1997). New carnivore material from the Plio-Pleistocene of Macedonia (Greece) with a description of a new Canid. *Münchner Geowissenschaftliche Abhandlungen*, 34: 33-63.

Koufos G.D. & Melentis J.K. (1983). New data from the Villafranchian mammal locality of Gerakarou (Macedonia, Greece). *Proceedings of the Academy of Athens*, 58: 185-191.

Kretzoi M. (1938). Die Raubtiere von Gombaszög nebst einer Übersicht der Gesamtfauna. *Annales Musei Nationalis Hungarici, Pars Mineralogica, Geologica, Palaeontologica*, 31: 88-157.

Kruuk H. (1976). Feeding and social behaviour of the striped hyaena (*Hyaena vulgaris* Desmarest). *African Journal of Ecology*, 14: 91-111.

Kurtén B. & Crusafont-Pairó M. (1977). Villafranchian Carnivores (Mammalia) from La Puebla De Valverde (Teruel, Spain). *Commentationes Biologicae*, 85: 1-39.

Lacombat F., Abbazzi L., Ferretti M., Martínez-Navarro B., Moullé P.-E., Palombo M., Rook L., Turner A. & Valli A.-M. (2008). New data on the Early Villafranchian fauna from Vialette (Haute-Loire, France) based on the collection of the Crozatier Museum (Le Puy-en-Velay, Haute-Loire, France). *Quaternary International*, 179: 64-71.

Lewis M.E. & Werdelin L. (2022). A revision of the genus *Crocuta* (Mammalia, Hyaenidae). *Palaeontographica, Abteilung A*, 322: 1-115.

Linnaeus C. (1758). Systema naturæ: per regna tria naturaæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. (In latín). Editio Decima Reformata. 823 pp. Laurentii Slavii, Holmiae.

Liu J., Liu J., Zhang H., Wagner J., Jiangzuo Q., Song Y., Liu S., Wang Y. & Jin C. (2021). The giant short-faced hyena *Pachycrocuta brevirostris* (Mammalia, Carnivora, Hyaenidae) from Northeast Asia: A reinterpretation of subspecies differentiation and intercontinental dispersal. *Quaternary International*, 577: 29-51.

Lordkipanidze D., Vekua A., Ferring R., Rightmire G.P., Agustí J., Kiladze G., Mouskhelishvili A., Nioradze M., Ponce de León M.S., Tappen M. & Zollikofer C.P.E. (2005). The earliest toothless hominin skull. *Nature*, 434: 717-718.

Lordkipanidze D., Jashashvili T., Vekua A., Ponce de León M.S., Zollikofer C.P.E., Rightmire G.P., Pontzer H., Ferring R., Oms O., Tappen M., Bukhsianidze M., Agustí J., Kahlke R., Kiladze G., Martínez-Navarro B., Mouskhelishvili A., Nioradze M. & Rook L. (2007). Postcranial evidence from early *Homo* from Dmanisi, Georgia. *Nature*, 449: 305-310.

Madurell-Malapeira J. & Vinuesa V. (2016). El yacimiento villafranquiense inicial de Villarroya (Logroño, España): colecciones del Institut Catalá de Paleontología Miquel Crusafont. *In* Alberdi M.T., Azanza B. & Cervantes E. (eds), Villarroya: yacimiento clave de la paleontología riojana, Instituto de Estudios Riojanos, La Rioja: 183-216.

Madurell-Malapeira J., Minwer-Barakat R., Alba D.M., Garcés M., Gómez M., Aurell-Garrido J., Ros-Montoya S., Moyà-Solà S. & Berástegui X. (2010). The Vallparadís section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe. *Quaternary Science Reviews*, 29: 3972-3982.

Madurell-Malapeira J., Morales J., Vinuesa V. & Boscaini A. (2015). Úrsidos, hiénidos y félidos del Pleistoceno inferior de Cueva Victoria (Cartagena, Murcia). *In* Gibert L. & Ferràndez-Cañadell C. (eds), Geología y Paleontología de Cueva Victoria. *MASTIA Revista del Museo Arqueológico Municipal de Cartagena*, 11-13: 401-432.

Madurell-Malapeira J., Alba D., Espigares M., Vinuesa V., Palmqvist P., Martínez-Navarro B. & Moyà-Solà S. (2017). Were large carnivorans and great climatic shifts limiting factors for hominin dispersals? Evidence of the activity of *Pachycrocuta brevirostris* during the Mid-Pleistocene Revolution in the Vallparadís Section (Vallès-Penedès Basin, Iberian Peninsula). *Quaternary International*, 431: 42-52.

Madurell-Malapeira J., Prat-Vericat M., Bartolini-Lucenti S., Faggi A., Fidalgo D., Marciszak A. & Rook L. (2024). A review on the latest Early Pleistocene Carnivoran guild from the Vallparadís Section (NE Iberia). *Quaternary*, 7: 40.

Marciszak A., Kropczyk A., Gornig W., Kot M. & Nadachowski A. (2023). History of Polish Canidae (Carnivora, Mammalia) and their biochronological implications on the Eurasian background. *Genes*, 14: 1-27.

Martínez-Navarro B. (1991). Revision sistematica y estudio cuantitativo de la fauna de macromammiferos del yacimiento de Venta Micena. 431 pp. Unpublished PhD Thesis, Universitat Autònoma de Barcelona, Barcelona.

Martínez-Navarro B. (2010). Early Pleistocene faunas of Eurasia and Hominin dispersals. *In* Fleagle J.G., Shea J.J., Grine F.E., Baden A.L. & Leakey R.E. (eds), Out of Africa I: The First Hominin Colonization of Eurasia, Vertebrate Paleobiology and Paleoanthropology, Springer, Dordrecht: 207-224.

Martínez-Navarro B. & Palmqvist P. (1995). Presence of the African machairodont *Megantereon whitei* (Broom, 1937) (Felidae, Carnivora, Mammalia) in the Lower Pleistocene site of Venta Micena (Orce, Granada, Spain), with some considerations on the origin, evolution and dispersal of the genus. *Journal of Archaeological Science*, 22: 569-582.

Martínez-Navarro B. & Palmqvist P. (1996). Presence of the African saber-toothed felid *Megantereon whitei* (Broom, 1937) (Mammalia, Carnivora, Machairodontinae) in Apollonia-1 (Mygdonia Basin, Macedonia, Greece). *Journal of Archaeological Science*, 23: 869-872.

Martínez-Navarro B., Belmaker M. & Bar-Yosef O. (2009). The large carnivores from 'Ubeidiya (early Pleistocene, Israel): biochronological and biogeographical implications. *Journal of Human Evolution*, 56: 514-524.

Martínez-Navarro B., Palmqvist P., Madurell-Malapeira J., Montoya S.R., Espigares-Ortiz M.P, Torregrosa V. & Pérez-Claros J.A. (2010). La fauna de grandes mamíferos de Fuente Nueva-3 y Barranco León-5: Estado de la cuestión. *In* Toro Moyano I., Martínez-Navarro B. & Agustí J. (eds), Ocupaciones Humanas En El Pleistoceno Inferior y Medio de La Cuenca de Guadix-Baza, Junta de Andalucía, Consejería de Cultura, Granada: 197-236.

Mazza P. (2006). Poggio Rosso (Upper Valdarno, Central Italy), a window on Latest Pliocene wildlife. *Palaios*, 21: 493-498.

Mazza P., Bertini A. & Magi M. (2004). The Late Pliocene site of Poggio Rosso (Central Italy): taphonomy and paleoenvironment. *Palaios*, 19: 227-248.

Medin T., Martínez-Navarro B., Madurell-Malapeira J., Figueirido B., Kopaliani G., Rivals F., Kiladze G., Palmqvist P. & Lordkipanidze D. (2019). The bears from Dmanisi and the first dispersal of early *Homo* out of Africa. *Scientific Reports*, 9: 1-16.

Mills M.G. (1989). The comparative behavioral ecology of hyenas: the importance of diet and food dispersion. *In* Gittleman J.L. (ed.), Carnivore behavior, ecology, and evolution, Springer, Boston MA: 125-142.

Mills M.G. (1990). Kalahari hyaenas: comparative behavioural ecology of two species. 320 pp. Unwin Hyman, London.

Moullé P.-E. & Tréguier J. (2006). Comparaison des dents déciduales de *Pachycrocuta brevirostris* et de *Crocuta crocuta spelaea*. *Bulletin du Musée d'Anthropologie préhistorique de Monaco*, 46: 21-33.

Mutter R.J., Berger L.R. & Schmid P. (2001). New evidence of the Giant Hyaena, *Pachycrocuta brevirostris* (Carnivora, Hyaenidae), from the Gladysvale Cave deposit (Plio-Pleistocene, John Nash Nature Reserve, Gauteng, South Africa). *Palaeontologia Africana*, 37: 103-113.

Nesti F. (1825). Lettere sopra alcune ossa fossili del Valdarno non per anco descritte. Sulla nuova specie di elefante fossile del Valdarno all'illustrissimo Sig. Dott. Prof. Ottaviano Targioni Tozzetti. Lettera prima. *Nuovo Giornale de' Letterati*, 11: 195-216.

Novelli M., Palombo M.R., Arca M. & Tuveri C. (2008). Hunter-Scheger Bands in *Cynotherium sardous* Studiati 1957 from Monte Tuttavista (Orosei, Central Eastern Sardina). *Geologica Romana*, 41: 65-70.

Owen R. (1846). A history of British fossil mammals, and birds. 560 pp. Van Voorst, London.

Owen R. (1870). On fossil remains of mammals found in China. *Quarterly Journal of the Geological Society of London*, 26: 417-434.

Palmqvist P., Torregrosa V., Pérez-Claros J.A., Martínez-Navarro B. & Turner A. (2007). A Re-evaluation of the diversity of *Megantereon* (Mammalia, Carnivora, Machairodontinae) and the problem of species identification in extinct carnivores. *Journal of Vertebrate Paleontology*, 27: 160-175.

Palmqvist P., Martínez-Navarro B., Pérez-Claros J.A., Torregrosa V., Figueirido B., Jiménez-Arenas J.M., Espigares M.P., Ros-Montoya S. & De Renzi M. (2011). The giant hyena *Pachycrocuta brevirostris*: modelling the bone-cracking behavior of an extinct carnivore. *Quaternary International*, 243: 61-79.

Palmqvist P., Campaña I., Granados A., Martínez-Navarro B., Pérez-Ramos A., Rodríguez-Gómez G., Guerra-Merchán A., Ros-Montoya S., Rodríguez-Ruiz M.D., García-Aguilar J.M., Hernández V. & Espigares M.P. (2024). The late Early Pleistocene site of Fuente Nueva-3 (Guadix-Baza Depression, SE Spain): a hyena latrine developed on a quicksand trap for megaherbivores? *Journal of Iberian Geology*, 50: 605-631.

Palombo M., Sardella R. & Novelli M. (2008). Carnivora dispersal in Western Mediterranean during the last 2.6 Ma. *Quaternary International*, 179: 176-189.

Pei W. (1934). On the Carnivora from Locality 1 of Choukoutien. *Palaeontologia Sinica, Series C*, 8: 1-216.

Pérez-Claros J.A. (2024). Unravelling the origin of the brown hyena (*Parahyena brunnea*) and its evolutionary and paleoecological implications for the *Pachycrocuta* lineage. *Palaeontologia Electronica*, 27: 1-25.

Petrucci M., Cipullo A., Martínez-Navarro B., Rook L. & Sardella R. (2013). The Late Villafranchian (Early Pleistocene) carnivores (Carnivora, Mammalia) from Pirro Nord (Italy). *Palaeontographica, Abteilung A*, 298: 113-145.

Qiu Z. (1987). Die Hyaeniden aus dem Ruscinium und Villafranchium Chinas. *Münchner Geowissenschaftliche*, *Abhandlungen A*, 9: 1-108.

R Core Team (2024). R: A language and environment for statistical computing, Vienna, Austria.

Randall R. (1981). Fossil hyaenidae from the Makapansgat Limeworks deposit, South Africa. *Palaeontologia Africana*, 24: 75-85.

Rook L. & Martínez-Navarro B. (2010). Villafranchian: The long story of a Plio-Pleistocene European large mammal biochronologic unit. *Quaternary International*, 219: 134-144.

Rook L. & Torre D. (1996). The wolf-event in western Europe and the beginning of the late Villafranchian. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, 8: 495-501.

Rook L., Croitor R., Delfino M., Ferretti M.P., Gallai G. & Pavia M. (2013). The Upper Valdarno Plio-Pleistocene vertebrate record: an historical overview, with notes on palaeobiology and stratigraphic significance of some important taxa. *Italian Journal of Geosciences*, 132: 104-125.

Schlager S. (2017). Morpho and Rvcg - Shape Analysis in R. *In* Statistical Shape and Deformation Analysis. Elsevier: 217-256.

Sotnikova M. & Rook L. (2010). Dispersal of the Canini (Mammalia, Canidae: Caninae) across Eurasia during the Late Miocene to Early Pleistocene. *Quaternary International*, 212: 86-97.

Spassov N. (2024). The final Pliocene and Early Pleistocene faunal dispersals from East to Europe and correlation of the Villafranchian biochronology between Eastern and Western Europe. *Quaternary*, 7: 43.

Stefen C. & Rensberger J.M. (1999). The specialized structure of hyaenid enamel: description and development within the lineage - including percrocutids. *Scanning Microscopy*, 13: 363-380.

Tappen M., Bukhsianidze M., Ferring R., Coil R. & Lordkipanidze D. (2022). Life and death at Dmanisi, Georgia: Taphonomic signals from the fossil mammals. *Journal of Human Evolution*, 171: 103249.

Teilhard de Chardin P. & Piveteau J. (1930). Les mammifères fossiles de Nihowan (Chine). *Annales de Paleontologie*, 19: 1-134.

Thunberg C.P. (1820). Beskrifning och teckning pa etr nytt species, Hyaena brunnea. *Kongliga Vetenskapsakademiens Handlingar för är* 1820: 59-65.

Tong H., Zhang B., Chen X., Jiangzuo Q., Liu J. & Wang X. (2023). New carnivoran remains from the Early Pleistocene Shanshenmiaozui site in Nihewan Basin, northern China. *Quaternary International*, 658: 60-79.

Toro-Moyano I., Martínez-Navarro B., Agustí J., Souday C., Bermúdez de Castro J.M., Martinón-Torres M., Fajardo B., Duval M., Falguères C., Oms O., Parés J.M., Anadón P., Julià R., García-Aguilar J.M., Moigne A.M., Espigares M.P., Ros-Montoya S. & Palmqvist P. (2013). The oldest human fossil in Europe, from Orce (Spain). *Journal of Human Evolution*, 65: 1-9.

Torre D., Ficcarelli G., Masini F., Rook L. & Sala B. (1992). Mammal dispersal events in the early Pleistocene of Western Europe. *Courier Forschungsinstitut Senckenberg*, 153: 51-58.

Tseng Z.J. (2011). Variation and implications of intra-dentition Hunter-Schreger band pattern in fossil hyaenids and canids (Carnivora, Mammalia). *Journal of Vertebrate Paleontology*, 31: 1163-1167.

Tseng Z.J. (2012). Connecting Hunter-Schreger band microstructure to enamel microwear features: new Insights from durophagous carnivores. *Acta Palaeontologica Polonica*, 57: 473-484.

Turner A. (2001). Remains of *Pachycrocuta brevirostris* (Carnivora, Hyaenidae) from the Lower Pleistocene Site of Untermassfeld. *In* Kahlke R.D. (ed.), Das Pleistozän von Untermassfeld bei Meiningen (Thüringen), Propylaeum, Heidelberg: 607-632.

Turner A. & Antón M. (1996). The giant hyaena, *Pachycrocuta brevirostris* (Mammalia, Carnivora, Hyaenidae). *Geobios*, 29: 455-468.

Turner A., Antón M. & Werdelin L. (2008). Taxonomy and evolutionary patterns in the fossil Hyaenidae of Europe. *Geobios*, 41: 677-687.

Valli A.M. (2004). Étude taphonomique et genèse du gisement Pliocène supérieur (Villafranchien moyen) de Saint-Vallier (Drome, France). *Géobios*, 37: S323-S348.

Vekua A. (1995). Die Wirbeltierfauna des Villafranchium von Dmanisi und ihre biostratigraphische Bedeutung. *Jahrbuch des Römisch-Germanischen Zentralmuseums Mainz*, 42: 77-180.

Vinuesa V., Madurell-Malapeira J., Ansón M. & Alba D. (2014). New cranial remains of *Pliocrocuta perrieri* (Carnivora, Hyaenidae) from the Villafranchian of the Iberian Peninsula. *Bollettino della Società Paleontologica Italiana*, 53: 39-47.

Vinuesa V., Madurell-Malapeira J., Fortuny J. & Alba D.M. (2015). The endocranial morphology of the Plio-Pleistocene bone-cracking Hyena *Pliocrocuta perrieri*: behavioral implications. *Journal of Mammalian Evolution*, 22: 421-434.

Vinuesa V., Iurino D.A., Madurell-Malapeira J., Liu J., Fortuny J., Sardella R. & Alba D.M. (2016). Inferences of social behavior in bone-cracking hyaenids (Carnivora, Hyaenidae) based on digital paleoneurological techniques: Implications for human–carnivoran interactions in the Pleistocene. *Quaternary International*, 413: 7-14.

Viret J. (1954). Le lœss à bancs durcis de Saint-Vallier (Drôme), et sa faune de mammifères villafranchiens (avec une analyse granulométrique et une analyse pollinique). *Nouvelle Archives du Musèum d'Histoire Naturelle de Lyon*, 4: 1-258.

Von Den Driesch A. (1976). A guide to the measurement of animal bones from archaeological sites 136 pp. Peabody Museum Press, Cambridge MA.

Werdelin L. (1999). *Pachycrocuta* (Hyaenids) from the Pliocene of East Africa. *Paläontologische Zeitschrift*, 73: 157-165.

Werdelin L. & Lewis M.E. (2000). Carnivora From the South Turkwel Hominid Site, Northern Kenya. *Journal of Paleontology*, 74: 1173-1180.

Werdelin L. & Lewis M.E. (2008). New species of *Crocuta* from the Early Pliocene of Kenya, with an overview of Early Pliocene hyenas of eastern Africa. *Journal of Vertebrate Paleontology*, 28: 1162-1170.

Werdelin L. & Peigné S. (2010). Carnivora. *In* Werdelin L. & Sanders W. (eds), Cenozoic Mammals of Africa, University of California Press, Berkeley: 609-663.

Werdelin L. & Solounias N. (1991). The Hyaenidae: Taxonomy, systematics and evolution. *Fossils and Strata*, 30: 1-104.

Werdelin L. & Solounias N. (1996). The Evolutionary History of Hyaenas in Europe and Western Asia during the Miocene. *In* Bernor R.L., Fahlbusch V. & Rietschel S. (eds), Later Neogene European biotic evolution and stratigraphic correlation, Columbia University Press, New York: 290-306.

Wickham H., Chang W. & Wickham M.H. (2016). Package 'ggplot2'. Create elegant data visualisations using the grammar of graphics. *Version*, 2: 1-189.

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