How many hyenas in North America? A quantitative perspective

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Dispersal events from Asia have played an important role in shaping some of the evolutionary faunas of Cenozoic terrestrial mammals of North America (Qiu, 2003; Figueirido et al., 2012, 2019). Hyenas of the genus Chasmaporthetes (Hay, 1921) are among the Asian immigrants that crossed Beringia in the early Pliocene and were the only members of this family to do so. Given the impact of predators on both present and past ecosystems (Van Valkenburgh et al., 2016), all evidence suggests that members of this genus played an important ecological role because they were the only representatives of the guild of high endurance cursorial predators in North America throughout the Pliocene and much of the Pleistocene.

The earliest representatives of Chasmaporthetes are from the late Miocene and are found in China, represented by C. exitelus and in Greece represented by C. bonisi. The precise taxonomic attribution of C. bonisi and the possible synonymy between these two taxa remains to be clarified, however (Werdelin and Solounias, 1991; Turner et al., 2008; Tseng et al., 2013; Vinuesa et al., 2016). The oldest uncontroversial species of the genus is C. australis, which occurs during the Messinian in Africa, where C. nitidula is also recorded during the Pliocene and early Pleistocene. In the early Pliocene, C. gangriensis is found in Asia. In Europe, C. melel has been described from the lower Pleistocene of Sardinia and C. borissiaki from the Pliocene of Russia, although Roock et al. (2004) question the validity of the latter species. The most abundant species of the genus and the most widespread in Eurasia is C. lunensis, which is considered to be the species that dispersed to North America. This form is distributed from Spain to China and its temporal range extends from the Pliocene to the early Pleistocene.

Two species have been described from North America: C. ossifragus (Hay, 1921) and C. johnstoni (Stirton and Christian, 1940). The two were subsequently synonymized by Kurtén and Werdelin (1988) (but see Berta [1981] and Galiano and Frailey [1977] for a contrary opinion). Kurtén and Werdelin (1988) also suggested the existence of a distinct species based on material found in Florida and described but not named by Berta (1981). Kurtén and Werdelin (1988) did not formally describe and name this species due to the scarcity of the material, but distinguished it from C. ossifragus on the basis of the ratio between the lengths of p4 and m1. This ratio is ∼1 in C. ossifragus but is ∼0.8 for the species from Florida. This has led to some debate as to whether there were one or several dispersals from Asia and also regarding attempts to relate the American Chasmaporthetes to specific Asian C. lunensis groups, i.e., the C. lunensis kani group in Sotnikova (1994) or the ‘B’ group in Tseng et al. (2013). New material of the genus has recently been described from the Arctic Circle (Tseng et al., 2019), which, although consisting only of a first molar and a lower third premolar, adds important new elements to this debate.

Here, we provide some evidence (metric in nature) that from a multivariate point of view the following assertions can be supported: (i) there is no reason to separate groups of C. lunenis on the basis of the ratio between lengths of the lower premolars and molar; (ii) it is reasonable to state that there are at least two distinct species of Chasmaporthetes in North America (i.e., C. ossifragus and C. species from Florida); (iii) such North American species are outside the range of variability observed for C. lunensis; and (iv) the remains found in the Arctic can be ascribed to the species from Florida.

To address these questions, a database was compiled using published literature measurements of lengths (L) and widths (W) for the third and fourth premolars and the first lower molars of Chasmaporthetes species, as well as measurements taken from museum specimens for extant durophagous hyenas (Tables S1 and S2, respectively). In those localities where there are no specimens preserving all variables simultaneously (Saint Vallier, Dañero 1, Layna and Old Crow 11 A) the mean values for all specimens were used. For those specimens where both right and left teeth are known, the corresponding measurements have been averaged.

Two principal component analyses were carried out: one using the lengths and widths of p4 and m1 and the other using those of p3 and m1. The use of two PCAs instead of a single PCA for m1, p3 and p4 is in order to maximize the sample size, because some specimens lack either p3 or p4, including the remains recovered from the Yukon. On the other hand, the results obtained by analyzing the six variables simultaneously are analogous to those presented here, which are shown in Figures 1 and 2 and in Table S3.

In both cases the first component, which encompasses 75% or more of the variance in the data, is a marker of size given that it shows positive loadings for all variables (and is especially high for the length of the carnassial). The second components, encompassing around 15% of the variance in the data, basically describe the length of the fourth (or third) premolar relative to the length of the m1.
FIGURE 1. Bivariate plot of the scores on the two first principal components of the p4 and m1 variables. The 95% confidence ellipse for *C. lunensis* is plotted as a dashed line. The convex hulls for the projections of the living species are in the upper right corner. The specimens of *C. australis* and *C. nitidula* have been joined by lines instead of by convex hulls to facilitate greater clarity of the figure. All the data are in Tables S1 and S2.

\[
\begin{align*}
PC_1 &= 0.316 Lp4 + 0.293 Wp4 + 0.828 Lm1 + 0.359 Wm1 \\
PC_2 &= 0.933 Lp4 - 0.162 Wp4 - 0.185 Lm1 - 0.261 Wm1
\end{align*}
\]

FIGURE 2. Bivariate plot of the scores on the two first principal components of the p3 and m1 variables. The 95% confidence ellipse for *C. lunensis* is plotted as a dashed line. The convex hulls for the projections of the living species are in the upper right corner. All the data are in Tables S1 and S2.

\[
\begin{align*}
PC_1 &= 0.432 Lp3 + 0.312 Wp3 + 0.759 Lm1 + 0.374 Wm1 \\
PC_2 &= 0.824 Lp3 + 0.228 Wp3 - 0.507 Lm1 - 0.114 Wm1
\end{align*}
\]
Two observations can be made in both analyses: the American specimens are outside the convex hulls defined by any group of *C. lunensis* and, taking *C. lunensis* as a reference, the position of *C. ossifragus* along the second principal component of each analysis is the polar opposite to that of the *Chasmaporthetes* from Florida.

An important question here is whether it is reasonable to establish groups within *C. lunensis* on the basis of the lower premolars and carnassials. For this purpose the sample of *C. lunensis* was divided into three groups: (i) Asian *C. lunensis* belonging to group ‘B’ of Tseng et al. (2013); (ii) Asian *C. lunensis* not belonging to group ‘B’; and (iii) European *C. lunensis*.

Figure 1 and, to a lesser extent, Figure 2 show a discontinuity between group ‘B’ and the rest. It is important to indicate that the criterion for separating the two groups of Asian *C. lunensis* is exclusively morphological, since there are no geographic or temporal reasons to separate the Asian localities of group ‘B’ (both morphotypes are found in Mazugou). In fact, it is possible to arbitrarily create other groups of *C. lunensis* specimens that would also be separated by an empty region of the morphospace. The question is whether such a discontinuity is the result of arbitrary selection of morphologically extreme individuals or actually reflects biological reality.

In order to clarify this point, a sample of each of the three extant species of durophagous hyenas has been projected onto the morphospaces (upper right corner in Figs. 1 and 2). It is important to note that data from the extant species have not been used in obtaining these principal components, and therefore, their projection (according to the multivariate metric of *Chasmaporthetes*) may give us some clue regarding intraspecific variation in *C. lunensis*. To compare intraspecific dispersion we used the multivariate extension of Levene’s test using the median instead of the mean (Van Valen, 1978).

If all the *C. lunensis* specimens are pooled into a single group then its mean dispersion with respect to the median in the analysis shown in Figure 1 is indistinguishable from that observed for living *Parahyaena brunnea* (Monte Carlo permutation *p* = 0.227) and is significantly lower than that for the *Crocuta crocuta* sample (*p* = 0.043), although it is higher than that of *Hyaena hyaena* (*p* = 0.034). In the case of the analysis shown in Figure 2 the results are clearer because the variability of *C. lunensis* as a whole is indistinguishable from that of *P. brunnea* (*p* = 0.282) or *H. hyaena* (*p* = 0.073), and is still statistically lower than that shown by *C. crocuta* (*p* = 0.045). These results are only indicative but suggest that the variability when pooling all groups of *C. lunensis* is equal to or less than that shown by extant hyenas. This is noteworthy considering that the temporal and geographic ranges of the *C. lunensis* sample are much greater. Consequently, the clusters within *C. lunensis* seem to reflect a choice of extreme morphologies rather than actual intraspecific variability. Furthermore, since the specimens of *C. ossifragus* analyzed as the first species recorded in the New World are already outside the variability observed for *C. lunensis*, the speciation process that resulted in this species must have occurred prior to Blancan IV (Piacenzian), which is the age of the oldest specimens assigned to the species.

Considering *C. lunensis* as a single group, the score on the second component in Fig. 1 (highly correlated with the Lp4/Lm1 ratio) does not best characterize the North American specimens, but rather the score on the second principal component of the analysis shown in Fig. 2, which corresponds to the Lp3/Lm1 ratio. In this analysis, all American specimens fall outside both the convex hull defined by *C. lunensis* specimens and their 95% confidence ellipse. In Fig. 2 it can also be observed that the American specimens project at opposite ends with respect to *C. lunensis*. On the other hand, the differences between the two species of *C. ossifragus* are due to size. It is remarkable that the Yukon specimen projects next to the Inglis IA specimen, indicating its affinity with the species from Florida. This would indicate that this species had an extensive geographic range.

It is not unreasonable that the morphological differences between *C. ossifragus* and the *C. species* from Florida are not random but reflect adaptation in opposite directions. The low population densities inferred for *Chasmaporthetes* (Tseng et al., 2013) may have promoted a phenomenon of rapid allopatric specialization through peripheral isolate populations followed by an episode of character displacement.

It is also interesting to point out here that it is common for closely related species of the ecotype to which *Chasmaporthetes* belongs to differ via a change in the ratio between the length of the carnassials with respect to that of the premolars (Coca-Ortega and Pérez-Claros, 2019). This differentiation occurs with little change in the widths of these teeth and has occurred in different lineages independently (homoplasies). This illustrates that there are no major developmental constraints that preclude natural selection from acting by changing such a ratio. In the case of fully developed bone crackers the ratio between premolars/carnassials is associated with the adaptation toward hunter or scavenger subniches (Pérez-Claros and Coca-Ortega, 2020). Consequently, it is not unreasonable to assume that this ratio also has ecological implications in the case of the American *Chasmaporthetes*. It is important to point out that the differences in ecology between present-day hunting (i.e., *C. crocuta*) and scavenging (i.e., *H. hyaena* and *P. brunnea*) durophages have been commonly ignored. However, the metric differences they show in dentition are remarkable, making it possible to apply them to infer the type of durophagy in extinct forms (Pérez-Claros and Coca-Ortega, 2020).

The species of the genus *Chasmaporthetes* are the culmination of a cladogenetic trend from members of the canid-like hyena lineage such as *Thalassocis* (Kurtén and Werdelin, 1988) toward a larger body size, more sectorial dentition, and a postcranial skeleton indicating greater cursorial than their extant durophagous relatives. These facts point to *Chasmaporthetes* playing an ecological role as an active predator (Berta, 1981; Kurtén and Werdelin, 1988; Tseng et al., 2013). This ecological role is also evidenced by the fact that in several Old World sites it coexists with *Pliocrocuta perrieri*, a scavenging form whose ecological role would be equivalent to present-day *H. hyaena* or, more likely, *P. brunnea* (Pérez-Claros and Coca-Ortega, 2020). Present-day scavenging durophages can coexist with hunting durophages such as *C. crocuta* because they occupy different portions of the durophagous niche.

When the first representatives of *Chasmaporthetes* reached the New World at the beginning of the Pliocene they found a vast territory without any competition because the guild of high-endurance cursorial predators in their size range was empty (*Miracinonyx*, the other cursorial predator, was a high-speed cursor). Just as in Eurasia, where the ecological niche of the bone crackers was occupied by *P. perrieri*, in North America its ecological equivalent was *Borophagus diversidens*, a terminal form extremely specialized for fracturing bone by hypertrophying the teeth adapted to this function (P4–M1 and m1–m2) and extremely reducing the rest, which can be found without wear (Wang et al., 1999).

Such a niche was occupied exclusively by *Chasmaporthetes* for two million years. The guild of large, high-endurance cursorial predators remained stable until the early Pleistocene with the appearance of *Canis armbrusteri*, which was probably the result of local evolution in North America from *Canis edwardii* (Perri et al., 2021), and the subsequent extinction of American forms of *Chasmaporthetes*. 
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