New cranial remains of *Pliocrocuta perrieri* (Carnivora, Hyaenidae) from the Villafranchian of the Iberian Peninsula

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**KEY WORDS -** Hyaenidae, Pliocrocuta, Villarroya, La Puebla de Valverde, Villafranchian, Plio-Pleistocene.

**ABSTRACT -** The hyaenid *Pliocrocuta perrieri* is one of the commonest large carnivorous species in the European Late Pliocene and Early Pleistocene, being recorded from more than 20 sites across the Old World. In spite of this, adult and fairly complete cranial specimens of this species have only been recovered from the French locality of Saint-Vallier (Early Pleistocene, MN17). Here we describe three new cranial remains of this bone-cracking hyena from the classic Iberian localities of *Villafranchia* (Late Pliocene, MN16a) and *La Puebla de Valverde* (Early Pleistocene, MN17). The morphology of the new crania is compared (both qualitatively and metrically) with that of previously known craniodental remains of *P. perrieri*, as well as with that of other extinct hyaenids, including its closest relative (*P. brevirostris*) and the contemporaneous Chasmaporthetes lunensis. The described skulls display many morphological and morphometric similarities with previously-known specimens of *P. perrieri*, including the relatively long muzzle, the triangular, slender and long nasals, the relatively short P2, and other occlusal details. In contrast, the new specimens display significant differences compared with both C. lunensis (the shorter muzzle, the more anterior orbits and more posterior infraorbital foramen, the triangular nasals, and the broader premolars with a relatively shorter P2) and Pa. brevirostris (smaller craniodental size, longer muzzle, and various dental occlusal details). The new skulls of *P. perrieri* reported here enable a more complete evaluation of intraspecific variability in this taxon, and the study of their internal anatomy might provide, in the future, new data on the paleoecology of *P. perrieri* and its phylogenetic relationships with other bone-cracking hyenas, both extant and extinct.

**RIASSUNTO -** I nuovi resti cranici di *Pliocrocuta perrieri* (Carnivora, Hyaenidae) dal Villafranchiano della Penisola Iberica. - Lo ienide *Pliocrocuta perrieri* è una delle specie di grandi carnivori più comuni nel Pliocene Superiore e Pleistocene Inferiore d’Europa, registrata in più di 20 siti in tutto il Vecchio Mondo. Tuttavia, crani adulti e abbastanza completi di questa specie sono noti solo nella località francese di Sant-Vallier (Pleistocene Inferiore, MN17). In questa nota vengono descritti tre nuovi crani di questa iberna frantumatrice di osso provenienti dalle note località della Penisola Iberica di Villarroya (Pliocene Superiore, MN16a) e *La Puebla de Valverde* (Pleistocene Inferiore, MN17). La morfologia dei nuovi crani viene confrontata (qualitativamente e metricamente) con quella dei resti craniodentari già conosciuti di *P. perrieri*, nonché con quella di altre specie estinte, inclusi il suo parente più vicino (*Pachycrocuta brevirostris*) e la specie coeva *Chasmaporthetes lunensis*. I crani descritti mostrano molte somiglianze morfologiche con gli esemplari già noti di *P. perrieri*, tra cui il muso relativamente allungato, i nasali triangolari, snelli e lunghi, il P2 relativamente corto, ed altri dettagli della morfologia occlusale. Al contrario, i nuovi esemplari mostrano differenze importanti rispetto a C. lunensis (il muso più corto, le orbite posizionate anteriormente e il foramen infraorbitale più posteriore, i nasali triangolari, e i premolari superiori più larghi, con il P2 relativamente più corto) e Pa. brevirostris (dimensioni craniodentali più piccole, muso più lungo, presenza di cuspidi accessorie mesiali in P2 e P3, ed altri dettagli della morfologia occlusale dei denti). L’attribuzione tassonomica degli esemplari descritti a *P. perrieri* è ulteriormente confermata dai risultati dell’analisi multivariata basata su dimensioni e proporzioni dei premolari superiori. I nuovi crani di *P. perrieri* rappresentano una aggiunta significativa alla conoscenza di questa specie di ienide, poiché permettono una valutazione più completa della variabilità interspecifica nelle caratteristiche craniodentali. Peraltro, lo studio dell’anatomia cranica interna negli esemplari descritti potrebbe fornire, in futuro, nuovi dati sulla paleoecologia di *P. perrieri* e sulle sue relazioni filogenetiche con le altre iberna frantumatrici di osso, sia attuali sia estinte.

**INTRODUCTION**

The bone-cracking hyena *Pliocrocuta perrieri* (Croizet & Jobert, 1828) (Carnivora, Hyaenidae) is one of the large carnivors most commonly recorded in the Early to Middle Villafranchian of Eurasia, being also frequently associated with the hunting hyena *Chasmaporthetes lunensis* (Del Campana, 1914). The chronological range of *P. perrieri* spans from MN15 to MN17 (4.2-2.0 Ma; Turner et al., 2008), whereas geographically it is widely distributed across Eurasia and Africa (Werdelin & Solounias, 1991; Turner et al., 2008). Until recently, it was generally considered that this species went locally extinct in Europe by the end of the Middle Villafranchian, so that its purported Middle Pleistocene record was interpreted as a second dispersal event from Africa (Turner et al., 2008). It is currently recognized, however, that its presumed second dispersal event corresponds in fact to that of another taxon, *Hyaena prisca* De Serres, Dubreuil & Jeanjean, 1828 (see Madurell-Malapeira, 2010). From a phylogenetic viewpoint, *Pliocrocuta* is considered the sister-taxon of *Pachycrocuta* Kretzoi, 1938 (Werdelin & Solounias, 1991;
Turner et al., 2008), or even its direct ancestor (Howell & Petter, 1980; Werdelin & Solounias, 1991; Arribas & Palmqvist, 1999; Olive, 2006; Turner et al., 2008).

*Pliocrocuta perrieri* is a large-bodied hyaenid dentally characterized by a non-reduced P4 protocone, as well as a short and massive m1 with no metaconid but with a wide talonid, in which both the entoconid and hypoconid are present (Werdelin & Sanders, 2010). Since its original description as *Hyaena perrieri* Croizet & Jobert, 1828, the taxonomic status of this taxon has been subject to considerable controversy (Turner, 1990; Werdelin & Solounias, 1991). Kretzoi (1938) erected the genus *Pliocrocuta*, which was subsequently synonymized with *Pachycrocuta* by several authors (Ficcarelli & Torre, 1970; Howell & Petter, 1980). More recently, Turner (1990) and Werdelin & Solounias (1991) resurrected the genus *Pliocrocuta* and further noted that *Pliocrocuta pyrenaica* (Depéret, 1890) and *Hyaena arvernensis* (Croizet & Jobert, 1828) must be considered junior subjective synonyms of *P. perrieri*.

In spite of being a relatively common taxon, *P. perrieri* is mostly known from dentognathic or isolated dental specimens. Thus, its postcranial anatomy is virtually unknown, and fairly complete crania have been only reported from the localities of Saint-Vallier (MN17, France) and Zhangwagou (MN15, China) (Viret, 1954; Qiu, 1987). Here we describe three fairly complete unpublished crania and associated mandibular remains of *Pliocrocuta perrieri* from the Iberian localities of Villarroya (MN16a) and La Puebla the Valverde (MN17), which provide new data on the intraspecific variability of the craniodental morphology of this taxon, and enable us to further review the differences of *Pliocrocuta* compared to other hyaenids.

**MATERIALS AND METHODS**

**Abbreviations**

ICP - Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona (Spain).

IPS - Acronym of the collections of the ICP. MNHN - Muséum National d’Histoire Naturelle, Paris (France).

**Comparative material**

We compared the described material with the two other known adult complete crania of *P. perrieri* (QSV20 and QSV48), from the French locality Saint Vallier (Viret, 1954; Howell & Petter, 1980; Werdelin & Solounias, 1991). The other available crania of this species (V7283, V7284), from the Chinese locality of Zhangwagou (Qiu, 1987), were not taken into account in the comparisons due to their juvenile condition. Dental measurements (in mm) for *P. perrieri*, *C. lunensis* and *Pachycrocuta brevirostris* (Gervais, 1850) (regarding the authorship of the taxon, see Alba et al., in press) were taken from the literature (Viret, 1954; Adrover & Soria, 1976; Howell & Petter, 1980; Qiu, 1987; Geraads, 1997; Turner, 2001; Argant, 2004; Baryshnikov & Tsoukalas, 2010; Werdelin & Lewis, 2012). When the two dental rows were available for a single individual, the averages of right and left measurements were used. Dental enamel microstructure in the described specimens was evaluated using light microscope, in order to identify the type of Hunter-Shreger bands (HSB; Koenigswald & Sander, 1997; Ferretti, 1999) displayed by them.

**Morphometric comparisons**

Craniodental measurements of the described specimens were taken to the nearest 0.01 mm with a digital caliper. Dental size and proportions were assessed using bivariate plots of buccolingual width vs. mesiodistal length for the P2, P3 and P4, as well as a plot of P2 length vs. that of the whole upper premolar series (P2-P4). With regard to multivariate comparisons, a canonical variate Discriminant Analysis (DA) was performed with SPSS v. 20.0, based on the mesiodistal lengths and buccolingual widths for the P2, P3 and P4. Three groups were defined a priori *(P. perrieri, C. lunensis and Pa. brevirostris)*, and two of the described crania were left ungrouped, being classified a posteriori by the analysis. Only IPS36758 and IPS36759 were included in the analysis, due to the impossibility of measuring tooth widths in IPS27340.

**GEOLOGICAL BACKGROUND**

**Villarroya**

The site of Villarroya is located in the Villarroya lacustrine Basin (Northern Iberian Peninsula; Fig. 1; Anadón et al., 2009). It is a classic paleontological site from the Early Villafranchian of Europe (Carvajal, 1926; Villalta Comella, 1952; Arribas Herrera & Bernad García, 1994; Jiménez García et al., 1999), from which more than twenty macromammalian species have been identified (Jiménez García et al., 1999). The age of Villarroya is currently correlated to MN16a (Arribas Herrera & Bernad García, 1994; Jiménez García et al., 1999), with an estimated age of ca. 2.6 Ma (Agusti & Oms, 2001).

**La Puebla de Valverde**

La Puebla de Valverde is located in the Sarrión plateau within the Teruel basin (Eastern Iberian Peninsula; Fig. 1; Gautier & Heintz, 1974). Like Villarroya, it is considered one of the most relevant mammal sites of studied sites within the Iberian Peninsula. 1: Villarroya; 2: La Puebla de Valverde.
the Middle Villafranchian of Europe (Crusafont Pairó et al., 1964; Adrover et al., 1974; Gautier & Heintz, 1974; Alcalá, 1994; Alberdi et al., 1997), with 21 identified macromammal species (Alberdi et al., 1997). The site is currently correlated to MN17 (Alcalá, 1994; Alberdi et al., 1997), with an estimated age of 2.14-1.95 Ma (Sinusía et al., 2004).

SYSTEMATIC PALEONTOLOGY

Order Carnivora Bowdich, 1821
Family Hyaenidae Gray, 1821
Subfamily Hyaeninae Gray, 1821
Genus Pliocrocuta Kretzoi, 1938

Type species - Hyaena perrieri Croizet & Jobert, 1828

Pliocrocuta perrieri (Croizet & Jobert, 1828)

Holotype - MNHN coll. Croizet No. 834, mandible from Les Étouaires (MN17, France).

Referred specimens - Cranium from Villarroya (IPS36758; Figs 2a, 3a); skull from Villarroya (IPS36759; Figs 2b, 3b); skull from La Puebla de Valverde (IPS27340; Fig. 2c).

Description and comparisons

Preservation - The cranium IPS36758 (Fig. 2a) is not completely preserved, missing the zygomatic arches, the tympanic bullae, and the posterior end of the sagittal crest. The specimen is also slightly distorted along its length, and displays abundant minor fractures, which are located along the braincase, the frontal and the nasals. The dentition (Fig. 3a) is heavily worn, but generally well preserved, although the left P2 is partially broken, and the canines and several incisors (right I1 and I2) are missing. The left I2 is preserved but incorrectly glued to the premaxilla (it is rotated and the apex-root axis is inverted). Part of the left mandibular corpus (with p2-p3 and the mesial portion of p4) is preserved, being attached to the cranium above the right maxilla.

The cranium IPS36759 (Fig. 2b) is undistorted and completely preserved, except for the two tympanic bullae and the zygomatic arches, which are missing. The morphology is generally well preserved, in spite of displaying a vertical fracture at about skull mid-length (just behind the orbits), which is oriented roughly along the coronal plane. There are several additional minor fractures, especially around the tooth rows, which are filled with plaster. The dentition (Fig. 3b) is very worn; only the two P1 are missing, although the left I1, P4, M1 and the right I1 and P4 are only partially preserved.

Unlike the two other specimens, IPS27340 (Fig. 2c) displays the mandible attached to the cranium in anatomical position. The cranium is more distorted, and displays a major fracture between the neurocranium and the nasals. Moreover, the posterior portion of the skull is slightly rotated and anteriorly displaced (overlapping with the nasals). The left side of the braincase is covered with sediment that was not removed during the preparation (due to the fragility of the specimen), so that only a portion of the sagittal crest is visible. The right side of the neurocranium is partially broken at the parietal and basicranial areas, exposing a large portion of the brain endocast and the tympanic bulla. In the anterior portion of the cranium, the left maxilla is almost complete, and part of the left zygomatic arch and orbit are also preserved, further displaying a fracture between P3 and P4. The infraorbital foramina, the nasals and the nasal fossa are missing. The right maxilla is poorly preserved, only

![Fig. 2 - Skulls of Pliocrocuta perrieri from Villarroya and La Puebla de Valverde. IPS36758: a1) left lateral view, a2) dorsal view, a3) basal view; IPS36759: b1) left lateral view, b2) dorsal view, b3) basal view, b4) frontal view; IPS27340: c1) left lateral view, c2) dorsal view.](image-url)
including the alveolar bone surrounding the tooth roots. The upper dentition is preserved except for the right P4, although the left P3 is misplaced (rotated) due to incorrect preparation. The mandible displays many fractures but is well preserved, except for some portions of the corpora and rami that have been reconstructed plaster. The lower dentition is completely preserved except for the right c1.

**Measurements** - See Tab. 1.

**Description** - The specimens reported here display an elliptic (higher than broad) nasal aperture as well as narrow triangular nasals, like *Hyaena* and *Parahyaena*. The nasal aperture is also wider than in *Crocuta*, more comparable to that of *Hyaena* and *Parahyaena*. The muzzle is long, with a very marked postcanine constriction, as in *Crocuta*. The frontomaxillary suture, as shown by IPS36759, is curved and posteriorly situated, most closely resembling in this regard both *Hyaena* and *Parahyaena*. The premaxillary suture, visible in IPS36759, does not reach the frontonasal suture, unlike in *Crocuta* and *Hyaena*, but are clearly separated as in *Parahyaena*. The marked postorbital processes display small lateral projections (only ascertainable in IPS36759 and IPS36758) as in *Crocuta*, whereas in *Hyaena* and *Parahyaena* these processes protrude basally. The tooth rows are markedly curved, as in *Crocuta* and *Parahyaena*. The palate, as seen in IPS36759 and IPS36758, is wide distally, thus resembling the condition in *Crocuta* and *Hyaena*. The basiocipital, observable in IPS36759 and IPS36758, more closely resembles that of *Parahyaena* in displaying a small central ridge as well as a transverse ridge at the beginning of the occipital condyles. The dorsal profile of the temporal region is slightly convex, with a degree of curvature intermediate between those of *Hyaena* (low curvature) and *Crocuta* (high curvature). The rostrum is relatively high and long (only preserved in IPS3658 and IPS36759), so that the nasals are more horizontally oriented than in extant bone-cracking hyenas. The anterior-most portion of the orbits is laterally situated at the level between P3 and P4, and the elliptical infraorbital foramen is situated at the level of the P3 protocone, as in the extant bone-cracking hyenas. The curvature of the nuchal crest (only well preserved in IPS36759) is marked, resembling the condition displayed by *Parahyaena*. In caudal view, the occipital outline (preserved in IPS36759 and IPS36758) is triangular, with marked nuchal and occipital crests, as in extant bone-cracking hyenas. The mandible is robust, as it is in the latter taxa.

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**Tab. 1 - Measurements (in mm) of the crania of *Pliocrocuta perrieri* from Villarroya and La Puebla de Valverde. Abbreviations: PA, prosthion-acrocranion length; SKL, prosthion-occipital condyles length; PB, prosthion-basion length; SB, synsphenion-basion length; PS, prosthion-synsphenion length; FA, frontal-acrocranion length; PN, prosthion-nasion length; PF, prosthion-frontal length; PT, prosthion-staphyilon length; LP1-P4, length of the upper premolar series; Woc, width of occipital condyles; WP4, palatal width at P4; WC, palatal width at C1; Hoc, occipital height; L, mesiodistal length; W, buccolingual width; LP4pr, mesiodistal length of fourth upper premolar protocone; LP4pas, mesiodistal length of fourth upper premolar parastyle; LP4pa, mesiodistal length of fourth upper premolar parastyle; LP4m, mesiodistal length of P4 metacone.**

![Image](image-url)
The dentition shows clear bone-cracking adaptations. The P1 is small and unicuspid, with a small buccal cingulum, as in extant bone-cracking hyenas (Fig. 3). The P2 displays a rectangular occlusal outline and bears two (mesial and distal) small but distinct accessory cusps, also as in extant bone-cracking hyenas. The P3 is stout (buccolingually broad) and displays well-developed accessory cusps, as in Crocuta, Hyaena and Parahyaena, the mesial cusp being rotated lingually. The P4 displays a well-developed and mesiolingually-oriented protocone, which is slightly larger and more mesially situated in IPS27340, as well as a paracone of the same length as the metastyle. The M1 is present, being relatively large and displaying a rectangular occlusal outline. This tooth is buccolingually broader than mesiodistally long (Fig. 3), as in Hyaena and Parahyaena, thus differing from that of Crocuta, which is usually smaller and rounder (if present at all). The lower premolars display a rectangular occlusal outline. The p2 displays a medium-sized protocone and no mesial accessory cusp. This tooth reaches its maximum width at the level of the posterior accessory cusp, which is moderately developed, as in extant bone-cracking hyenas. The p3 lacks the mesial accessory cusp, unlike Hyaena, and displays a well-developed protocone and a wide distal accessory cusp, like Parahyaena. The p4 displays both mesial and distal accessory cusps, as well as a well-developed protocone, as in extant bone-cracking hyenas. The mesial accessory cusp is smaller than the distal cusp, and situated on the lingual portion of the crown, being more developed than in Crocuta. In contrast, the p4 distal accessory cusp is more mesially situated, thus resembling the condition of both Hyaena and Parahyaena. The m1 is rather small, with a long paraconid and a short protoconid. The buccal margin of the paraconid displays a small cingulid. The m1 talonid is long and bicuspid, contrasting with the short and unicuspid talonid of Hyaena and Parahyaena, as well as with the almost completely reduced talonid of Crocuta. The presence/absence of metaconid in the m1 cannot be ascertained.

Regarding enamel microstructure, due to preservational reasons, HSB were only observable on the outer enamel surface of two of the studied specimens (IPS36758 and IPS36759). They are well separated from one another and display a marked zigzag pattern (Fig. 4), with a mean angle α < 90°. This morphology is characteristic of the three extant bone-cracking hyenas and the extinct Pachycrocuta, clearly distinguishing the studied specimens from Chasmaporthetes, which displays less steeply folded bands that are more closely packed with one another (Ferretti, 1999).

Morphological comparisons - The morphology of the described specimens (IPS36759, IPS36758 and IPS27340) closely resembles that of the Saint-Vallier specimens (QSV20 and QSV48; Viret, 1954) in the following features: convex superior cranial profile with only a small concave depression at the frontonasal region; relatively long muzzle; short braincase not extended posteriorly by the sagittal crest; slender, long and triangular nasals lacking intermaxillary contact; maxillae barely elevated above the orbits; not markedly broad palate; robust anterior teeth relative to the cheek teeth; P1 present; relatively small P2; robust P3 with a high main cusp and mesial and distal crests; P4 with a large and high parastyle, an elongate metacone longer than the paracone, and a well-developed protocone that is not expanded towards the parastyle; and well-developed M1 with a marked parastyle lobe.

In spite of the similarities mentioned above, the studied specimens display several minor differences among them and/or compared with the Saint-Vallier material. Thus, the three described crania display a conspicuous postcanine constriction, which is less marked in one of the Saint-Vallier specimen (QSV20), and most developed in IPS27340. All the specimens possess postorbital processes with small lateral projections (except QSV48, which displays more marked projections). The occipital protuberance is proportionally more protruding in IPS36759. A markedly-developed P4 root is present in all the specimens, although it is less marked in QSV20 and IPS27340. The nasal fossa is slightly wider in QSV48 than in the other specimens. The curvature of the tooth rows is slightly variable, being least marked in QSV20, which further displays a narrower palate as well as narrower and more protruding occipital condyles than the remaining specimens. Dental differences among the various available specimens are minor, the most variable character being the position of P1. This tooth is situated between the canine and P2 in all the specimens except QSV48, in which it is more lingually situated (next to the distolingual aspect of the canine).

In contrast with the minor differences reported above, when compared with other skulls of P. perrieri, the described specimens (IPS36759, IPS36758 and IPS27340) display major differences compared with the sympatric hunting hyena C. lunensis (Viret, 1954; Antón et al., 2006; Ferretti, 2007) and the Early Pleistocene giant short-faced hyena Pa. brevirostris (Boule, 1893; Kretzoi, 1938; Werdelin & Sanders, 2010). Thus, the described crania differ from C. lunensis in the more anteriorly situated...
orbits, the more posterior infraorbital foramen, the more strongly developed postorbital process, the triangular nasals, the longer muzzle, the comparatively larger I3 and the steeply folded HSB with a marked zigzag pattern on the outer enamel surface. In turn, the described crania differ from *Pa. brevirostris* in the smaller overall size, the longer rostrum, the presence of mesial accessory cusps in the P2 and P3, the less developed premolar protocones, and the slenderer P4 paracone.

**Morphometric comparisons** - The size and proportions of the premolars in the described specimens are compared to those of previously-known specimens of *P. perrieri*, *C. lunensis* and *Pa. brevirostris* in Fig. 5. Standard bivariate plots of width vs. length of the upper premolars (P2-P4; Fig. 5a-c) overlap to some degree among the various species in all instances, with *Pa. brevirostris* displaying largest absolute dimensions for the three premolars. For both the P3 (Fig. 5b) and the P4 (Fig. 5c), *P. perrieri* shows similar proportions but intermediate sizes between *C. lunensis* (smaller) and *Pa. brevirostris* (larger), only with some overlap. For the P2 (Fig. 5a), *Pa. brevirostris* overlaps more extensively with *C. lunensis* in length, although many specimens of the latter tend to display a relatively wider P2. Among the studied specimens, IPS36758 exclusively overlaps with the scatter of *P. perrieri* (thus confirming the attribution to this taxon), whereas IPS36759 does not overlap with any of the studied hyaenid species for the P2 (falling close to both *P. perrieri* and *C. lunensis*), overlaps with both *P. perrieri* and *C. lunensis* for the P3, and overlaps only with *C. lunensis* for the P4. Overall, upper premolar proportions are not reliable for providing a secure taxonomic attribution, since they do not enable a clear and unambiguous discrimination among these taxa.

In contrast, the length of the P2 relative to the P2-P4 row provides a much better discrimination among the three studied species (Fig. 5d), since the P2 of *P. perrieri* is relatively shorter than in *C. lunensis*, only with a very minimal overlap. *Pachycrocuta brevirostris*, in turn, differs from both *P. perrieri* and *C. lunensis* by the larger dental size of the former, with only a very minimal overlap with the largest specimens of *P. perrieri*. Regarding this feature, all the studied specimens (further including IPS27340, for which premolar width is not available) exclusively overlap with *P. perrieri*, thus supporting our taxonomic attribution to this taxon on the basis of qualitative morphological features.

The DA (Tab. 2 and Fig. 6) yields two discriminant functions (DF), with a Wilk’s lambda significant at p<0.001 (DF1) and p<0.01 (DF2). Based on these functions, the analysis provides a very good discrimination between the three extinct hyaenids included, by correctly classifying 95.2% of the original cases (85.7% when cross-validation is employed). DF1 separates *Pachycrocuta* (positive values) from both *Pliocrocuta* (generally rather negative values, only minimally overlapping with *Pachycrocuta*) and *Chasmaporthetes* (highly negative values, with no overlap with *Pachycrocuta*), being mostly driven by size (especially P3 width and P4 length). DF2, in turn, mostly discriminates between *Pliocrocuta* (negative values) and *Chasmaporthetes* (positive values), with *Pachycrocuta* displaying values around zero that largely overlap with the two other taxa. This axis is mostly driven by P2 length and width (the larger the P2, the more positive the values along DF2) as well as P3 width (the wider the P2, the more negative the values along DF2). The analysis therefore shows that *Pliocrocuta* dentally differs from *Pachycrocuta* mostly by displaying smaller teeth, whereas in contrast...
it differs from *Chasmaporthetes* by dental proportions (especially the smaller P2 and the stouter P3).

With regard to the new crania described here, the analysis classifies them both as *Pliocrocuta* in first instance, with a classification probability of $p=0.956$ for IPS36758 and $p=0.473$ for IPS36759 (and posterior probabilities of $p=0.981$ and $p=0.867$, respectively); as a second alternative, the new skulls are classified as *Chasmaporthetes*, with much lower posterior probabilities ($p=0.010$ in IPS36758 and $p=0.133$ in IPS36759). This can be clearly seen in the plot of DF2 versus DF1 (Fig. 6), in which the two described crania are much closer to the *Pliocrocuta* centroid (Mahalanobis squared distances of $D^2=0.09$ for IPS36758 and $D^2=1.498$ for IPS36759) than to that of *Chasmaporthetes* ($D^2=9.34$ and $D^2=5.248$, respectively).

**Artistic reconstruction** - In Fig. 7 we provide a reconstruction of the skull and life appearance of the head of *Pliocrocuta perrieri*, which is mainly based on the crania described here, further complemented (when necessary to reconstruct areas damaged in the described specimens) by data from the Saint-Vallier specimens QSV20 and QSV48 (Viret, 1954).

**DISCUSSION AND CONCLUSIONS**

The studied hyaenid skulls from Villarroya and La Puebla de Valverde closely resemble the previously-known material of *Pliocrocuta perrieri* (Viret, 1954; Howell & Petter, 1980) in both cranial morphology (e.g., relatively long muzzle, short braincase, slender and triangular nasals) and dental features (presence of P1 and broad premolars, with a relatively short P2). In contrast, the described material displays marked differences compared with both *Chasmaporthetes lunenis* (shorter muzzle, more anterior orbits, more posterior infraorbital foramen, triangular nasals, stouter upper premolars with a relatively shorter P2, and zigzag pattern of HSB on tooth enamel) and *Pachycrocuta brevirostris* (including smaller cranial and dental size, longer muzzle, less developed premolar protocones and several occlusal details). An attribution to *P. perrieri* of the described specimens is further confirmed by the multivariate analyses performed here based on dental size and proportions.

The described skulls show some degree of intraspecific variability in various craniodental features, both among themselves and/or compared with specimens from other localities. These features include the development of the postcanine constriction, the projection of the postorbital processes, the occipital protuberance and the occipital condyles, the development of the P4 root, the width of the nasal aperture and the palate, and the position of the P1. Such differences are however very minor (compared
to the differences between *P. perrieri* and other hyaenid taxa) and do not merit any taxonomic value. The skulls of *P. perrieri* described here therefore enable to better evaluate the intraspecific variability in cranial morphology in this taxon, for which relatively complete adult skulls were only previously known from the locality of Saint-Vallier. Overall, the Iberian material of *P. perrieri* confirms that, in spite of some degree of variation in cranial features, this taxon consistently differs in craniodental morphology from both the contemporaneous hyena *C. lunensis* and its purported descendant *Pa. brevirostris*. Moreover, the future study of the internal cranial anatomy of the new specimens of *P. perrieri* described here may shed new light on the paleoecology and phylogenetic relationships of this taxon compared to the extant and other extinct bone-cracking hyenas.

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