



THE LOST HYENA FROM PACIANO (UMBRIA, ITALY) RECONSIDERED.

Alessio Iannucci¹, Marco Cherin², Raffaele Sardella¹

¹ Dipartimento di Scienze della Terra (PaleoFactory lab.), Sapienza Università di Roma, Roma, Italy.

² Dipartimento di Fisica e Geologia, Università degli Studi di Perugia, Perugia, Italy.

Corresponding authors: A. Iannucci <alessio.iannucci@uniroma1.it>

ABSTRACT: We redescribe and revise the taxonomic attribution of a lost hyena hemimandible recovered from Paciano (Umbria, Italy), originally reported in the early 1900s, by comparing it with relevant samples of Pliocene, Pleistocene, and extant species. The mandible of the Paciano hyena was initially attributed to *Hyaena striata* (= *Hyaena hyaena*) and subsequently listed as a record of the giant hyena *Pachycrocuta brevirostris*, but is here assigned to another “bone-cracking” hyena, the Pliocene-Early Pleistocene *Pliocrocuta perrieri*. The Paciano hyena contributes to the discussion on the relationships and turnover between *Pl. perrieri* and *P. brevirostris*. On the one hand, the two species are very similar in craniodental morphology; their isolated remains are often separated by size; and *P. brevirostris* is thought to derive from a large-sized population of *Pl. perrieri*. On the other, a larger size is not an aspect to disregard in hyenas as it usually correlates with the acquisition or better development of “bone-cracking” features; remains attesting the co-occurrence of *Pl. perrieri* and *P. brevirostris* are known from some sites dated at around 2.0–1.8 Ma; and the observed size differences between the two species exceed those recorded between extant and (at times) sympatric species. Therefore, taken alone the competition with *P. brevirostris* does not explain the extinction of *Pl. perrieri*, but considering it together with the concurrent spread and resulting peak of carnivoran diversity in Late Villafranchian faunas might. *Pliocrocuta perrieri* was outcompeted by its larger descendent in scavenging carcasses, while other carnivorans limited its options to deviate to other resources or adopt a different feeding behavior (e.g., active hunting). The case of Paciano is also significant in that it offers an example of the importance and feasibility of reconsidering historical collections, even when the original material is lost entirely. In general, the seek for “novelty” that permeates current scientific literature ensues in few descriptions or reconsiderations of historical samples, especially if the new examinations confirm old results, but we emphasize the significance of such efforts in making old data truly available for the scientific community. In addition, the hyena from Paciano has a biochronological and stratigraphic value, confirming the occurrence in western Umbria of a depositional cycle older than the late Early Pleistocene one (well represented by the rich assemblages from Pietrafitta and Selvella; Farneta Faunal Unit).

Keywords: Hyaenidae, Carnivora; Quaternary; Europe; historical collections.

1. INTRODUCTION

Hyenas were once an ecologically diverse group that showed adaptations to many different feeding behaviors, from the probable insectivory/omnivory of civet-like and mongoose-like species, to hypercarnivory and “bone-cracking” (Kurtén, 1956; Howell & Petter, 1980; Werdelin & Solounias, 1991, 1996; Semenov, 2008; Turner et al., 2008; Tseng et al., 2013; Coca-Ortega & Pérez-Claros, 2019; Koufos, 2021; Iurino et al., 2022; Lewis & Werdelin, 2022). The latter is almost the only ecomorphotype (or ecomorph; Werdelin & Solounias, 1996) that survived to the present day. Indeed, with the exception of the aardwolf, *Proteles cristatus* (Sparrmann, 1783), which is a specialized termite eater (Kruuks & Sands, 1972; Cooper & Skinner, 1979), the other three living hyenas, *Crocuta crocuta* (Erleben, 1777), *Hyaena hyaena* (Linnaeus, 1758), and *Parahyaena brunnea* (Thunberg, 1820), display a suite of craniodental traits that highlight their ability of cracking bones. This capacity gave bone-cracking hyenas access to resources out of reach of most other predators and scavengers, apart mainly from hominins, who could also crack and deflesh bones using tools. Therefore, Quaternary hyenas are often considered as potential

competitors of hominins, stimulating research with vibrant paleoecological and taphonomic implications, but also engendering debate on the magnitude of *Homo*-hyena interactions and relationships (Stiner, 1991; Turner & Antón, 1996; Boaz et al., 2000; Lewis & Werdelin, 2010; Espigares et al., 2013; Madurell-Malapeira et al., 2017; Iannucci et al., 2021b).

An interesting period on which our knowledge on the evolution of hyenas is still rather imperfect is around 2.0–1.8 Ma. At the time, the giant hyena *Pachycrocuta brevirostris* (Gervais, 1850) spread into Europe, becoming soon after the only bone-cracking carnivoran for most of the Early Pleistocene (Iannucci et al., 2021b). In some of the earliest localities where *P. brevirostris* is recorded, the giant hyena is accompanied by other species that will be no longer present in later faunas, namely the hunting hyena *Chasmaporthetes lunensis* (Del Campana, 1914) and another bone-cracker, *Pliocrocuta perrieri* (Croizet & Jobert, 1828). *Chasmaporthetes lunensis* is a more gracile and cursorial species than the others, and its ecology is often discussed in comparison to carnivorans other than bone-cracking hyenas (Kurtén & Werdelin, 1988; Ferretti, 1999; Antón et al., 2006; Tseng et al., 2011, 2013; Pérez-Claros et al., 2021; Konidaris, 2022; Marciszak et al., 2022). Conversely,



Fig. 1 - Geographic location of Paciano (red star). The extensional basins cited in the text are highlighted.

Pliocrocota and *Pachycrocota* are considered ecomorphologically very close and indeed placed by some authors in the same genus (e.g., Qiu et al., 2004; Liu et al., 2021). Arguments in favor of a “sharp” separation between *Pliocrocota* and *Pachycrocota* are some morphological differences, especially the lack of a metaconid in the lower carnassial in *P. brevirostris* (Werdelin & Solounias, 1991) and the co-occurrence of the two species in some European localities at ~2.0 Ma (Iannucci et al., 2021b). On the other hand, localities where hyaenid fossils have been assigned to both species are not but a few, and attributions are merely based on the size of the remains (Iannucci et al., 2021b). From an ecological point of view, the increase in size in hyenas is nonetheless significant, as it is generally correlated to the acquisition or better development of “bone-cracking” craniodental features (Werdelin & Solounias, 1991). Moreover, despite the paucity of available remains in relevant localities, the reliability of such size-based repartition would be corroborated by the low level of sexual dimorphism –in craniodental measurements– observed in *C. crocuta* (e.g., García, 2003; Lewis & Werdelin, 2022), assuming that the same holds true for *Pliocrocota* and *Pachycrocota*. In general, the spotted hyena is definitely

the most studied amongst extant hyenas (e.g., Kruuk, 1972; Frank, 1986a, b; Kolowski et al., 2007; Holekamp et al., 2012), somehow “skewing” considerations on hyenas as a whole (Werdelin & Solounias, 1991; Lewis & Werdelin, 2022). However, considering how many aspects of *C. crocuta* biology and ecology are regarded as peculiar in comparison to other extant bone-cracking hyenas (e.g., Kruuk, 1972; Frank, 1986a, b; Mills 1982, 1990) and that it has been suggested that several features might have evolved recently (Werdelin & Lewis, 2008), it remains to be answered to what extent similar characteristics were present in extinct hyenas (Iannucci et al., 2022).

In this framework, there is a critical need of description of more material that might be key to clarify. Notwithstanding the importance of the recovery of further fossils from new excavations, revising historical collections might also offer new insights. The rediscovery of important specimens or new research in old localities is often the impetus for revising historical collections (e.g., Bona, 2021; Fabbi et al., 2021; Mecozzi et al., 2021, 2022), but reconsiderations of many samples are never attempted, especially if represented by few specimens. The number of “sporadic” findings, that is, those

Measurement	Value
c1 L	23 ¹
p2 L	15 ²
p2 W	10 ²
p3 L	20
p3 W	12,5
p4 L	22
p4 W	11,5
m1 L	25
m1 W	11,5
m1 pa-pr	13
m1 bhpa	13
m1 bhpr	11,5
m1 hmt	8,5
Di	14
c1-m1	121
p2-m1	86
Hfp2	42
Hbm1	47
Wbm1	12
TpL	158 ³

Tab. 1 - Measurements (in mm) of the hyena right hemimandible from Paciano provided by Bortolotti (1905). L = length, W = width, m1 pa-pr = distance between paraconid and protoconid, m1 bhpa = buccal height of the crown at the paraconid, m1 bhpr = buccal height of the crown at the protoconid, m1 hmt = height of the crown at the metaconid, Di = length of diastema c1-p2, c1-m1 = inclusive length of c1-m1, p2-m1 = inclusive length of p2-m1, Hfp2 = dorsoventral height of the mandible in front of p2, Hbm1 = dorsoventral height of the mandible behind m1, TpL = total preserved length of the mandible between the base of c1 and the rear of the ascending ramus.

¹ Approximate value according to Bortolotti (1905).

² We also consider these values approximations, as Bortolotti (1905) reported that the tooth was fragmented above the base of the crown.

³ The true total length of the mandible would have been greater than the reported value.

not recovered during systematic excavations, can be substantial in localities with a long research tradition and/or when fossiliferous formations span vast areas (e.g., Argenti, 2004; Iannucci et al., 2021c; Mecozzi et al., 2021). Extensive fossil samples remain undescribed in museums and other institutions, which might be seen as a particular case of the “taxonomic impediment” (Rodman & Cody, 2003) in one of its worst forms, that is, not necessarily due to the lack of proper expertise, but to the poor motivation to undertake dedicated studies, given the long effort needed and the meager credit taxonomic and descriptive works might have (Godfray, 2002; Agnarsson & Kuntner, 2007). In several cases, historical samples were the subject or works carried out at the time of their discovery, but then went entirely lost or destroyed for disparate reasons. Notorious incidents that caused immeasurable loss of natural history collections span from the bombing of several museums and institutions during World War II (e.g., Crumly, 1984) to the recent fire of the National Museum of Brazil in 2018 (Escobar, 2018). Implications for such losses are huge, and the existence of historical descriptions can have great importance from purely taxonomic and nomenclatural considerations to all that follows

(e.g., Pape et al., 2018). Paradoxically, however, the existence of previous works also adds further difficulties in offering stand-alone reconsiderations of historical samples, as they might be perceived as not original, the seek for “novelty” being a key aspect of current scientific publication practice (Makel & Plucker, 2014).

In this context, Umbria (central Italy) represents an emblematic case. In fact, despite the small geographical extension but thanks to the considerable (vertical and horizontal) development of Plio-Pleistocene sedimentary basins on the territory, it has played and still plays a key role for the understanding of the faunal turnovers that occurred in the last 3 Ma or so (Cherin, 2013). The historical collections of fossil mammals from Umbria have been known to science since the beginning of the 19th century (e.g., Cuvier, 1821) and were often the preserve of nobles or other prominent personalities of culture and society (as was the case in many other parts of Europe at that time). The recent reconsideration of some of these collections or of individual fossils has led to interesting knowledge advances. For instance, the revision of part of the mammal assemblage (Cicioni and Bellucci Collections) recovered from Villa Spinola (Perugia) in 1894-95 (Tuccimei, 1895) led to the description of the only partial skeleton of the felid *Panthera gombaszogensis* (Kretzoi, 1938) known in Umbria to date (Argenti & Sardella, 2003). Similarly, a recently reappraised mandible of *Tapirus arvernensis* Croizet & Jobert, 1828 from the lignite mines of Spoleto (Clerici Collection; Clerici, 1895) was recognized as the southernmost record of this species in Italy (Pandolfi & Kotsakis, 2017).

Here, we redescribe and revise the taxonomic attribution of a lost hyena hemimandible recovered from Paciano (Umbria, Italy; Fig. 1), originally reported by Bortolotti (1905), comparing it with relevant samples of Pliocene, Pleistocene, and extant species.

2. MATERIALS AND METHODS

The original hyena right hemimandible recovered from Paciano and described by Bortolotti (1905) is apparently lost, as reported by Argenti (2004) when listing fossil localities of Umbria and as confirmed by our own surveys in relevant institutions. In detail, the Paciano hyena was part of the ancient Canali Collection, a historical collection that went lost after the first decades of the last century (Argenti, 2004). Only a fraction of the Canali Collection is still curated in the Regional Direction for Museums of Umbria, including some other specimens described by Bortolotti (1904). Nonetheless, even if the original material is not available for direct examination, Bortolotti (1905) provided measurements and comments that allow to compare and contextualize this important specimen in an updated taxonomic framework. Bortolotti (1905) attributed the Paciano hyena to *Hyaena striata* (= *Hyaena hyaena*), while Argenti (2004) referred it to *P. brevirostris*. However, Iannucci et al. (2021b) did not mention Paciano among the occurrences of the giant hyena.

The massive and straight mandibular corpus of the hyena from Paciano adheres in morphology to that of a bone-cracking hyena. Therefore, the mandible was compared with that of extinct and extant bone-cracking hye-

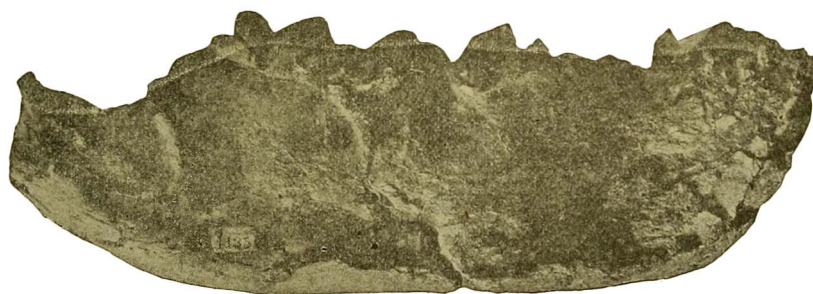


Fig. 2 - The hyena right hemimandible recovered from Paciano. Modified from Bortolotti (1905).

nas, namely *Pl. perrieri*, *P. brevirostris*, *C. crocuta*, “*Hyaena*” *prisca*, *H. hyaena*, and *Pa. brunnea*. The sample from Longdan (Qiu et al., 2004), considering his potentially “transitional” position between *Pliocrocota* and *Pachycrocota* (Iannucci et al., 2021b), is analyzed separately. Length (L) and width (W) of third premolar (p3), fourth premolar (p4), and first molar (m1) were included in the analysis. Here, the choice of variables was dictated by the availability of reliable measurements provided by Bortolotti (1905), but previous biometric analyses similarly relied on the p3-m1 series (Iannucci et al., 2021b). We used the dataset assembled by Iannucci et al. (2021b), with the addition of the Paciano specimen, as the input for two PCA analyses on the variance-covariance matrix of the considered measurement, in the first case using log-transformed values (referred to as logPCA in the text) and in the second “size-adjusting” raw measurements by dividing them by the geometric mean (gmPCA) of all measurements for that specimen (Mosimann, 1970; Mosimann & James, 1979; Jungers et al., 1995), the latter being an effective method to produce dimensionless variables widely adopted in studies on fossil mammals (e.g., Ercoli et al., 2019; Iannucci et al., 2021a). The software PAST version 4.04 (Hammer et al., 2001) was used for the analysis.

To avoid confusion when referring to different taxa, *Pachycrocota* is abbreviated to *P.*, *Pliocrocota* to *Pl.*, and *Parahyaena* to *Pa.*, when appropriate. Measurements of the Paciano hyena and related abbreviations are provided in Table 1.

3. RESULTS

3.1. Description

Bortolotti (1905) provided only a figure of the Paciano right hemimandible, from which the morphology of the dentition is not very clear (Fig. 2). Still, the robust and straight corpus of the hemimandible is indicative of a bone-cracking hyena, similar in proportions to all species considered in the comparison except for *C. crocuta*, in which the body is shallower near the symphysis (Palmqvist et al., 2011; Iannucci et al., 2022). According to Bortolotti (1905), the mandible of Paciano preserved the right p3-m1 series, with p2 and c1 also present but severely damaged. The author did not provide many details in his description of the specimen, but he emphasized the presence in m1 of a metaconid [“tubercolo

interno del ferino” (= “internal tubercle of the carnassial”; own translation from the original Italian)] and a well-developed talonid hosting two cuspids (one buccally and one lingually) separated by a valley.

3.2. Biometric comparison

The results of the PCA are consistent with those obtained by Iannucci et al. (2021b). In logPCA, the morphospace projection onto the first two components (Figure 3) separates specimens mainly according to their size (along PC1, 86.5% of explained variance) and relative elongation of m1 (along PC2, 8.6% of explained variance). The large-sized *P. brevirostris* is placed on the right of the scatter plot and *C. crocuta* separated towards positive values on PC2. The other species are grouped on the left and are mainly, but not completely (apart from *H. hyaena* and “*H.*” *prisca*), distinct by size. Some specimens of *Pl. perrieri*, especially that from Paciano, plot towards positive values along PC2, meaning they have relatively elongated m1.

When the effect of size is adjusted in gmPCA, the morphospace projection of the first two components (Figure 4) separates specimens mainly on the base of the elongation of m1 (along PC1, 66.0% of explained variance) and the proportions of the premolars (along PC2, 21.4% of explained variance). The latter differences are mainly intraspecific and place specimens with widened premolar towards more negative values along PC2. Basically, in gmPCA only *C. crocuta* clearly occupies a distinct area of the morphospace, while there is overlap between all other species. Also in this case, there are, however, few specimens of *P. brevirostris* and *Pl. perrieri*, especially Paciano, that plot closer to values observed for *C. crocuta*, having relatively elongated m1.

Detailed bivariate comparisons of length and width of each tooth confirm the differences in size observed with the PCA (Figure 5). *Hyaena hyaena* is the smallest species in all considered measurements, while *P. brevirostris* is the largest in all but m1 L, in which it is surpassed by several specimens of *C. crocuta*. In terms of dental proportions, all species are similar, apart from *C. crocuta*, which is almost completely separated by other hyenas according to its relatively more elongated m1 (Figure 5C). In general, measurements of the hemimandible from Paciano place it among small-sized specimens. In detail, in the p3 scatter plot it falls within the ranges of *H. hyaena* and *Pl. perrieri*, and not far from the smallest specimens of brown and spotted hyenas

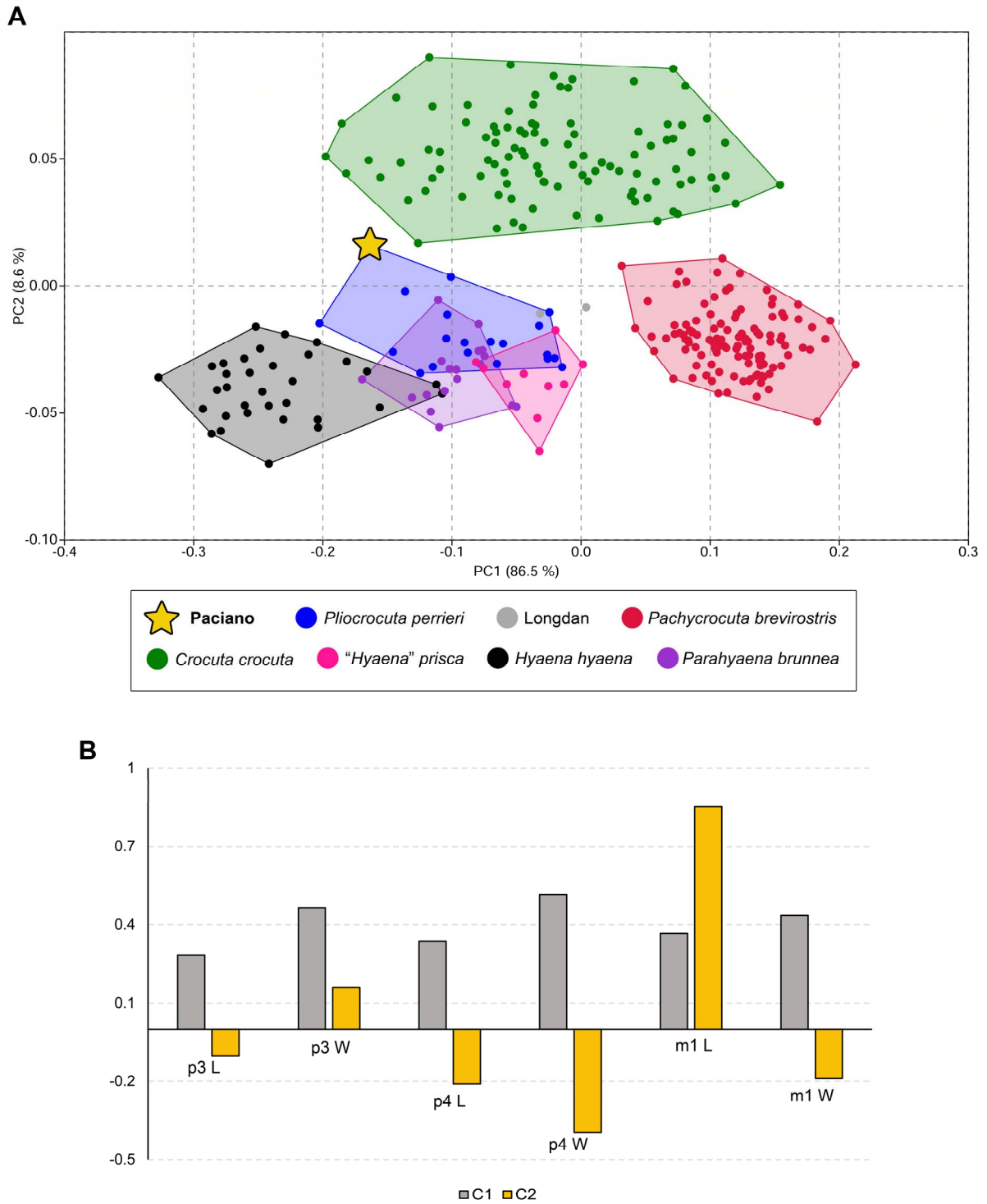


Fig. 3 - Scatter plot (A) and loadings (B) of the first two principal components of logPCA. For raw data and detailed references, see Iannucci et al. (2021b).

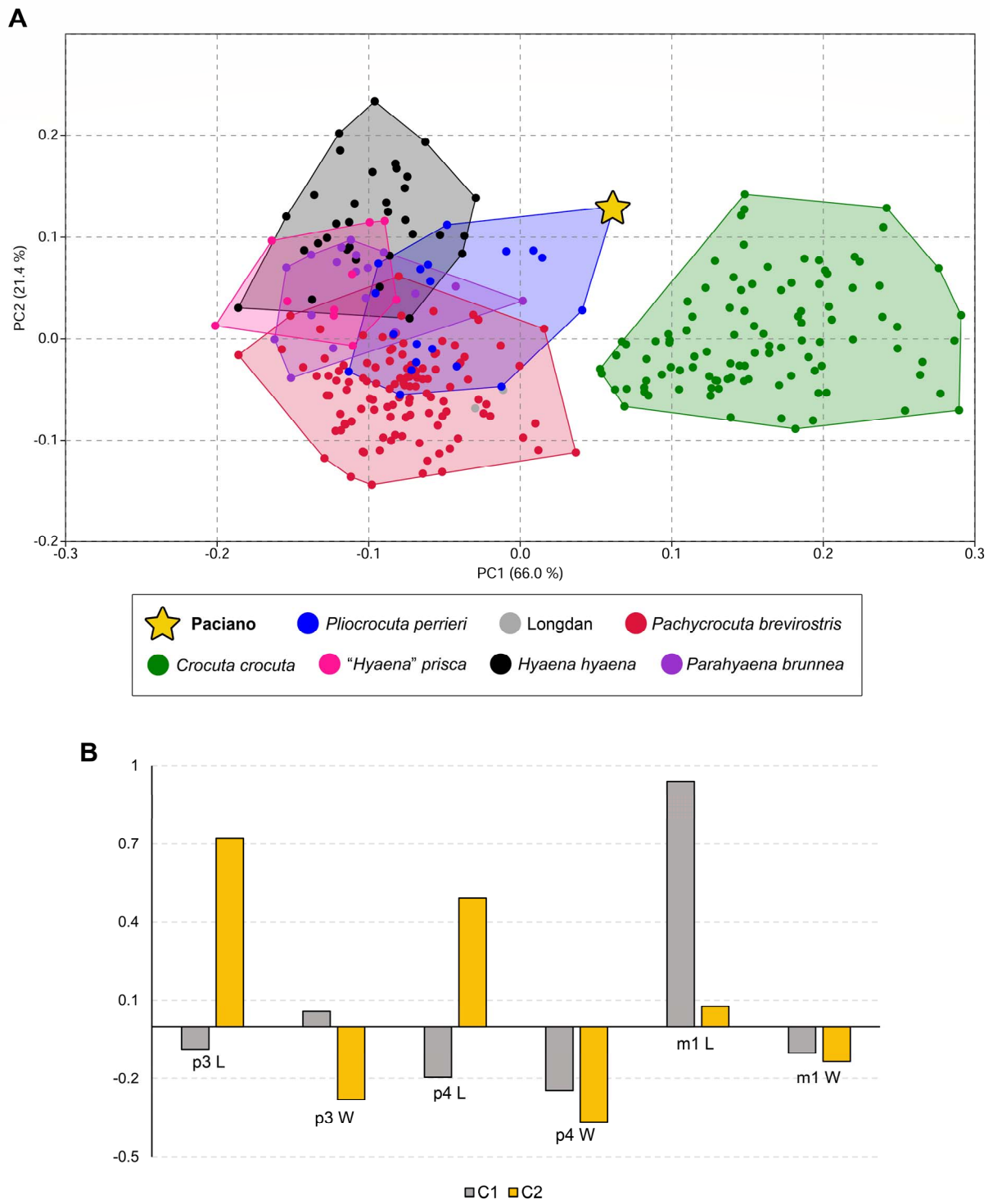


Fig. 4 - Scatter plot (A) and loadings (B) of the first two principal components of gmPCA. For raw data and detailed references, see Iannucci et al. (2021b).



Fig. 5 - Bivariate plots comparing L and W (in mm) of p3 (A), p4 (B), and m1 (C) of the hyena from Paciano and several samples of extinct and extant bone-cracking hyenas.

(Figure 5A). In the bivariate comparison of p4 measurements, Paciano is somewhat distinct from other species but closer to *C. crocuta* (Figure 5B). Considering length and width separately, in p4 L, Paciano is compatible with *C. crocuta*, *H. hyaena*, *Pa. brunnea*, and *Pl. perrieri*, while p4 W only fits with *H. hyaena* and smallest values of *C. crocuta*. In m1 measurements, Paciano again does not plot confidently in the range of one of the groups of the comparative sample, but it is close to specimens of *C. crocuta*, *Pa. brunnea*, and *Pl. perrieri*.

4. DISCUSSION

Bortolotti (1905) attributed the Paciano hyena to *H. striata* (= *H. hyaena*), noting an overall resemblance with *H. arvernensis* (= *Pl. perrieri*) but judging the specimen too small to belong to that species. Indeed, our comparisons showed that there is some overlap, though limited, between the largest specimens of *H. hyaena* and the smallest of *Pl. perrieri* in most measurement considered (Figure 5). However, although the Paciano hyena is apparently among the smallest specimens of *Pl. perrieri*, it has a larger and proportionally more elongated m1 than that of *H. hyaena*, which separates it from this species. This evidence allows to identify the Paciano hyena as *Pl. perrieri*. Considering the paucity of comparative material Bortolotti (1905) had in his disposal, his taxonomic opinion represented the best fit for the then available evidence, but can now be confidently revised.

Pliocrocuta perrieri and the giant hyena *P. brevirostris* have a very similar morphology, and remains of the two species are often separated by size (Iannucci et al., 2021b). In this respect, the small size of the Paciano hyena clearly excludes an attribution to *P. brevirostris*, which was tentatively suggested by Argenti (2004). Bortolotti (1905) also underlined the presence of a well-developed metaconid in the m1 of the Paciano hyena, a feature that reinforces its assignment to *Pl. perrieri* (Werdelin & Solounias, 1991; Iannucci et al., 2021b).

In some measurements, the Paciano hyena seems peculiar in comparison to other specimens of *Pl. perrieri*. In detail, the p4 W (11.5 mm) is slightly below the minimum value of the sample of *Pl. perrieri* included in the comparison (12.1 mm), although not outside the range known for the species (a minimum value of 9.3 mm is reported by Coca-Ortega & Pérez-Claros, 2019). Moreover, although the specimen is small in most measurement, the value of m1 L is relatively high, denoting a proportionally elongated carnassial. However, considering the fragmentary nature of the specimen and that Bortolotti (1905) evidently adopted a “coarse” approximation at 0.5 mm in his measurements, the observed differences are likely spurious.

For completeness, it is worth mentioning that a reference of the Paciano hemimandible to *C. lunensis*, a species that might have been compatible with the putative age of the fossil locality, is clearly discouraged by morphological and biometric traits, including the robust and straight mandibular corpus, the presence of a metaconid in m1, and the widened teeth, among others (Werdelin & Solounias, 1991; Tseng et al., 2013).

The presence of *Pl. perrieri* at Paciano has also

implications for the age of the fossil deposit. The latest occurrences of *Pl. perrieri* in Europe are dated at ~2.0–1.8 Ma (Iannucci et al., 2021b), and the species is certainly more abundant in older localities (e.g., Viret, 1954; Howell & Petter, 1980; Qiu, 1987; Werdelin & Solounias, 1991).

In Umbria, most Plio-Pleistocene mammal assemblages have been discovered within the Tiberino Basin, which extends across the center of the territory for ~1800 km² (Cherin et al., 2019). Other findings are reported from the smaller Tavernelle-Pietrafitta Basin, south of Lake Trasimeno, including the extremely rich assemblage from the Pietrafitta lignite mines (Martinetto et al., 2014; Sorbelli et al., 2021, and references therein). Finally, some other mammal remains have been recovered from the Valdichiana Basin, whose deposits crop out in few areas of western Umbria (Figure 1). Among the latter discoveries, it is worth mentioning the assemblages from Selvella and Vigna Nuova. The former was originally dated at ~1 Ma (De Giuli, 1987), but then referred to the Farneta Faunal Unit (FU; ~1.5 Ma; Alberdi & Palombo, 2013; Cirilli et al., 2020), similarly to the aforementioned assemblage from Pietrafitta. The case of Vigna Nuova is intriguing because taphonomic and geological evidence have allowed the sample to be divided into two assemblages (Azzarà et al., 2022). The younger, including only remains of cf. *Leptobos* collected from conglomerates (“upper layer”), can be correlated with other well-known Valdichiana assemblages (e.g., Selvella, Farneta), thus dated at ~1.5 Ma. The older sub-sample, coming from a putative paleosol (“lower layer”) no longer visible in the field, includes cf. *Megantereon*, *Canis* sp., Mustelidae indet., Proboscidea indet., *Equus* cf. *senezensis*, cf. *Leptobos*, *Croizetoceros ramosus*, *Pseudodama* sp., Cervidae indet. (large size), and *Sus* cf. *strozzi*. Azzarà et al. (2022) referred this assemblage to the Coste San Giacomo FU (late Middle Villafranchian; ~2.2–2.1 Ma).

Unfortunately, the exact provenance of the hyena from Paciano is unknown. On the basis of the geographical location of the municipality of Paciano (Figure 1), the fossil could come from deposits of either the Valdichiana or Tavernelle-Pietrafitta Basin. Therefore, given that the last occurrence of *Pl. perrieri* is attested at the beginning of the Late Villafranchian (but the species is certainly more abundant in Europe in the Middle Villafranchian), its presence in Paciano could (1) confirm the presence of a late Middle Villafranchian sedimentary cycle in the Valdichiana Basin, in agreement with the recent discoveries at Vigna Nuova (Azzarà et al., 2022) or (2) suggest the presence of a similar sedimentary cycle also in the Tavernelle-Pietrafitta Basin, not reported so far. Unfortunately, as it is not possible to define whether the fossil comes from one or the other basin, this doubt cannot be resolved.

The Paciano hyena likely falls in a time-span of great interest for the evolution of hyenas in Europe, when some localities still document the presence of *C. lunensis* and *Pl. perrieri*, but also the contemporaneous occurrence of *P. brevirostris* (Iannucci et al., 2021b). If the coexistence between *C. lunensis* and the other species is easily justifiable by their different inferred ecology (e.g., Werdelin & Solounias, 1991, 1996; Tseng et al.,

2011, 2013), that between *Pl. perrieri* and *P. brevirostris* might seem to necessitate some further explanation, as they are very similar in craniodental morphology.

A somewhat similar case that is worth considering here is the extinction in Europe of *P. brevirostris*. After ~1 Ma since its appearance in the European fossil record, the rule of the specialized bone-cracker came to an end close the Early-Middle Pleistocene boundary, ~0.8 Ma, approximately coinciding with the arrival of *C. crocuta* and “*H. prisca*” (Iannucci et al., 2021b). Competition between *P. brevirostris* and *C. crocuta* has often been advocated as a factor potentially favoring the disappearance of the former (e.g., Kurtén, 1968; Palombo et al., 2008). Iannucci et al. (2021b) argued instead that the newcomers hardly played a significant role in the extinction of *P. brevirostris*, considering paleoecological and paleobiogeographical aspects, but mostly revising the putative records previously deemed to attest a persistence of the giant hyena in Europe beyond the Early-Middle Pleistocene boundary and its coexistence with *C. crocuta*. The authors also reasoned that although the error ranges associated with the available dating estimates for the last occurrences of *P. brevirostris* and the firsts of *C. crocuta* in the Iberian Peninsula do not allow to exclude an overlap in the chronological range of the two species—one of the aspect that might permit to hypothesize some sort of competition—from a biochronological point of view the arrival of Galerian newcomers such as *Cervus elaphus*, *Sus scrofa*, and *C. crocuta* at Gran Dolina and Cueva Negra (earliest localities with *C. crocuta*) likely supports a separation from Vallparadís EVT7 (latest calibrated occurrence of *P. brevirostris*). This remark has now received further support from the revised chronological constraints for the lower levels of Gran Dolina (Duval et al., 2022), which, among the other things, are incompatible with the previous paleomagnetic correlation for the normal polarity intervals of the unit TD7 with the Kamikatsura (846 ± 10 ka) and/or Santa Rosa (932 ± 5 ka) magnetic excursions (Parés et al., 2013). The new dating constraints rather point to a correlation with the Matuyama-Brunhes precursor, which is not older than 794 ± 4 ka but perhaps even younger (Channell et al., 2020; Haneda et al., 2020; Duval et al., 2022). The previous interpretation was the main reason to consider *C. crocuta* potentially present in Europe prior 0.9 Ma (e.g., Martínez-Navarro, 2010; Palombo, 2014), as TD7 overlies levels with hyaenid remains in the sequence of Gran Dolina. Therefore, the “*C. crocuta* event”, as it is often referred to (Martínez-Navarro, 2010), likely occurred ~0.8 Ma. This age is close to the earliest occurrence of *C. crocuta* in Italy from the layer of gravels and sands of Cava di Breccia di Casal Selce, which is dated around 0.75–0.70 Ma and yielded the reference fauna of the Ponte Galeria FU, at the beginning of the Galerian European Land Mammal Age (Petronio & Sardella, 1999; Sardella & Petrucci, 2012; Strani et al., 2022).

In this case, competition between hyenas hardly played a significant role in the extinction of *P. brevirostris*, although it might have influenced the late dispersal of *Crocuta* in Europe after its spread outside Africa (Iannucci et al., 2021b). However, *Pl. perrieri* and *P. brevirostris* were definitely closer in craniodental mor-

phology (and hence inferred ecology) than the giant hyena was to *C. crocuta*, and their remains are recovered together in some localities (Iannucci et al., 2021b). Even so, looking at the dimensional differences in dental measurements between the extant species (Figure 5), we observed a much larger overlap than that between *Pl. perrieri* and *P. brevirostris*. Therefore, even considering size alone, it seems reasonable to assume that the two species were different enough to occupy different niches, not impeding their coexistence. Further support for this consideration comes from the behavioral plasticity of living bone-cracking hyenas. The proportion between hunting and scavenging, diurnal or nocturnal activity, and the location of denning sites, among others, are all factors that can vary and thus facilitate coexistence between living species (Kruuk, 1972; Mills, 1982, 1990; Wiesel, 2006). On the other hand, the “*P. brevirostris* event” was accompanied by an important reorganization of mammalian faunas and indeed witnessed a peak in carnivoran diversity, particularly of hypercarnivorous and ambush-hunting felids (Azzaroli, 1983; Palombo et al., 2008; Konidaris, 2022). Envisioning *Pl. perrieri* mainly as a solitary scavenger, led to the paradox that after its extinction the “place” of a middle-sized scavenger in the carnivoran guild of the Late Villafranchian remained unoccupied (Konidaris, 2022), which might have implications for early hominin dispersal into Europe (Konidaris & Tourloukis, 2021; Konidaris, 2022). However, few species are exclusively adapted to a specific feeding behavior and if *Pl. perrieri* had to coexist with *P. brevirostris*, it likely had to deviate to a more active hunting behavior and/or to target smaller preys. At the same time, this was likely not an easy task, facing the arrivals of several new competitors. It is thus conceivable that *Pl. perrieri* managed to maintain a place in Late Villafranchian carnivoran guild only for a short geological period, perhaps while other carnivorans were becoming widespread.

If the evolution of *P. brevirostris* was a punctuated event, the likely source area would be eastern Asia. Indeed, the sample from Longdan referred to *Pachycrocuta* by Qiu et al. (2004), is intermediate in several measurements between *Pl. perrieri* and *P. brevirostris*, although somewhat closer to the former species (Figure 5). Further discovery and description of new (and old) material is needed to understand if a tendency towards larger dimensions occurred in other samples across Eurasia, especially focusing on late samples of *Pl. perrieri*. Although the trend is not strong, chronologically younger specimens of *P. brevirostris* are generally larger than earlier representatives of the species, supporting the view of a progressive specialization during the evolution of the giant hyena (Iannucci et al., 2021b, 2022), which might have started from the separation of *P. brevirostris* from *Pl. perrieri* (Werdelin & Solounias, 1991), or perhaps even in some late samples of the latter species.

5. CONCLUSIONS

Although the hyena hemimandible from Paciano went lost over the years, critically revising and contextualizing the description and measurements provided by Bortolotti (1905) in an updated comparative and taxo-

onomic framework allowed to reattribute the specimen to *Pl. perrieri*. This species is not documented by extensive samples in Italy and testifies to a relatively old age for the fossil locality, thus offering an interesting additional record in the study of Early Pleistocene European hyenas and underlining the importance and the feasibility of revising historical collections, even when the original remains are lost. In general, there is a relative paucity of descriptions or reconsiderations of historical samples, especially if excluding publications that change previous interpretations, as a likely consequence of the seek for “novelty” that permeates current scientific literature. Here, we revised the taxonomic attribution of the Paliano hyena, but we emphasize that even confirming an attribution to *P. brevirostris*, as proposed in the latest work mentioning this sample (Argenti, 2004), would have been a significant outcome, and that confirmatory results are worth to share with the scientific community. The giant hyena *P. brevirostris* likely originated from a large-sized stock of *Pl. perrieri*, but around 2.0–1.8 Ma, while *P. brevirostris* spread into Europe, some populations of *Pl. perrieri* remained relatively small-sized and survived for a short time alongside the giant hyena. The impact of competition between extant hyaenid species is generally compensated by their behavioral plasticity, but the evolution of the specialized giant hyena on one side, and the concurrent spread of other Late Villafranchian carnivores on the other, might have pushed *Pl. perrieri* towards the limits of its ecological tolerance, eventually triggering its extinction. In any case, there are few localities that document a co-occurrence of *Pl. perrieri* and *P. brevirostris*, which complicates elucidating the issue.

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