Unravelling the origin of the brown hyena (*Parahyena brunnea*) and its evolutionary and paleoecological implications for the *Pachycrocuta* lineage

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ABSTRACT

The dentition of several species of hyenas within the lineages leading to *Parahyaena brunnea* and *Pachycrocuta brevirostris* was analysed from a multivariate point of view. The probable origin of these lineages can be traced back to China in the late Miocene or early Pliocene, from an initial stock that dispersed across the Old World during the Zanclean. This ancestral stock is believed to comprise *Parahyaena howelli* and *Pliocrocuta perrieri* from the Zanclean and is suggested to be grouped into *Pachycrocuta pyrenaica*. The subsequent *Pliocrocuta perrieri* arose from such a stock and is proposed to be reassigned to *Pachycrocuta perrieri*. The findings obtained substantiate the hypothesis that *Pachycrocuta bellax* represents a species distinct from *Pachycrocuta brevirostris*. *Pachycrocuta perrieri* is posited as the ancestor of *Pachycrocuta brevirostris* in Eurasia, and *Parahyaena brunnea* in Africa. The sequence *Pachycrocuta pyrenaica, Pachycrocuta perrieri,* and *Pachycrocuta brevirostris* delineates an evolutionary trend marked by greater specialization in the scavenging niche, manifested through augmented overall dentition size and development of bone-breaking part of the dentition at the expense of a reduction in its cutting region. Present-day forms of *Parahyaena brunnea* also exhibit such specialization, but the size of the dentition is similar to that of *Pachycrocuta perrieri*. *'Hyaena' prisca* is considered a basal form of *Parahyaena brunnea*, akin to specimens recovered from Elandsfontein approximately 1 million years ago, which recolonized Europe following the extinction of *Pachycrocuta brevirostris*. The degree of divergence of the extant forms of *Parahyaena brunnea* from *'Hyaena' prisca* justifies their classification as distinct species. A proposal is made to integrate both the brown hyena and *'Hyaena' prisca* into the genus *Pachycrocuta*.

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INTRODUCTION

One of the central species of this paper is *'Hyaena perrieri'* or hyena of Perrier, as originally named by Croizet and Jobert in 1828. The fossil assemblage where this hyena was described has special significance in the beginning of both Paleontology and Geology. Such an assemblage was composed of extinct species of still extant genera, which together with the fact that the materials where the remains were recovered were stratigraphically far below lava flows covering the region, was used by Lyell and Murchison (1829) as arguments to indicate that such a fossil assemblage was of immense antiquity and that the deep excavation of the valleys by the erosive action of the rivers observed in the French Auvergne region indicated current geological forces acting over an incalculable period of time. These arguments supported a uniformitarian interpretation as opposed to the catastrophist thesis maintained by Cuvier, which Buckland even tried to associate with the biblical deluge (Rudwick, 1985). More than 150 years later, Howell and Peter (1980) assigned *'Hyaena perrieri'* to the genus *Pachycrocuta* and differentiated it from *Pachycrocuta pyrenaica* (Depéret, 1890). Subsequently, Werdelin and Solounias (1991) synomized both, reassigning them to *Pliocrocuta perrieri*.

Pliocrocuta perrieri is one of the most abundant and widespread hyenas during the Pliocene of the Old World. This species exhibits dental adaptations typical of the ecomorph fully developed bone-crackers of Werdelin and Solounias (1996). This type of trophic adaptation has arisen independently within the family Hyaenidae on several occasions in both, the subfamily Percrocutinae (Pérez-Claros, 2023) and the subfamily Hyaeninae, with *Allohyaena sarmatica* (Semenov, 1994) being the first representative of the latter subfamily at the beginning of the Tortonian (Pérez-Claros, 2022).

The durophagous ecomorph can be further subdivided into two distinct sets of adaptations that are metrically reflected in their dentition (Coca-Ortega and Pérez-Claros, 2019; Pérez-Claros and Coca-Ortega, 2020): social hunting durophages with the spotted hyena (*Crocuta crocuta* [Erxleben, 1777]) as its only present-day representative and solitary scavenging durophages with the striped and brown hyena (*Hyaena hyaena* [Linnaeus, 1758] and *Parahyaena brunnea* [Thunberg, 1820], respectively) as living species of the latter. Such differences may explain the sympatry of *C. crocuta* with the other two hyenas and the allopatry between *H. hyaena* and *Pa. brunnea*, since the similarity in body size and ecomorphological adaptations between them can be interpreted in terms of competitive exclusion (Pérez-Claros, 2022).

On the other hand, the common adaptations observed in *H. hyaena* and *Pa. brunnea* are the consequence of an evolutionary convergence, since they come from ancestors that had not developed the fully developed durophagous characteristics they share. In fact, the ecomorphological analysis by Coca-Ortega and Pérez-Claros (2019) showed that *Parahyaena howelli* (Werdelin, 2003), an early member of the *Pa. brunnea* lineage according to Werdelin and Lewis (2008), although nominally associated with the fully developed bone cracker ecomorph, shows a position in the morphospace of both the upper and lower dentition relatively close to the transitional bone cracker ecomorph of Werdelin and Solounias (1996). Since *Ikelohyaena abronia* (Hendey, 1974), which is an early member of the lineage that gave rise to *H. hyaena*, also belongs to the transitional bone cracker ecomorph, the fully durophagous characteristics observed in *H. hyaena* and *Parahyaena brunnea* must have evolved independently. On the other hand, considering that *Pa. howelli* is known only from the localities of Kanapoi and Laetoli (Werdelin, 2003; Werdelin and Dehghani, 2011) both of Zanclean age around 4 Ma, the separation of the lineages that gave rise to *H. hyaena* and *Pa. brunnea* must have taken place earlier, well into the early Pliocene or even the late Miocene.

Parahyaena brunnea and *Pl. perrieri* show adaptations typical of the solitary scavenging durophagous ecomorph (Coca-Ortega and Pérez-Claros, 2019; Pérez-Claros and Coca-Ortega, 2020). Both forms are evolutionarily close although their exact phylogenetic relationships have been interpreted differently by different authors. Figure 1 shows some examples of mandibles, stratigraphic ranges, and geographic occurrences of those scavenging durophagous species related to the *Pa. brunnea* lineage (as indicated, the rest of the extant durophagous hyenas: *H. hyaena* and *C. crocuta* do not belong to such a lineage).
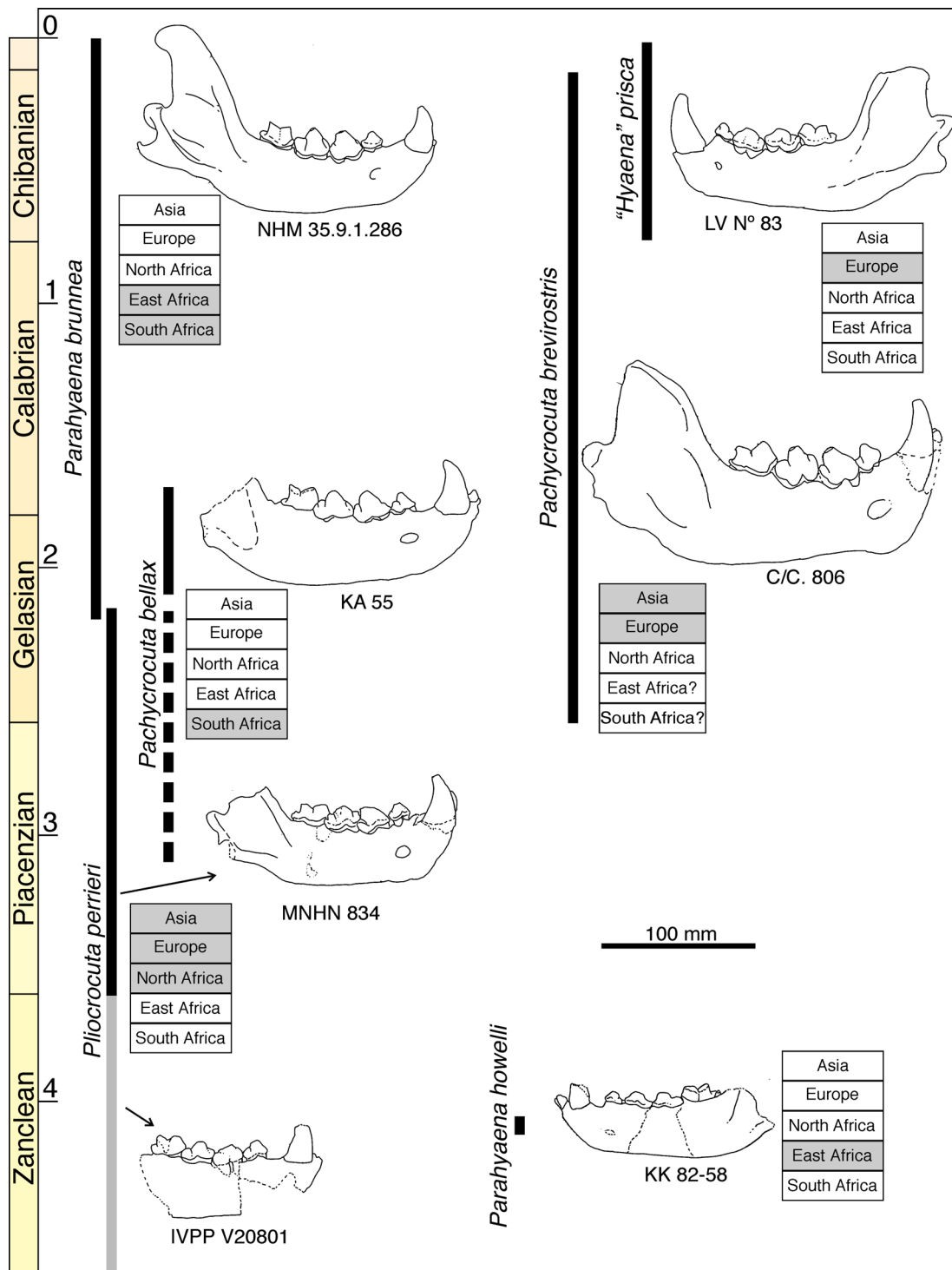
FIGURE 1. Stratigraphic range of the species belonging to the analyzed lineages, their paleogeographic distribution (squares with gray background), and some examples of lower mandibles in labial view. IVPP V20801: *Pliocrocuta perrieri* from Zanclean (Zanda Basin, China), drawn from Tseng et al. (2016). KK 82-58: *Parahyaena howelli* (Laetoli, Tanzania), drawn from Werdelin and Dehghani (2011). MNHN 834: *Pliocrocuta perrieri* post-Zanclean (holotype from Mont Perrier, Muséum national d'histoire naturelle, Paris. C/C. 806: *Pachycrocuta brevirostris* (Zhoukoudian, China) drawn from Pei (1934). KA 55: *Pachycrocuta bellax* (Kromdraai A, South Africa) drawn from Ewer (1954a). *'Hyaena' prisca* (holotype from Lunel-Viel, France) drawn from Brugal et al. (2021). NHM 35.9.1.286: *Parahyaena brunnea* (Karroo Valley, South Africa, housed at the Natural History Museum, London).

Both Kurtén (1954) and Howell and Petter (1980) considered that *Pa. brunnea* and *Pl. perrieri* came from a common ancestor in the Pliocene. Howell and Petter (1980) specified that this common ancestor was *P. pyrenaica*. That is, according to the scheme followed by Howell and Petter (1980), *Pachycrocuta pyrenaica* would be the ancestor of both *P. perrieri* and *Pa. brunnea*. On the other hand, Turner (1990) proposes that *P. perrieri* and *Pa. brunnea* would be conspecific. The similarity between these species is undeniable, and according to Turner (1990), if *P. perrieri* were recovered from a site in South Africa, it would be directly assigned to *Pa. brunnea*.

As indicated above, Werdelin and Solounias (1991) grouped *Pachycrocuta pyrenaica* and *Pachycrocuta perrieri* within *Pliocrocuta perrieri* on the grounds that the metric distinction made by Howell and Petter (1980) mixed specimens and individuals, which concealed variation within *Pliocrocuta perrieri*. However, the discrepancy between Werdelin and Solounias (1991) and Howell and Petter (1980) is more taxonomic than evolutionary in nature. Indeed, the former recognize that specimens of *Pliocrocuta perrieri* from the Zanclean (i.e., *Pachycrocuta pyrenaica* sensu Howell and Petter, 1980), considered as a whole, tend to have more primitive characteristics than those from the Piacenzian and Gelasian, which gradually change to the condition seen in *Pachycrocuta brevirostris*.

Werdelin and Solounias (1991) also grouped within *Pliocrocuta perrieri* another form unique to the Middle Pleistocene of Europe known as *'Hyaena' prisca*. Such grouping creates a discontinuity within the stratigraphic range of *Pliocrocuta perrieri*, since this species disappears from the fossil record at the end of the Gelasian. Recently, Lannucci et al. (2021) have shown metric arguments that reject the conspecificity of *Pliocrocuta perrieri* and *'Hyaena' prisca*.

Finally, there are two additional species of the genus *Pachycrocuta* phylogenetically close to the species previously considered: *P. brevirostris* (Gervais, 1850) and *P. bellax* (Ewer, 1954a). *Pachycrocuta brevirostris* is widely known from the Early Pleistocene of Eurasia, disappearing from Europe at the end of the Early Pleistocene (Lannucci et al., 2021), although it persisted in China until the Middle Pleistocene (Liu et al., 2021). There is some consensus that *Pliocrocuta perrieri* is the ancestor of *P. brevirostris* (Howell and Petter, 1980; Qiu, 1987; Werdelin and Solounias, 1991). The clearest difference between *Pl. perrieri* and *P. brevirostris* is

the larger size of the latter in addition to the fact that the former has a metaconid on the first lower molar and in general *P. brevirostris* does not. Ecomorphological and paleoecological studies show that this species would be a highly specialized scavenger (Palmqvist et al., 2011; Pérez-Claros and Coca-Ortega, 2020).

Pachycrocuta bellax is known from few remains in South Africa. Turner (1990) suggested its conspecificity with *P. brevirostris*, and although its relationship to the *Pliocrocuta perrieri–P. brevirostris* lineage seems clear (Howell and Petter, 1980; Werdelin and Solounias, 1991), certain primitive features (e.g., a clearly differentiated metaconid) do not allow it to be clearly integrated into *P. brevirostris* without a re-evaluation of the variation of the latter (Werdelin and Solounias, 1991). In fact, Howell and Petter (1980) indicated that *P. bellax* has some characteristics that resemble *P. perrieri* and others resemble *P. brevirostris*.

Although some morphological data that have served as a basis for establishing phylogenetic relationships between the hyena species analysed here are certainly important, metric data such as those studied in the present study are indispensable. Morphometric analyses are necessary as some morphological data, such as the presence/absence of a metaconid or the number of cusps of the talonid of the lower molar, have been questioned in some cases for taxonomic classification as they are certainly variable (e.g., Kurtén, 1956). A classic and widely used method of analysing metric data for phylogenetic purposes has been the use of ratio diagrams (e.g., Kurtén, 1956; Howell and Petter, 1980; Werdelin and Solunias, 1991). Another way to analyse metric data to establish phylogenetic relationships is by coding them as discrete variables to be subsequently incorporated into cladistic analyses (e.g., Werdelin and Solunias, 1991).

In addition to the discovery of new paleontological sites, important compilations of metric data have been published in recent years (e.g., Liu et al., 2021; Lewis and Werdelin, 2022), which allow evaluation of the degree of overlap and morphological continuity of the species of this and other lineages from a multivariate statistical point of view (e.g., Pérez-Claros et al., 2021). Lannucci et al. (2021) assessed with such methodology the relationships among most species of this lineage together with other social durophages, including living *C. crocuta*. The results obtained in such a study, like others published previously (Coca-Ortega and Pérez-Claros, 2019; Pérez-Claros and

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Coca-Ortega, 2020), indicated a clear separation between the two types of durophagous ecomorphs based on the relative increase in the length of the lower carnassial in the case of social hunters (e.g., genus *Crocuta*). On the other hand, Lannucci et al. (2021) obtained some separation in size between the different species belonging to each type of durophages, although the degree of overlap in morphology for the species that integrate each category is remarkable.

The aim of the present work is to re-evaluate the relationships between the species that are part of or closely related to the lineage leading to *Pa. brunnea* and *P. brevirostris* from a multivariate metric perspective and its paleoecological and paleogeographical implications. For this purpose, the sample analysed has been expanded with respect to previous studies both qualitatively and quantitatively, also including the upper dentition. In addition, the samples are analysed at the individual level as well as at the fossil assemblage level by averaging the different variables in each fossil locality. This makes it possible to analyse fossiliferous localities that, although providing several remains, lack complete individuals. In cases where there are a reasonable number of remains, the mean can be considered a value close to the population mean. Finally, in all analyses, the three living durophagous species have been incorporated to evaluate the effect of individual versus population variation.

MATERIALS AND METHODS

The analysed sample consists of the mesio-distal lengths (L) and bucco-lingual widths (W) of the last two lower premolars and first molar (p3, p4,

m1) and the last three upper premolars (P2, P3, P4) for the three living durophagous hyenas *(H. hyaena, Pa. brunnea,* and *C. crocuta)* as well as for the previously mentioned extinct species: *Pa. howelli, Pl. perrieri, P. brevirostris, P. bellax,* and *'H.' prisca*.

For certain analyses the sample of *Pl. perrieri* has been divided into the Zanclean specimens and those of later age (Piacenzian and Gelasian) as well as the sample of *Pa. brunnea* that has been divided into its living and fossil representatives. To complement the sample with fossil representatives of the hunting durophagous ecomorph, *C. spelaea* (sensu Lewis and Werdelin, 2022) has been included in the analyses, since this species is known from a high number of remains and is well delimited both geographically and temporally. The sample sizes for each species are listed in Table 1.

Virtually all data come from literature sources, except for certain specimens of *H. hyaena* from the Western Sahara obtained from the Museum of the Estación Biológica de Doñana (Seville, Spain). The length of the trigonid of m1, if not explicitly reported by the authors, has been estimated directly from photographs of the specimens (if figured), following Werdelin and Solounias (1991). The numerical age assigned to the paleontological sites was the midpoint of the reported time interval. All measurements and approximate ages of the specimens related to the lineages under study, as well as the references where they have been extracted, are shown in the Appendix 1.

Four individuals attributed to *H. hyaena* by Cardoso (1993) and two to *Hyaena* sp. by Geib (1915) have been excluded from the analysed sample of extant species. A previous discriminant

TABLE 1. Sample sizes for the species analyzed as a function of dentition type and analysis performed.

Species	Lower Dentition		Upper Dentition	
	Nº Individuals	Nº Fossil Sites	Nº Individuals	Nº Fossil Sites
P. brunnea (living)	23	–	20	–
P. brunnea (fossil)	9	9	2	3
H. hyaena	56	–	47	–
C. crocuta	69	–	35	–
'Hyaena' prisca	10	6	4	4
P. brevirostris	119	26	44	16
P. bellax	1	1	2	2
Pl. perrieri (Zanclean)	4	6	1	2
Pl. perrieri (Piac., Gel.)	29	25	14	13
Parahyaena howelli	5	2	1	1
Crocuta spelaea	105	25	42	20

analysis showed in the first case that the upper or lower dentition (or both) of such specimens (MNHN 1877-113, MNHN 1922-301, MNHN A-1536, and MNHN A-7940) were attributed to *Pa. brunnea* with a probability close to 1. In the case of Geib (1915), one of the dentitions (upper or lower) of the specimens A.1.14 and 583/A. 235b was attributed to *Pa. brunnea* and the other to *H. hyaena*, with probabilities close to 1. It is not possible to ascertain whether these are nomenclatural errors of the museum or truly atypical *H. hyaena* individuals. Atypical individuals, although perfectly acceptable from a biological point of view, can negatively affect statistical procedures (Reyment, 1990), and for this reason have been excluded. Nevertheless, the sample size of *H. hyaena* analysed was comparatively high (N = 56, Table 1), so it is expected that the sample reflects the biological variability of this species.

The specimen from the Lunel-Viel site (France) LVI-4-1412 attributed to *Crocuta spelaea intermedia* by Bonify (1971) has been assigned to *'Hyaena' prisca* fossils in agreement with Lewis and Werdelin (2022). Specimen CD 3218 from the Cooper's Cave site (South Africa) assigned to *Pa. brunnea* by Kuhn et al. (2017) has not been incorporated into the analysis since the values fall outside the range observed for such a species (Kuhn et al., 2017, figure 2c shows that CD 3218 projects outside the convex hull of *Pa. brunnea* and within the region occupied by *C. crocuta* and *C. ultra*).

Specimens HMV 1201 and HMV 1202 from the Londang site (Linxia Basin, China) attributed to *Pachycrocuta licenti* by Qiu et al. (2004) have been initially attributed to *Pl. perrieri* according to Lannucci et al. (2021), although as will be discussed below they are intermediate forms between *Pl. perrieri* and *P. brevirostris* (as indicated by Qiu et al., 2004 in the diagnosis of *P. licenti*). Finally, specimen V 7296 from Baihaicum locality 26 (Yushe Basin, China) attributed to *Crocuta honanensis* by Qiu (1987) has been considered *Pl. perrieri*; the justification for this assignment is presented below in the results section. These three specimens have not been included within *Pl. perrieri* in the plots and have been represented with different symbols to facilitate identification.

The data corresponding to the fossils have been analysed at the individual level for those cases where it is possible to estimate the values for the six variables in the same individual and also at the fossil locality level by averaging the values of all the individuals. In some cases, the data for the individual and the population coincide since only a single complete individual is known. The different levels (or cave members) of the fossil localities have been considered as independent samples in case they have been differentiated. Similarly, the early and late forms of *Pa. brunnea* described by Hendey (1974) in Elandsfontein have been considered as independent observations. In order to have a frame of reference for intraspecific variability, the living species have not been grouped into populations.

Principal component analysis was performed independently for both lower and upper dentition variables using covariance matrices since all variables are measured on the same scale. For the test of multivariate means the non-parametric multivariate analysis of variance (PERMANOVA) of Anderson (2001) was used with Euclidean distances between scores on the retained principal components, using 9999 replicates. PERMANOVA is more robust to heterogeneity in balanced designs than other nonparametric rank-based alternatives such as Clarke's (1993) Analysis of Similarities (ANOSIM) and is more specific for testing the differences in centroids (Anderson and Walsh, 2013). This is especially important due to the nature of the data analysed here given that there are differences in the correlations between variables as well as in the sample sizes of the groups analysed. Bonferoni's sequential p-values have been considered for the acceptance or rejection of the null hypotheses in the case of multivariate tests. All analyses were performed using free software for scientific data analysis PAST v. 3.24 (Hammer et al., 2001).

RESULTS

Attribution of V 7296 to *Pliocrocuta perrieri*

As discussed in the previous section, specimen V 7296 described by Qiu (1987) from the Baihaicum locality has been assigned to *Pl. perrieri* rather than to *C. honanensis* based on the morphology and metrics of m1. This specimen is severely worn and difficult to identify. Paradoxically, this fact has some advantages, given that hunting-durophages are distinguished from scavengers in the type of wear. One aspect derived from the relative shortening of m1 (while maintaining its width) shown by solitary scavengers versus social hunters (i.e., genus *Crocuta*) is that the wear facets of m1 in the former tend to be wider and bilobed, whereas in the latter, they are more elongated and continuous.
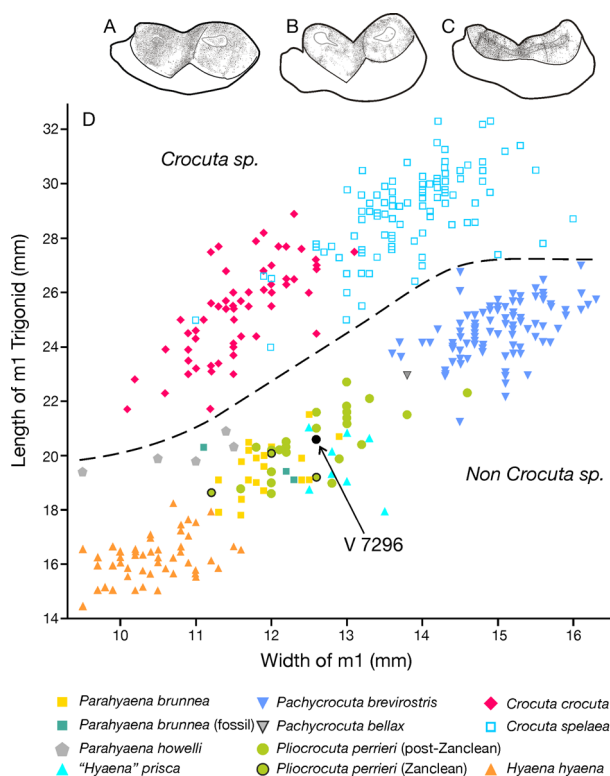
FIGURE 2. Several examples of worn lower first molars. **A**, V 7296 from Baihaicum (from Qiu, 1987). **B**, *Pliocrocuta perrieri* (Se 312, Senèze, France). **C**, *Crocuta crocuta* (no id. Naturkundemuseum Berlin). **D**, plot of m1 trigonid length on m1 width for the species analyzed in this study. Note that there is a clear separation between *Crocuta* and Non *Crocuta* species. Additional explanations have been provided in the text.

Figure 2A shows the m1 of V 7296 in lingual view, whereas Figure 2B-C show a worn m1 of *Pl. perrieri* and *C. crocuta*, respectively. As can be seen, V 7296 is more similar to *Pl. perrieri* than to *Crocuta*. The attribution of V 7296 to *Pl. perrieri* is further corroborated by its position on the plot of the length of the trigonid against its width (Figure 2D). This plot makes it possible to clearly discriminate the genus *Crocuta* from the rest of the species. Such a plot for m1 serves the same purpose as figure 2 of Kurtén (1956), which shows the metastyle length versus the total length for P4 for discrimination of *Crocuta*. The attribution of V 7296 to *Pl. perrieri* makes the fossil assemblage from Baihaicum more typical of the Pliocene, as it is relatively common to find *Pl. perrieri* together with the more slender hyaenid *Chasmaporthetes*, which has also been recovered at such a locality.

Principal Component Analysis. General Aspects

The first three principal components were retained in the four analyses performed because all of them could be biologically interpreted. The loading coefficients and explained variance are listed in Table 2. The three components encompassed more than 97% of the variance in all the four cases. The structures of the first three components were relatively similar in all the analyses. The first component reflected the dentition size and explained the largest percentage of variance. The second component is an axis of variation in shape and expresses the relative shortening/elongation of carnassials (m1 or P4) with respect to the rest of the variables, explaining between 6% and 14% of the variance depending on the case. This second axis separates the scavenging durophagous forms (shortening of the carnassials) from the hunting durophagous forms (lengthening of the carnassials). In the case of the upper dentition, the reduction in the length of the carnassial is correlated with a clear increase in the length of the second premolar. The third component is also a shape axis, in which the lengths score negatively and the widths score positively. Although this principal component explained a relatively low percentage (between 1.4% and 2.3%), it can be clearly interpreted as a robustness/sectoriality axis of the dentition.

The Mantel test for the covariance matrices between the variables obtained for individuals and localities (N = 99999) is significant for both the lower (p = 0.004) and upper dentition (p = 0.001) indicating a similar structure for both matrices. In the case of individuals, another way to support the previous result is through correlations between the scores obtained directly in the PCA and those using the principal component loadings for the localities (where they have not participated in the construction of the components). In practically all cases, the correlation values were higher than 0.9 and significant with p < 10^{-53}, both for the upper and lower dentition. These results indicate that the information reported by the analyses of individuals and localities was very similar.

The correlations between the scores obtained in the principal component analysis and those corresponding to the between group principal components (using species as groups) are higher than 0.94 (p < 10^{-76}) for all principal components for both the analysis of individuals and paleontological sites and for both the lower and upper dentition. The only exception was the third component of the lower dentition, whose correlations were somewhat

TABLE 2. Principal component loadings and variance explained for the four analyses performed.

	PC I	PC II	PC III	PC I	PC II	PC III
	Lower Dentition (individuals)			Lower Dentition (localities)		
Lp3	0.318	0.274	-0.644	0.304	0.271	-0.529
Wp3	0.372	0.106	0.225	0.384	0.120	0.303
Lp4	0.373	0.430	-0.355	0.350	0.418	-0.511
Wp4	0.363	0.369	0.480	0.320	0.408	0.429
Lm1	0.638	-0.746	-0.064	0.682	-0.702	-0.039
Wm1	0.287	0.192	0.418	0.264	0.278	0.426
% Var.	82.2	14.0	1.5	83.3	12.7	1.4
	Upper Dentition (individuals)			Upper Dentition (localities)		
LP2	0.259	0.634	-0.425	0.240	0.641	-0.421
WP2	0.247	0.167	0.216	0.256	0.169	0.235
LP3	0.365	0.349	-0.318	0.348	0.329	-0.369
WP3	0.320	-0.026	0.406	0.343	0.002	0.449
LP4	0.708	-0.605	-0.279	0.715	-0.595	-0.275
WP4	0.367	0.285	0.655	0.357	0.315	0.595
% Var.	89.3	6.1	1.9	87.0	7.9	2.3

lower, but equally significant ($p < 10^{-13}$). This indicates that the number of observations per species does not affect the overall results obtained, especially for the first two components of each analysis.

In the species of the lineages analysed, no significant differences were detected among the means for the third principal component, except between *Pa. brunnea* and *Pl. perrieri* for the upper dentition (individuals and localities), indicating a greater robustness of the former ($p < 0.001$). Since the percentage of variance explained by this component barely exceeds 2%, the following sections are focused on the first two principal components.

Principal Component Analysis. Lower Dentition

Figure 3A-B depicts the projections onto the first two principal components of the analysis for both the sample of individuals and paleontological sites, respectively. Both analyses yield similar results. The first component separates species based on size with *H. hyaena* at one end and *P. brevirostris* and *C. spelaea* at the other, while the second component separates hunting durophages such as *C. crocuta* from scavengers such as *Pa. brunnea* or *P. brevirostris*.

Pachycrocuta bellax is just at the limit of variation of *P. brevirostris* in the plot corresponding to individuals, but falls well outside the range in the fossil locality plot.

The two Longdan specimens are right on the border of *Pl. perrieri*, although in the region closest to *P. brevirostris*. Specimen V 7296 projects within

the region of *Pl. perrieri*, which corroborates its assignment to *Pl. perrieri* made above.

A noteworthy aspect observed in Figure 3 is the significant correlation between size and shape (allometry) within *Pl. perrieri, Pa. brunnea* and *P. brevirostris*, both at the level of individuals and fossil locality (Table 3). The correlation in *Pa. brunnea* as a whole is due to the fossil sample, being absent in the extant sample. These results carry significance for taxonomy as organisms of the same species with different sizes can exhibit different morphology. A related noteworthy fact seen in Figure 3A-B is the relative continuity through the morphospace of the sequence *Pl. perrieri* from the Zanclean, *Pl. perrieri* from the Piacenzian and Gelasian and *P. brevirostris*, which favors the interpretation of a gradual evolution from the former to the latter.

Crocuta crocuta, C. spelaea, H. hyaena and *P. brevirostris* occupy distinctly separated regions in morphospace, resulting in PERMANOVA analyses showing statistically significant differences both among themselves and with the remaining species ($p = 0.0001$, both for individuals and localities).

As shown in Figure 3, in the case of the remaining species there is an enormous degree of overlap in the morphospace, although some increase in the value of the second component is observed from *Pa. howelli* to *'H.' prisca* following the sequence: *Pa. howelli, Pl. perrieri, Pa. brunnea* (fossil), *Pa. brunnea* (living) and *'H.' prisca*.
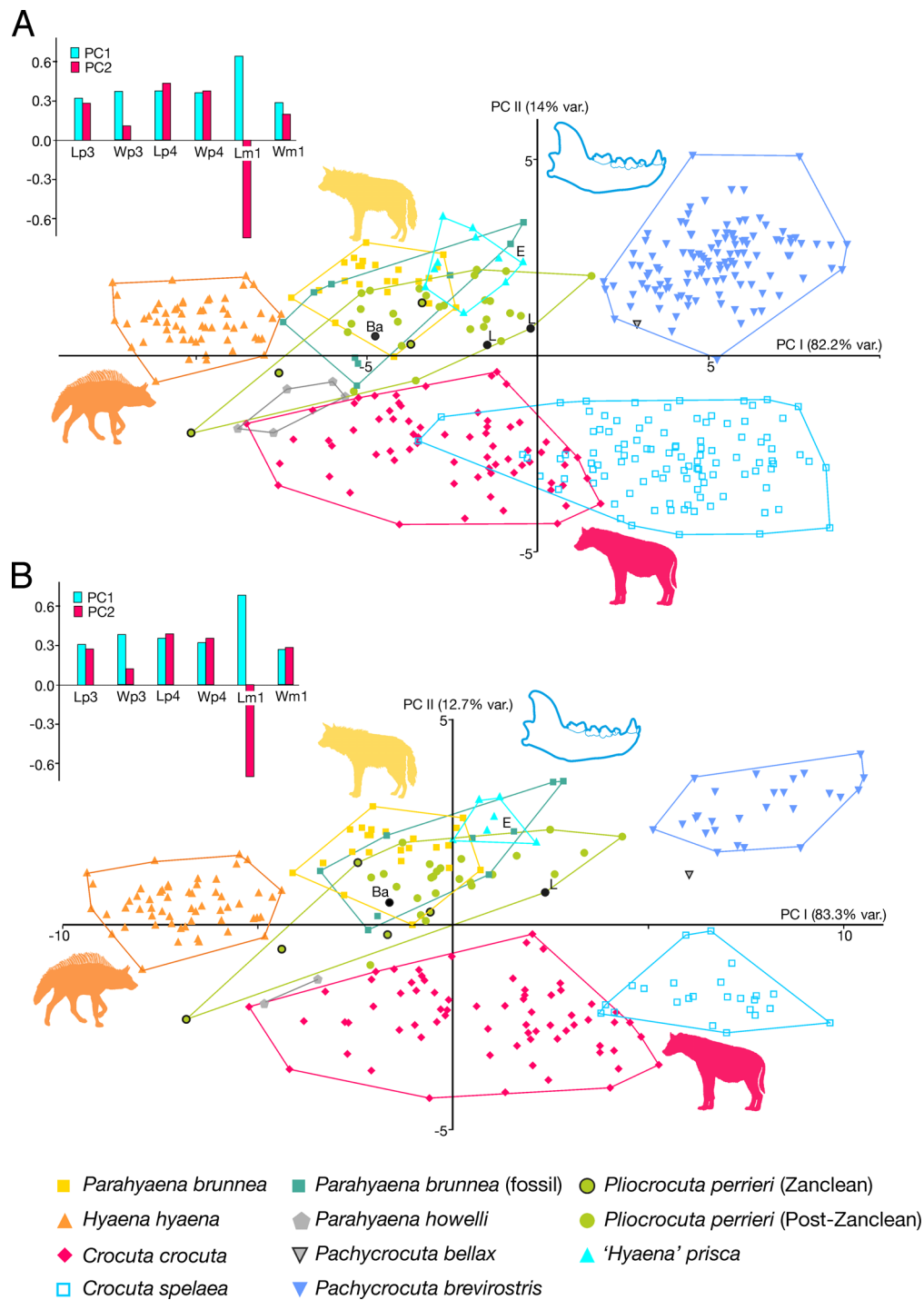
FIGURE 3. Bivariate plots of the scores on the lower dentition two first principal components and their corresponding component loading plots for (**A**) analysis for fossil individuals and (**B**) analysis for paleontological localities. Ba: Baihaicum. E: Elandsfontein. L: Longdan.

Table 4 summarizes the results of testing the null hypotheses of centroid equality. Similar results are obtained for both individuals and localities. *Parahyaena howelli* is excluded in the case of the localities since it has only been recovered in two of them (Kanapoi and Laetoli). It cannot be rejected that *Pa. brunnea* (fossil) is statistically different from any other species. Notably, *Pl. perrieri* from the Zanclean is statistically different from that from the Piacenzian and Gelasian, but its difference

TABLE 3. Correlations between the scores on the first two principal components of the lower dentition for the different species analysed. Significant differences at 95% in bold type.

	Individuals			Localities		
	r (PC I–PC II)	p	N	r (PC I–PC II)	p	N
Pa. brunnea	**0.384**	**0.0299**	**32**	**0.419**	**0.0169**	**32**
Pa. brunnea (fossil)	**0.675**	**0.0457**	**9**	**0.767**	**0.0158**	**9**
Pa. brunnea (living)	-0.012	0.9550	23	0.064	0.7702	23
Pl. perrieri	**0.753**	**0.0003**	**33**	**0.730**	**0.0000**	**31**
Pl. perrieri (Zanclean)	**0.951**	**0.0491**	**4**	**0.828**	**0.0419**	**6**
Pl. perrieri (Piac., Gel.)	0.313	0.0988	29	**0.552**	**0.0042**	**25**
Pa. howelli	0.753	0.1420	5	–	–	2
P. brevirostris	**0.294**	**0.0010**	**119**	**0.544**	**0.0041**	**26**
'H'. prisca	0.003	0.9930	10	-0.100	0.8511	6
H. hyaena	-0.035	0.798	56	0.075	0.5826	56
C. crocuta	**-0.318**	**0.008**	**69**	-0.181	0.1365	69
C. spelaea	-0.121	0.219	105	-0.136	0.5155	25

TABLE 4. Results of the PERMANOVA comparisons between the different sets analyzed using the scores on the first three principal components of the lower dentition. Values above the main diagonal correspond to localities and those below to individuals.

	Pa. brunnea (living)	*Pa brunnea* (fossil)	*Pa. howelli*	*Pl. perrieri* (Zanclean)	*Pl. perrieri* (Piac., Gel.)	"H." prisca
***Pa. brunnea* (living)**	–	No Rejected	–	No Rejected	0.0002	0.0001
***Pa brunnea* (fossil)**	No Rejected	–	–	No Rejected	No Rejected	No Rejected
Pa. howelli	0.0001	No Rejected	–	–	–	–
***Pl. perrieri* (Zanclean)**	No Rejected	No Rejected	No Rejected	–	0.0019	0.0017
***Pl. perrieri* (Piac., Gel.)**	0.0003	No Rejected	0.0001	0.004	–	No Rejected
"H." prisca	0.0001	No Rejected	0.0004	0.001	No Rejected	–

from *Pa. howelli* cannot be rejected. *'Hyaena' prisca* is statistically different from *Pa. brunnea* (living), *Pl. perrieri* from the Zanclean and *Pa. howelli*. Another interesting result as discussed below is the significant difference between *Pa. brunnea* (living) and the Piacenzian and Gelasian *Pl. perrieri*.

Principal Component Analysis. Upper Dentition

The morphospace regions occupied by the species, as illustrated in Figure 4, exhibit a general similarity to those identified in the preceding analysis. The second principal component effectively distinguishes scavenging species from hunting species. However, with the exception of *P. brevirostris*, there is a significant overlap between the species of the lineages analysed.

In contrast to the previous section, the number of fossils is notably smaller in this analysis. The bibliographic search for the data used in the present work reveals that it is 2.6 times more likely to find a specimen with all three dental elements ana-

lysed for the lower jaw than for the upper jaw. In the case of localities, it is 1.6 times more likely to find a paleontological site with at least one tooth of each of the three analysed for the lower jaw than for the upper jaw. Although not the focus of this investigation, this substantial reduction in sample sizes may be attributed to certain taphonomic factors. This strong reduction does not have the same importance for all the species analysed; for example, the sample of *Pa. howelli* or *Pl. perrieri* from Zanclean (inherently scarcer) are notably reduced with respect to the lower dentition. Perhaps such a reduction might contribute, in part, to the absence of significant correlations between the two factors for the species of the lineages studied in contrast to those obtained for the lower dentition shown in Table 3.

Despite reduced dataset, Figure 4 facilitates additional significant inferences concerning the phylogenetic relationships within the clade. A considerable overlap persists between *Pa. brunnea*
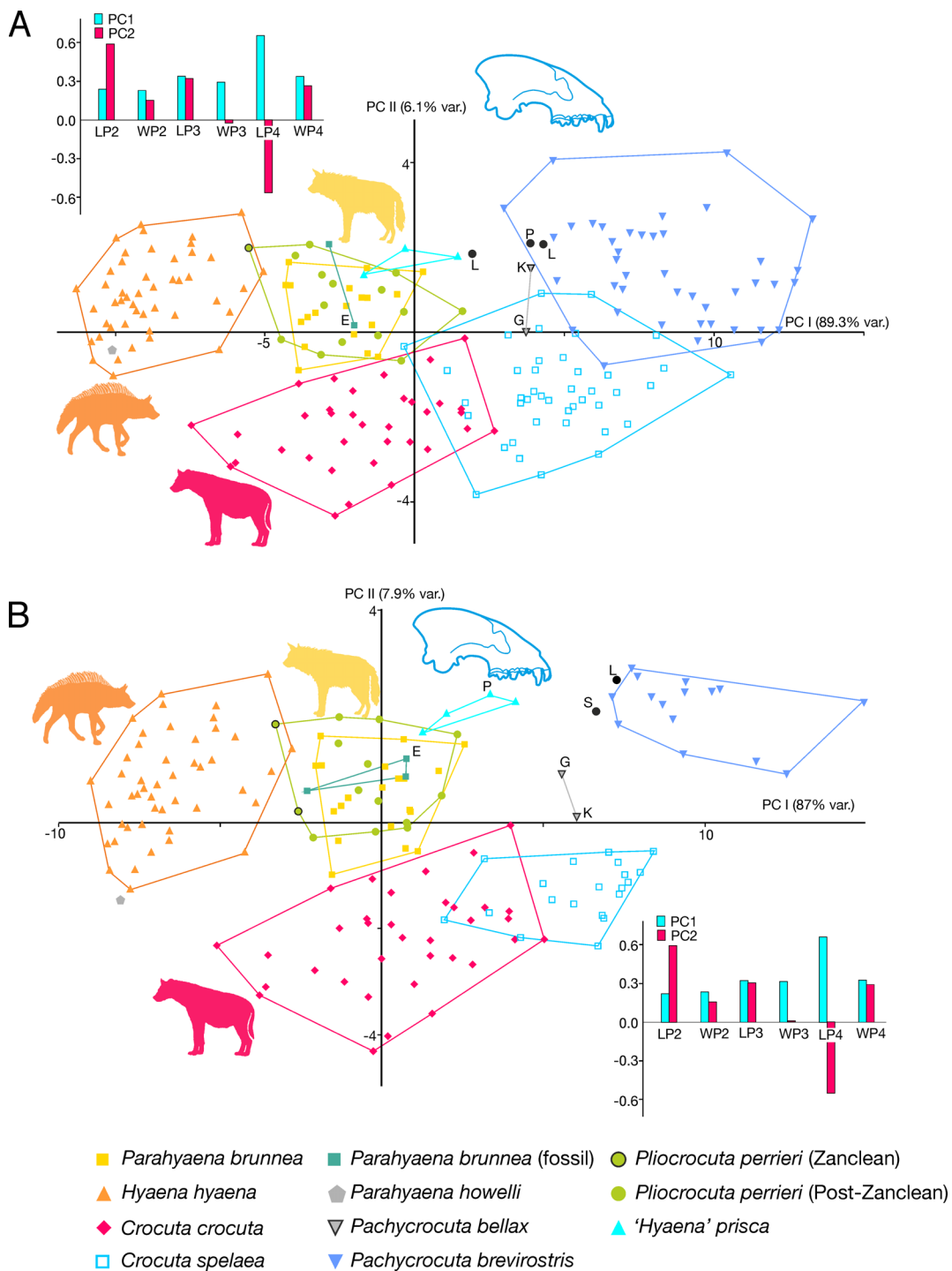
FIGURE 4. Bivariate plots of the scores on the upper dentition two first principal components and their corresponding component loading plots for (**A**) analysis for fossil individuals and (**B**) analysis for paleontological localities. E: Elandsfontein. G: Gladysvale Cave. K: Kromdraai A. L: Longdan. S: Ségriès-le Réservoir.

(both living and fossil) and *Pl. perrieri*. In this case *'H.' prisca* exhibits a slight separation due to its larger size. The two specimens from Londang show different positions in Figure 4A, one falling within the convex hull of *P. brevirostris* but the other closer to *'H.' prisca*.

On the other hand, specimen PEC 18 from Petralona, assigned to *Pl. perrieri* by Baryshnikov and Tsoukala (2010) and nominally assigned here

to *'H.' prisca* falls within *P. brevirostris*. The South African individuals K55 (Komdraai A) and GV 3914 (Gladysvale Cave) project outside the region occupied by *P. brevirostris* in both individual and locality analyses (Figure 4A-B, respectively), supporting the hypothesis that both are conspecific and belong to *P. bellax*.

Another noteworthy observation concerns the Ségriès-le Réservoir sample (Cornillet, France) dating back to MN17a, approximately 2.6–2.5 million years ago (Dubar, 2014). Although originally assigned to *Pl. perrieri* by Dubar et al. (1978), its projection indicates a higher affinity with *P. brevirostris*, implying a potential first occurrence of this species in Western Europe. This point will be further discussed below.

Only one or two specimens are available for *Piacenzian perrieri* from the Zanclean and *Pa. howelli*, depending on the analysis considered, which project within or very close to the convex hull of *H. hyaena* because of their small size. Due to the small size of the upper dentition sample only the hypotheses of equal centroid have been statistically compared for some of the analysed species (*C. crocuta, C. spelaea, H. hyaena, P. brevirostris, Pl. perrieri* from the Piacenzian and Gelasian, *Pa. brunnea* [living] and *'H.' prisca).* In all cases, statistically significant differences between them are obtained for both individuals and localities (p = 0.0001).

Change in Principal Components Over Geological Time. Lower Dentition

The variations through geological time of the scores on the first two principal components of the lower dentition for the lineages analysed is presented in Figure 5. As previously mentioned, there exists a certain degree of correlation between the two components for the species of the lineages under investigation, leading to a certain degree of parallelism between changes in shape and size, although the change in size is more conspicuous than the change in shape.

Figure 5 shows for both individuals and localities an evolution from small dentitions with relatively elongated m1 (*Pa. howelli* and *Pl. perrieri* from Zanclean) to larger forms with relatively shorter carnassials (*Pl. perrieri* from Piacenzian and Gelasian). Subsequently, during the first third of the Piacenzian, *Pl. perrieri* seems to split into three lineages: two that continue to progress in the preceding trend giving rise to *P. brevirostris* in Eurasia and *P. bellax* in Africa and another set that

practically remains in stasis giving rise to *Pa. brunnea*.

For *P. brevirostris*, a significant positive correlation between the first principal component and geological age is observed for both individuals (r = 0.333, p = 2.6 10^{-4}) and localities (r = 0.519, p = 0.011), which is evidence of a significant increase in size until its extinction (Figure 5A-B, respectively). Additionally, this species shows a significant increase of the second component over time (reflecting relative shortening of m1) for individuals (r = 0.249, p = 0.007), although it is not significant for localities (Figure 5C-D, respectively).

A noteworthy observation is the fact that virtually the entire *Pa. howelli* sample is included within the convex hull of *Pl. perrieri* from the Zanclean. On the other hand, despite the limited sample of *Pa. brunnea* fossils, the distinction made by Hendey (1974) between early and late morphotypes (small and large, respectively) seems appropriate.

In almost all the plots shown in Figure 5, *'H.' prisca* is practically encompassed in the convex hull of *Pa. brunnea* fossil. It is further observed that *'H.' prisca* appears to be derived from the late morphotype of *Pa. brunnea* as that recovered from Elandsfontein. A significant inverse correlation between both scores and geological age is observed for individuals of *'H.' prisca* (r = -0.702, p = 0.024), though this correlation is not statistically significant for localities.

Change of Principal Components Over Geologic Time. Upper Dentition

Despite the reduced number of observations for the upper dentition, Figure 6 shows that the relative positions of the species through geological age closely resemble those obtained for the lower dentition.

Similarly, to the previous section, *P. brevirostris* exhibits a direct correlation between PC I (size) and geological age for both individuals (r = 0.540, p = 0.031) and localities (r = 0.509, p = 4.9 10^{-4}). However, unlike the lower dentition, a significant inverse correlation between the second principal component and geological age is obtained for both individuals (r = -0.644, p = 0.007) and localities (r = -0.647, p = 2.8 10^{-6}).

This result can be interpreted as a consequence of the difference in functions within the upper carnassial. As indicated by Ewer (1954b) in her ecomorphological analysis of present-day hyenas, scavenging durophages, such as those of the lineages analysed here, show a greater development of the P4 parastyle, which has a greater role
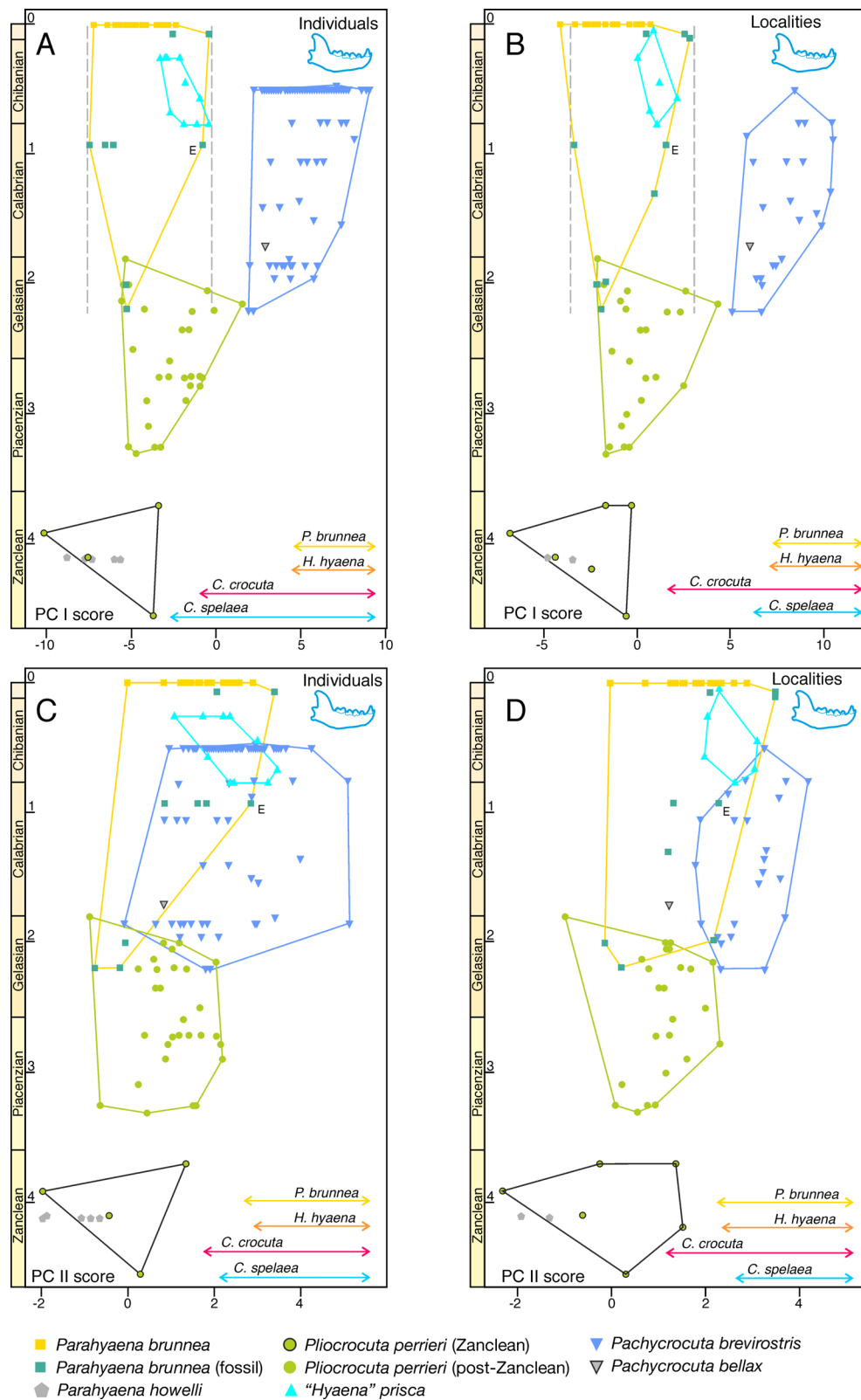
FIGURE 5. Bivariate plots of geological age on the scores for the lower dentition two first principal components. **A-B**, PC I for fossil individuals and paleontological localities, respectively. **C-D**, PC II for fossil individuals and paleontological localities, respectively. E: Elandsfontein. At the base of each figure are shown the ranges for the extant species and *C. spelaea* in each principal component.
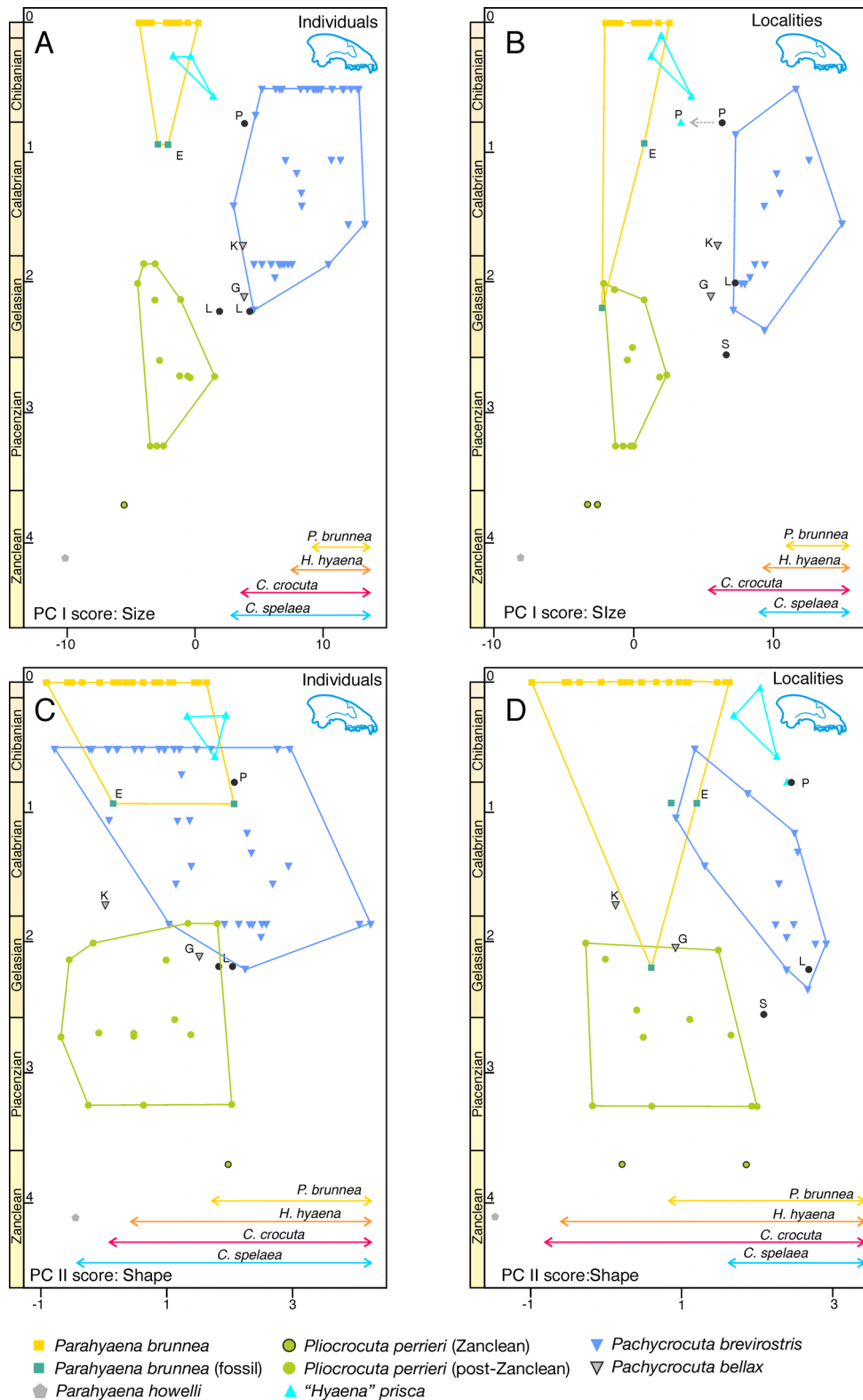
FIGURE 6. Bivariate plots of geological age on the scores for the first two principal components of the upper dentition (**A**) and (**B**) PC I for fossil individuals and paleontological localities, respectively. **C-D**, PC II for fossil individuals and paleontological localities, respectively. E: Elandsfontein. G: Gladysvale Cave. K: Kromdraai A. L: Longdan. P: Petralona (circle: PEC 18, triangle: mean for Petralona). S: Ségriès-le Réservoir. At the base of each figure are shown the ranges for the extant species and *C. spelaea* in each principal component.
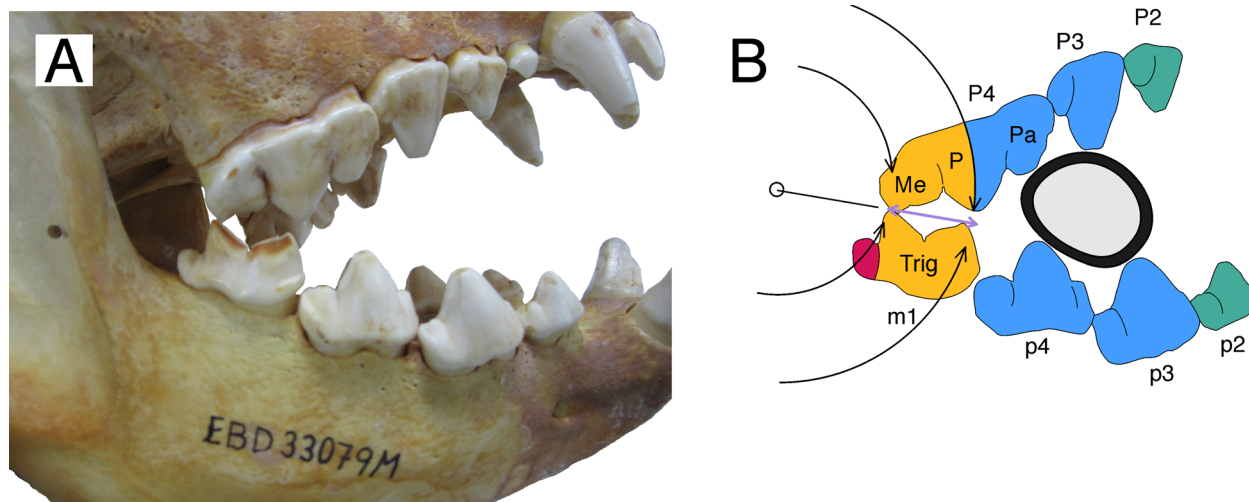
FIGURE 7. In **A** is shown a lateral view of an articulated skull and jaw of a *H. hyaena* specimen (EBD 33079M, Doñana Biological Station, Seville) and its corresponding schematic drawing in **B**, showing different functional regions of the dentition during the mandibular occlusion process. The main regions involved in cutting meat are the trigonid (Trig) of m1 in the lower dentition and the metastyle (Me) and the distal part of Paracone (P) of the upper fourth premolar (P4). The main elements involved in bone breaking are the two lower premolars (p4 and p3) that occlude with the upper third premolar (P3) and the mesial part of the paracone and the parastyle of the upper P4.

as a bone crusher than in *Crocuta*. In fact, this function extends to the mesial region of the P4 paracone (when the jaw is wide open), leaving the cutting function of the P4 confined to the metastyle and the distal region of the paracone (Figure 7). Thus, while almost the entire length of the lower carnassial corresponds to the trigonid (cutting function), the upper carnassial has a dual function (cutting and bone crusher). This is important for the functional interpretation of the second principal component of the lower and upper dentition, given that the lengths of the carnassials (m1 and P4, respectively) are the most important variables in them. To analyse how the bone-breaking part of P4 varies with respect to the total length of P4 in *P. brevirostris* one can appeal to the fact that the lower and upper dentition have to be functionally integrated, i.e., the trigonid (cutting part of m1) should be approximately equivalent to the cutting region of P4 (Figure 7). This implies that if the length of the trigonid is subtracted from the total length of the P4, the result should be approximately the length of the P4 involved in crushing (the mesial part of the paracone and the parastyle). There are not many fossil individuals in which m1 and P4 are preserved simultaneously, but it is possible to perform the above calculation for some fossil sites. Figure 8 presents the percentage of the crushing length of P4 versus the total length of P4 for some populations of *P. brevirostris*, obtaining a positive and significant correlation between them (r
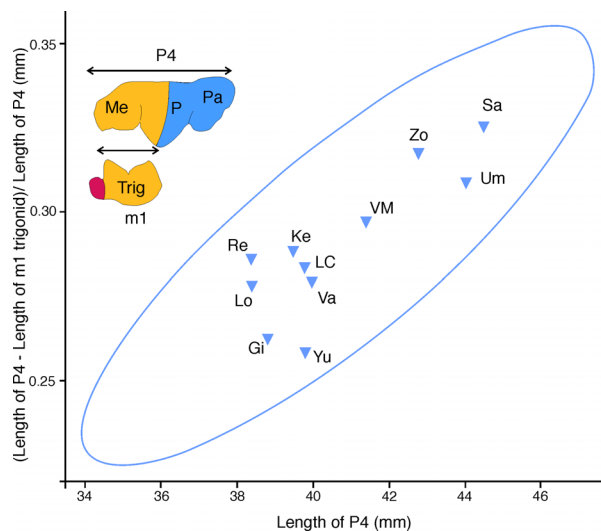

FIGURE 8. Relative size of the bone-breaking region of P4 versus the size of P4 for some localities of *P. brevirostris*. The correlation coefficient between both variables is significant ($r = 0.844$, $p = 0.002$). The ellipse corresponds to the expected region for the population at 95% confidence. Gi: Gigantopithecus Cave, Ke: Kedung Brubus, Lo: Longdan, LC: Longgu Cave, Re: Renzi Cave, Sa: Sainzelles, Um: Untermasfeld, Va: Val d'Arno, VM: Venta Micena, Yu: Yuanmou, Zo: Loc.1 of Zhoukoudian.

= 0.844, p = 0.002). Such correlation evidences an increase in the length of the crushing part of P4 with increasing LP4, that is, a positive intradental allometry. In other words, in *P. brevirostris*, a simple increase in P4 size leads to an increase in bone-breaking specialization. Therefore, the inverse correlation of the second principal component and geological age observed in this species is a consequence of the inverse covariation of these components with LP4.

As in the previous section some observations of some importance can be made in Figure 6. In the case of Londang the two specimens analysed (HMV1200 and HMV1203) show an intermediate position between *Pl. perrieri* and *P. brevirostris*.

The Komdraai A and Gladysvale Cave fossils fall virtually outside of all convex hulls encompassing *P. brevirostris*, supporting the hypothesis of the validity of *P. bellax* as a distinct species from the former.

In the case of Petralona, Figure 5B shows the only individual with complete upper dentition from this locality (PEC 18) and the average for the paleontological site. In terms of size, the position changes from a value close to *P. brevirostris* for PEC 18 to one close to that of *'H.' prisca* for the average of the locality, which points to PEC18 being *P. brevirostris* and the rest of the specimens being *'H.' prisca*. That is, both taxa are present in that cave.

DISCUSSION

The results obtained are consistent with the gradual evolution of the lineage from an initial stock of populations distributed throughout the Old World at the beginning of the Zanclean, whose oldest specimen included in this study is V7289 originally attributed to *Pliohyaena pyrenaica orientalis* by Qiu (1987), (= *Pachycrocuta pyrenaica* in Qiu et al., 2004) from the Chinese locality of Wangjiagou. The site is at the base of the Nanzhuanggou Member of the Gaozhuang Formation, bounded by two unconformities dated at 4.9 and 4.2 Ma, respectively (Flynn and Qiu, 2013). Qiu (1987) also assigns specimen V7288 (an anterior skull fragment with very worn dentition) to this species. The locality where such a specimen was found (Lok. ?14, Hsingyangcun) was reassigned to Loc. 44 (Taoyangts'un) by Tedford et al. (2013: p. 32). Such a locality is included in the Taoyang Member of the aforementioned formation, which is bounded by two unconformities dated at 5.8 and 5.2 Ma, respectively. This implies that the origin of the lineage may even reach the Late Miocene.

Regarding this issue, the results obtained raise two related questions: the first is the conspecificity of *Pa. howelli* and *Pliocrocuta perrieri* from the Zanclean (= *Pachycrocuta pyrenaica* in Howell and Petter, 1980; Qiu, 1987 and Qiu et al., 2004) and the second whether there is reason to separate *Pliocrocuta perrieri* into the two taxa proposed by Howell and Petter (1980): *Pachycrocuta pyrenaica* and *Pachycrocuta perrieri*.

Howell and Petter (1980) addressed both questions. Indeed, the conspecificity of *Pa. howelli* and *P. pyrenaica* was proposed by these authors, indicating the existence of a perfectly preserved right mandible from the Kanapoi locality (south of Lake Turkana, Kenya) that has not yet been described (KNM-K. 069/6702), which corresponds to specimen KNM-KP 10033 in Werdelin (2003). Howell and Petter (1980) highlighted the good accommodation (from a morphological and metrical point of view) of this individual within the *P. pyrenaica* sample from Odesa Catacombs (Ukraine). On the other hand, Tseng et al. (2016) highlighted the remarkable similarity between *Pa. howelli* and the Zanclean *Pliocrocuta perrieri* specimen recovered from Zanda Basin (IVPP V20801). Although there are insufficient data to compare the upper dentition metrically, the results obtained here for the lower dentition are consistent with the conspecificity of these two species, given not only the proximity in morphospace but also that *Pa. howelli* also falls within the temporal range of *Pliocrocuta perrieri* during the Zanclean. In fact, Leaky and Werdelin (2010) indicate that, as is the case in the Miocene, during the Zanclean carnivores migrated preferentially from Eurasia to Africa than in the opposite direction. In other words, if there were no major geographic or ecological barriers to the dispersal of other carnivores to Africa during this stage, there is no reason to think that there were specific dispersal constraints for a taxon such as *Pliocrocuta perrieri* that ranged throughout Eurasia, from Spain to China.

The second question about the co-specificity of *P. pyrenaica* and *P. perrieri* can be rephrased as whether it is reasonable to divide the lineage into two segments: *Pl. perrieri* from the Zanclean and those from the Piacenzian and Gelasian. The results presented here indicate a gradual anagenetic evolution from the former to the latter. Certainly, continuity of a lineage can be an argument for not splitting it, but it should also apply to the transition between *Pl. perrieri* and *P. brevirostris* since the change is also gradual, and yet there is consensus that they are distinct species. For

example, the morphological distance between the specimen of *Pl. perrieri* Se 312 from Senéze (France) and that of the specimen of *P. brevirostris* V13932.1 from Renzi Cave (China) is much smaller than that shown by many individuals of *Pl. perrieri* from each other (Figure 2A).

The division of any lineage into successive species segments (chronospecies) is undoubtedly arbitrary. However, the application of the typological concept of species in paleontology is not without arbitrariness. Besides being alien to the idea of evolution, sometimes the characters chosen to separate two species from a typological point of view are essential for some species and irrelevant for others, which is questionable from a biological point of view. Moreover, from a practical point of view, a specimen may resemble the holotype of one species in some characteristics and the holotype of another species in others. In addition, as features evolve, discontinuities separating paleontological species often fade as new intermediate fossils appear between them. Or put in another way, the hypodigms of two species of a lineage (ancestor and descendant) expand as new fossils appear until the two eventually touch or even overlap. In such cases, the holotypes may be markedly different, giving the false appearance of a clear separation between the species, but actually, the boundary between the two species is as arbitrary as the division of a lineage into segments.

The temporal dimension makes the biospecies concept in paleontology inapplicable and after decades of long and fruitless debates, there is no consensus on how to translate the biological species concept to paleontology (Sepkoski, 2016). However, despite these conceptual difficulties, species in paleontology has a practical value, both in biostratigraphy and paleoecology. Here, two arguments are proposed that may be useful as purely practical criteria for separating segments within the lineage studied. It is important to emphasize that such criteria are not intended to be conceptual tools but purely pragmatic.

The first element that can be used as a guide is whether there are significant differences between the multivariate means of the two sets that are assumed to belong to different chronospecies. Another point that may help is whether the variability of a quantitative characteristic important for defining species within the lineage analysed exceeds that observed for related extant species. Thus, if a segment of a lineage exceeds the range observed for phylogenetically close biospecies, it could be divided into at least two arbitrary subseg-
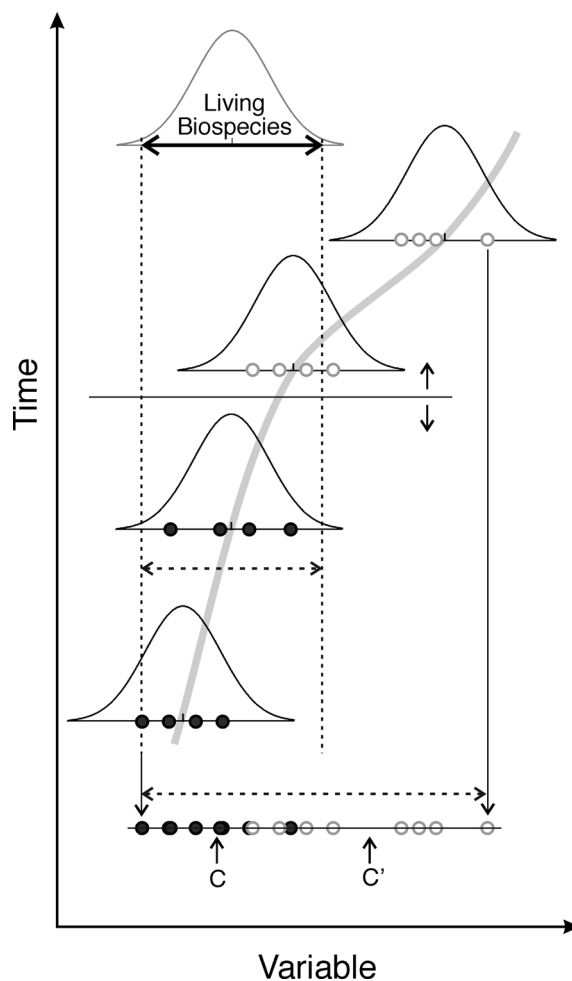

FIGURE 9. Illustration of the two criteria used in this study as a practical guide to separate segments within a lineage. Successive values of a lineage with four populations and four fossils per population are shown. At the top, the range of variation observed for the variable considered in a related present-day biospecies. Taking the lowest value of the first population as an arbitrary reference point, the lineage will be divided into two segments for that time value at which the observed range for the biospecies is surpassed, and at the same time, the difference between the means of the two sets (C and C', respectively) becomes significant.

ments of chronospecies. Obviously, the boundaries between two chronospecies can vary if new remains recovered change such means or ranges. Figure 9 graphically illustrates both criteria.

As presented in the results section, the first criterion is met for the lower dentition of *Pl. perrieri* from the Zanclean with respect to those from the Piacenzian and Gelasian, as well as for the latter with respect to *P. brevirostris*. Figure 5 shows that the size and shape range of *Pl. perrieri* taken as a

whole also surpasses that exhibited by the living species, so it could be divided into two segments.

Similarly, the union of the Piacenzian and Gelasian *Pl. perrieri* together with *P. brevirostris* exceeds the range of variation observed for the extant species and it also meets the first criterion. Consequently, the proposal of Howell and Petter (1980) seems the most consistent with the two proposed guides, which implies dividing the lineage into three successive chronospecies of greater size and degree of specialization in the scavenging niche: *P. pyrenaica, P. perrieri,* and *P. brevirostris*.

This division carries certain paleoecological implications given that although the early forms of the lineage could play an ecological role similar to that of the later species, it is unlikely that they did so in exactly the same way given that they have not fully developed the morphological adaptations to do so. On the other hand, the differentiation of the lineage into three chronospecies also has some biostratigraphic value, since selection pressures maintained in the same direction have resulted in mean values of both shape and size varying in approximately the same direction over geological time.

While *Pachycrocuta perrieri* in Eurasia gradually evolved into *P. brevirostris*, in Africa, *P. perrieri* gave rise to *Pa. brunnea* (and perhaps to *P. bellax*). As can be seen in Figures 5–6, the dentition of the earliest specimens ascribed to *Pa. brunnea* (Member 1 of Swartkrans, Kromdraai B and Malapa) is virtually indistinguishable in both size and shape from that of the smaller specimens of *P. perrieri* from the late Gelasian. It is relevant to note here that *P. perrieri* has been identified in North Africa in both the Piacenzian (L'Aïn Brimba) and the Gelasian (Ahl al Oughlam). These results corroborate Turner's (1990) claim of conspecificity at least for the earliest representatives of *Pa. brunnea* and *P. perrieri*: the main reason for ascribing the first South African specimens to *Pa. brunnea* rather than to *P. perrieri* is that they are in South Africa, as are their present-day descendants. As Geraads (2006) shows almost all ungulate genera from Ahl al Oughlam are also known in East and/or South Africa, implying that the Sahara did not act as an insurmountable geographical barrier to large mammals that prevented free faunal exchange between North Africa and the rest of the continent. In fact, even in today's arid conditions the striped hyena is distributed from North to East Africa, reaching Tanzania (Hofer and Mills, 1998).

An inescapable question at this point is the conspecificity of present-day *Pa. brunnea* and the late forms of *P. perrieri*. Werdelin and Solunias (1991) indicated that there are certain characteristics, especially the basioccipital shape in which the two species differ. On the contrary, Vinuesa et al. (2014) show that two adult and fairly complete crania of *P. perrieri* (IPS36759 and IPS36758) recovered from the Spanish localities of Villaroya and La Puebla de Valverde, respectively, exhibit similar morphologies to *Pa. brunnea*, including the presence of a small central ridge on the basioccipital. Regardless of the shape of the basioccipital, the greater reduction of the m1 at equal size of the rest of the dentition can be assessed as an autapomorphy of living *Pa. brunnea* with respect to *P. perrieri*. As can be seen in Figure 5A-B, the size of the lower dentition of *Pa. brunnea* practically remains in stasis from *P. perrieri*, but in Figure 5C-D it is observed that *Pa. brunnea* shows a relative reduction of the carnassial compared with *P. perrieri*, converging with *P. brevirostris*. In this case, both the criteria for considering *P. perrieri* and *Pa. brunnea* (living) as distinct species are met, as there are significant differences between them (Table 4) and the range of values of the union of *P. perrieri* and *Pa. brunnea* (living) is greater than that of *Pa. brunnea*.

A question that may arise here is whether the fossil and extant forms of *Pa. brunnea* have diverged sufficiently to be considered distinct chronospecies. Although the range of values of living *Pa. brunnea* increases somewhat when including the fossil forms (Figure 5), no significant differences are obtained between them and therefore they must be considered conspecific.

In the case of *'H.' prisca* no significant differences are obtained with the fossils of *Pa. brunnea*, but there are significant differences with its living representatives. Additionally, the union of *'H.' prisca* with *Pa. brunnea* (living) slightly expands the range observed for the latter, and consequently, both criteria are met. Although, as discussed below, the probable ancestor of *'H.' prisca* is *Pa. brunnea*, the latter may be considered to have diverged sufficiently from *'H.' prisca* to be considered a distinct species at present. In fact, the two species are clearly separated in the morphospaces of the lower and upper dentition (Figures 3–4).

Regarding the origin of *'H.' prisca*, in addition to its morphological similarity to *Pa. brunnea*, the results obtained show the high metric similarity with the lower dentition of *Pa. brunnea* specimens from the South African locality of Elandsfontein, especially with the late morphotype (Figures 3–6). This fact supports the hypothesis that *'H.' prisca* origi-

nated from *Pa. brunnea*, which colonized Europe through the Levantine corridor during the Middle Pleistocene. One element that clearly supports this hypothesis is the fact that *Pa. brunnea* is detected in East Africa during the Middle Pleistocene (Werdelin and Barthelme, 1997), consequently this species could have reached the Levantine corridor and finally Europe, where it evolved in allopatry. This colonization of Europe must have occurred after the extinction of *P. brevirostris* since both belong to the scavenging morphotype and a competitive exclusion in sympatry would be probable.

In this regard, it is interesting to comment on the case of Petralona cave. In agreement with Lannucci et al. (2021), the specimen PEC 17 assigned to *P. brevirostris* by Baryshnikov and Tsoukala (2010) is probably another taxon, possibly *Crocuta*. Paradoxically specimen PEC 18 assigned to *Pl. perrieri* (i.e., '*H.' prisca*) by Baryshnikov and Tsoukala (2010) clearly projects within the convex hull of *P. brevirostris*. Figure 6B shows the projection of PEC 18 and the mean for the entire Petralona locality. As can be seen, the mean change from a point close to *P. brevirostris* to another one close to '*H.' prisca*, what suggests that there is a mixture of taxa in the sample. Therefore, both taxa are present at this locality. These specimens lack stratigraphic context, but it is reasonable to assume that '*H.' prisca* and *P. brevirostris* were not coeval due to the principle of competitive exclusion mentioned above.

As shown, evolution from *P. perrieri* to *P. bevirostris* is a gradual process. The upper dentition specimen from the Longdan locality described by Qiu et al. (2004) is an example of this. However, the lower dentition specimens HMV 1201 and HMV 1202 clearly fall within the hypodigm of *P. perrieri*. Qiu et al. (2004) indicate that some fossils were purchased from local fossil collectors and perhaps these specimens come from a lower stratigraphic position. It is possible that in Linxia Basin it occurs as in the Val d'Arno Basin, where *P. perrieri* is detected in the lower strata and *P. brevirostris* in the upper ones.

Similarly, in the case of Western Europe, the sample from the French locality of Ségriès-le Réservoir can be considered as a transitional form between *P. perrieri* and *P. brevirostris* equivalent to those from the Chinese locality of Londang. Even given its greater similarity to *P. brevirostris* than to *P. perrieri*, this locality could be considered the first occurrence of *P. brevirostris* in Western Europe. This site is dated between 2.6–2.5 Ma (Dubar, 2014), just at the boundary between the Piacen-

zian and the Gelasian. It is important to note here that the fossil assemblage found at Ségriès-le Réservoir presents a typical Piacenzian fauna (e.g., *Nyctereutes megamastoides, Gazella borbonica, Croizetoceros ramosus,* etc.). This reinforces the idea that the evolutionary process from *P. perrieri* to *P. brevirostris* was gradual and explainable by an anagenetic transformation of the Eurasian populations of *P. perrieri* and independent of the evolution or dispersal of other species with which it is typically found in other Gelasian fossil assemblages. In fact, the anagenetic evolution of *P. brevirostris* adapting in both size and shape toward greater specialization to the scavenging niche continued in China during the Middle Pleistocene until its final extinction.

The results obtained indicate that South African specimens from Komdraai A and Gladysvale Cave are outside the range of variation of *P. brevirostris*, which reinforces the hypothesis that *P. bellax* is a distinct species that would have evolved locally in Africa. This would imply that the similarities between *P. brevirostris* and *P. bellax* are an evolutionary convergence resulting from independent adaptation as specialized scavengers.

The record of *P. bellax* is extraordinarily scarce and probably restricted to South Africa. Werdelin (1999) proposed the conspecificity of this taxon with *P. brevirostris* and its occurrence at some localities in the Turkana Basin in chronologies between 3.5 and 2.5 Ma. However, such a hypothesis is supported by few poorly preserved remains that had originally been attributed to a large *Crocuta* by Harris et al. (1988). In fact, Werdelin and Lewis (2008) subsequently reassigned some of such material to *C. eturono* (Werdelin and Lewis, 2008), a large *Crocuta* described from the Turkana Basin in such chronologies. Without additional evidence, the presence of a large *Pachycrocuta* species in East Africa must be cautiously discounted until assessing whether the remaining East African material is within the variability of *C. eturono*.

The situation in South Africa is no better, except for Kromdraai A and Gladysvale, the remains attributed to *P. bellax* (or *P. brevirostris*) in Member 3 from Makapansgat Limeworks and Members 4 and 5 from Sterkfontein, lack other diagnostic value except that they are large. Assuming that the remains recovered from Makapansgat belong to *P. bellax*, the origin of that species must predate the age of Member 3 of that cave, which has been estimated to be between 2.9 and 2.6 Ma (Herries et al., 2013). This age is significantly older
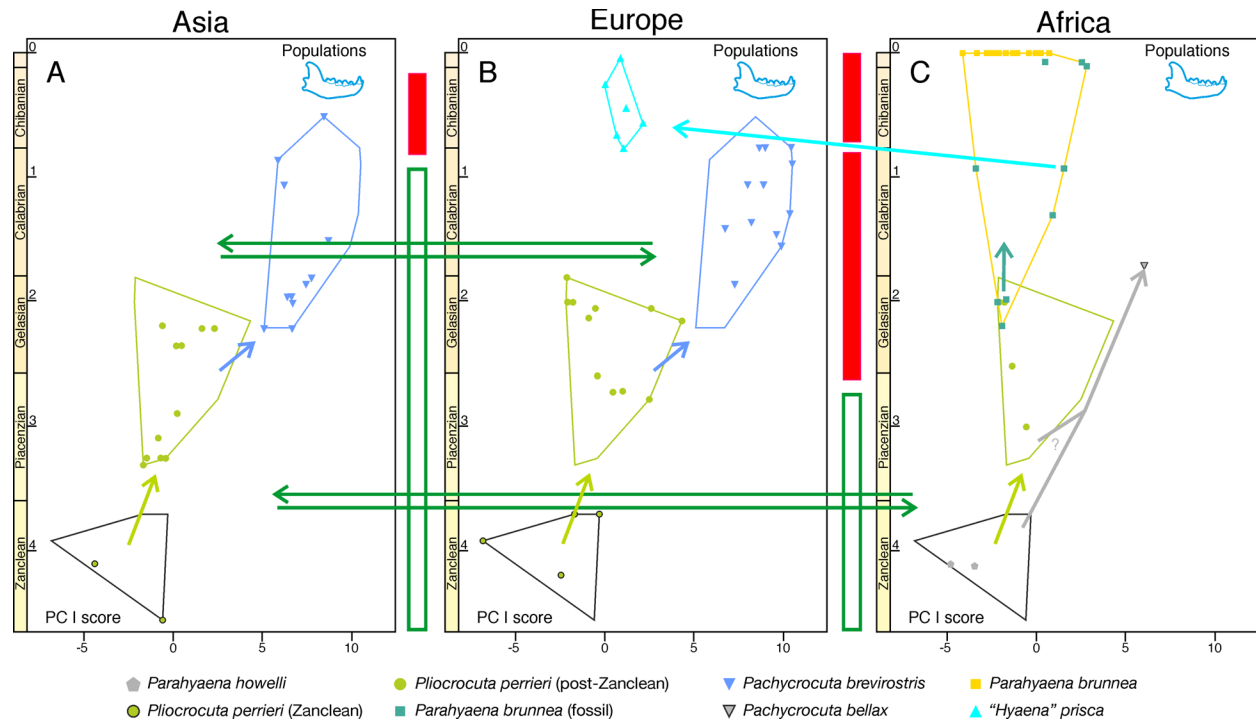
FIGURE 10. Evolutionary and paleobiogeographic hypotheses proposed in this work illustrated with the plot of the first principal component for the lower dentition. Double horizontal lines indicate bidirectional migratory flows. Empty rectangles indicate the absence of barriers to dispersal between the last three regions considered, and solid rectangles indicate geographic isolation. See the text for a more detailed explanation.

than that of the earliest Eurasian *P. brevirostris* and corresponds approximately with that of the earliest *P. perrieri*. Consequently, *P. bellax* must have originated from the local evolution either from a basal stock of African *P. perrieri* such as those found in North Africa or even from a South African stock of *P. pyrenaica / Pa. howelli*. Without additional data it is not possible to specify its ancestor.

This result also raises the question of sympatry between early *Pa. brunnea* and *P. bellax* since competitive exclusion between them would be expected. There are two alternatives for the allopatry between these two taxa. One possibility is that *Pa. brunnea* was relegated to a marginal ecological refuge that was difficult to access for *P. bellax*. Such an ecological refuge could be the Namib Desert, which is separated by more than 1000 km and has different ecological conditions from those observed at Cradle of Humankind, where the Komdraai and Gladysvale Cave localities are located. At least at present *Pa. brunnea* is a species adapted to the extreme conditions of the Namib Desert, one of the oldest in the world, whose biome is maintained by the Benguela Current (Van Zinderen Bakker, 1975). Another possibility is the local extinction and subsequent recolonization of *P. per-*

rieri from North Africa after the extinction of *P. bellax* (similar to the colonization of Europe by *'H.' prisca,* after the extinction of *P. brevirostris*), given that in this period there are no barriers to prevent it (Geraads, 2006).

As a summary, Figure 10 shows the evolutionary hypotheses presented here from a paleogeographic perspective using the lower dentition for localities to illustrate it. *Pachycrocuta pyrenaica* would be a taxon with a wide distribution in the Old World that would evolve anagenetically to *P. perrieri*, which would later give rise to *P. brevirostiris* in Eurasia and perhaps also to *P. bellax* in Africa. These evolutionary changes determine an evolutionary trend towards an increase in size and in the bone-breaking adaptation of the dentition. In Africa *P. perrieri* would also give rise to *Pa. brunnea*. Basal forms of *Pa. brunnea* would colonize Europe in the Middle Pleistocene, evolving into *'H.' prisca*. To meet the requirements of competitive exclusion, it is proposed that there must have been barriers to the dispersal of *P. brevirostris* to Africa during the Early Pleistocene and from Asia to Europe in the Middle Pleistocene, which allowed the isolation of *P. bellax* in Africa and the colonization of Europe by *'H.' prisca*.

A final question that emerges from the results is whether *Parahyaena brunnea* should be assigned to genus *Pachycrocuta*. Although a more detailed study would certainly be necessary, with little taxonomic redefining it would be possible to accommodate the brown hyena within the genus *Pachycrocuta*. In fact, the differences between *Pa. brunnea* and *P. perrieri* are smaller than those observed between the three species of *Pachycrocuta*. Therefore, it seems appropriate to accept the proposal of McKenna and Bell (1997) to place *Pa. brunnea* within the genus *Pachycrocuta*, and consequently, *'H.' prisca* as well.

CONCLUSIONS

According to Howell and Petter (1980), the synonymy of *Parahyaena howelli* and *Pliocrocuta perrieri* from the Zanclean is proposed, both of which would be integrated within *Pachycrocuta pyrenaica*.

Pliocrocuta perrieri from the Piacenzian and Gelasian would be reassigned to *Pachycrocuta perrieri*. The results obtained support the hypothesis that *Pachycrocuta bellax* is a different species from *Pachycrocuta brevirostris*.

Pachycrocuta perrieri would be the ancestor of *Pachycrocuta brevirostris* in Eurasia and of *Parahyaena brunnea* (and perhaps *Pachycrocuta bellax*) in Africa.

The sequence *P. pyrenaica, P. perrieri, P. bellax,* and *P. brevirostris*, implies a greater specialization in the scavenging niche by increasing size and the breaking part of the dentition.

Basal forms *Parahyaena brunnea* would recolonize Europe after the extinction of *P. brevirostris* originating *'H.' prisca. Parahyaena brunnea* has now diverged sufficiently to be considered a distinct species from *'H.' prisca*. A change of genus is proposed for the brown hyena, which would be integrated into *Pachycrocuta*, as well as *'H.' prisca*.

ACKNOWLEDGEMENTS

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APPENDIX 1.

Measurements, ages and references of the specimens analyzed. (Spreadsheet available for download at https://palaeo-electronica.org/content/2024/5173-the-origin-of-the-brown-hyena)