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Skull shape evolution in durophagous carnivorans

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In this paper we investigate convergent evolution towards durophagy in carnivoran skull shape using geometric morphometrics in a sample of living and extinct species. Principal components analysis indicate that, in spite of the different dietary resources consumed by durophages –i.e., bone-crackers and bamboo-feeders– both groups of carnivorans share portions of skull phenotypic spaces. We identify by discriminant analyses a shared set of adaptations towards durophagy in the skull of carnivores. However, ancestral states indicate that although durophages reached similar phenotypes, the evolutionary pathways that they followed are different depending upon the family to which they belong. Furthermore, while the carnivoran cranium more closely reflects the nature of the resources consumed –i.e., soft or hard and tough items– the mandible shows particular feeding adaptations –i.e., bamboo or bone. This finding supports the interpretation that the mandible has more evolutionary plasticity than the cranium, which is more limited to evolve towards a particular feeding adaptation. However, we find that the shapes of the cranium and the mandible are highly integrated for the whole order Carnivora. Published studies of teratological cats and dogs indicate that the role of internal constraints in shaping this pattern of integration is absent or weak and malleable by selection.

Key words**:** Evolutionary convergence, morphometrics, phenotype, durophagy, Carnivora

INTRODUCTION

The problem

Convergent evolution is a central topic in evolutionary biology (Madsen et al. 2001; Nevo 2001; Winter and Oxnard 2001; Wroe and Milne 2007; Futuyma 2010). Despite this, interpretations on its potential causes are not clear-cut (e.g. Stayton 2008; Losos 2011; Olson 2012) and most contemporary surveys recognize two different points of view for explaining of the evolutionary convergence of traits: internalist and externalist explanations (e.g., Wake 1991). From an externalist point of view, convergent evolution is exclusively an evidence of adaptation due to the powerful action of natural selection (e.g., Schlueter 2000; Conway-Morris 2003; Blackledge and Gillespie 2004; Grenier and Greenberg 2005; Langerhans et al. 2006; Stayton 2008). Under this perspective of understanding phenotypic evolution, convergent traits are optimal solutions to repeated environmental problems (Losos 2011). In contrast, the internalist point of view argues that convergence is the result of internal constraints, which hamper the production of phenotypic variability upon which natural selection can operate (e.g., Alberch and Gale 1985; Maynard-Smith et al. 1985; Alberch 1989; Wake 1991; Schwenk 1995; Schwenk and Wagner 2003, 2004; Jaekel and Wake 2007; Figueirido et al. 2011a).

Although both adaptation and constraint give account of order and discreteness in phenotypic spaces (Gould 2002), the two concepts have become divorced due to a dichotomous attitude about them (Schwenk and Wagner 2004). Good examples of these “rival traditions” in evolutionary morphology are the seminal articles on this topic published recently by Losos (2011) and Olson (2012). Both reviews indicate the need for integrative studies of the effects of natural selection and constraints using different kinds of approaches for understanding phenotypic evolution.

In this article, we investigate the evolutionary convergence towards durophagy in the skull of mammalian carnivores and discuss the role of natural selection and different kinds of constraints in shaping this pattern. The order Carnivora is an excellent choice for this study because its evolution represents one of the most spectacular cases of repeated and independent evolution of similar morphologies on a limited range of ecologies (Van Valkenburgh 2007; Wroe and Milne 2007; Wroe et al. 2007; Wroe 2008). In fact, convergent patterns in the evolution of carnivoran skull shape have been reported by a number of researchers, either towards hypercarnivory (e.g., Van Valkenburgh 1991; Holliday and Steppan 2001; Van Valkenburgh 2007; Wroe and Milne 2007; Goswami et al. 2011; Figueirido et al. 2011a), bone-cracking (Van Valkenburgh et al. 2003, 2007; Palmqvist et al. 2011; Tseng and Wang 2011) or even herbivory (Figueirido et al. 2010b). However, it is worth noting that convergent trends towards durophagy are still unexplored. Furthermore, durophagous carnivorans open the possibility of testing if two distantly related groups of carnivorans –e.g., living pandas and hyaenas, which belong to suborders Caniformia and Feliformia, respectively– adapted to feed on extremely different resources –i.e., bamboo and bones, respectively– converge in skull biomechanics as a consequence of the required performance to feed on hard and tough foods. In order to test this hypothesis, we applied landmark-based methods of geometric morphometrics in a large sample of living and extinct representatives of the order Carnivora. We define convergent evolution as the repeated and independent evolution of similar traits towards the same environmental regimes (Futuyma 2010). Therefore, we include under evolutionary convergence both parallel and convergent evolution, because many authors cast doubts on whether there is a clear-cut theoretical distinction between these two evolutionary phenomenona, which are frequently envisaged as extremes of a continuum (e.g., Meyer 1999; Gould 2002; Desutter-Grandcolas et al. 2005; Arendt and Reznick 2008; Hall 2007; Abouheif 2008).

Hard and tough food

We classify as durophagous carnivorans those species that usually feed on bones and bamboo. Bone and bamboo are hard materials because they have high values of yield strength (σ) –i.e., a large force is required to produce a material failure. Furthermore, they are also tough because they have high values of toughness (Jc) –i.e., a high capacity to absorb a large amount of energy before breaking (e.g., Wegst & Ashby 2004). The combination of these parameters relative to the Young's Modulus (i.e., elasticity) unequivocally indicates that both biomaterials are almost identical in hardness and toughness (see Fig. 1A,B). As a consequence, osseous tissue –i.e., calcium phosphate in the hydroxylapatite chemical arrangement– is a hard organic material (Schmidt-Nielsen 1984) and the physical and mechanical properties of bamboo are comparable to those of hard materials such as low-carbon steel and glass-reinforced plastics, which leads to its frequent use in industry for constructing scaffolds and as a reinforcement for cement, rubber, thermoplastic, and even aluminum (Low et al. 2005).

Bone-crackers and bamboo-feeders as durophagous carnivorans

Bone-crackers are considered strict hypercarnivores because they feed primarily on limb bones, with high nutritional content of blood and fat-rich marrow tissues (e.g., Kruk 1972; Palmqvist et al. 1999, 2011; Van Valkenburgh 2007). As indicated by fossil data, the bone-cracking ecomorph evolved independently at least four times during the Cenozoic: in Hyaenidae, Percrocutidae†, and twice within Canidae –in the Aelurodontina and Borophagina subtribes of subfamily Borophaginae†– (e.g., Van

Valkenburgh 1999; Wang 1999; Van Valkenburgh 2007; Tseng and Wang 2011). In contrast, bamboo-feeders are considered as strict herbivores feeding almost entirely on bamboo (e.g., Gittleman 1994; Figueirido et al. 2010). Similarly, data from the fossil record suggest that the bamboo-feeding ecomorph evolved independently in two living species of carnivorans: the giant panda (*Ailuropoda melanoleuca*) within Ursidae and the red or lesser panda (*Ailurus fulgens*) within Ailuridae (e.g., Flynn et al. 2000, 2005). However, despite that both species feed entirely on bamboo they also differ in their feeding behavior. The giant panda usually eat on bamboo leaves and trunks depending upon the season (from March to July they feed almost entirely on trunks in the wild; Schaller et al. 1985). However, they remove the outer, green, smooth and waxy layer of the trunks before chewing or biting because this is their less nutritive part (Hansen et al. 2010). Although the red panda, feed almost entirely on leaves supplemented by arboreal fruits and bamboo shoots (Reid et al. 1991; Wei et al. 1999) sometimes they also feed on peeled trunks. Furthermore, it is worth noting that both pandas are the only carnivorans adapted to feed regularly on leaves –i.e., a fibrous material with high contents in lignin, cellulose and hemicellulose. Other herbivorous carnivorans like the kinakajou (*Potos flavus*) or the Andean bear (*Tremarctos ornatus*) mostly feed regularly on fruits and shoots but not on leaves (Figueirido et al. 2010b; Figueirido et al. 2011b, Figueirido et al. 2012).

Therefore, we considered both bamboo-feeders and bone-crackers as durophages because they feed regularly on hard and tough materials such are bamboo and bones, respectively.

Anatomical and functional traits shared by bone-crackers and bamboo-feeders

Previous researchers have noted qualitatively an external morphological resemblance between the skulls of bamboo-feeders and bone-crackers (e.g., Davis 1964) which have leaded to analyze both groups of carnivorans jointly in functional studies (e.g., Christiansen and Wroe 2007). In fact, a brief review of the literature indicates that both types of durophages share a number of morphological traits in the skull that could be considered potential adaptations to feed on hard and tough foods. These traits include a robust craniodental morphology with a raised and dome-like frontal region of the cranium, enlarged areas for the attachment of masticatory muscles, well-developed frontal sinuses, enlarged premolars, and microstructurally reinforced tooth enamel (Dong 2008; Figueirido et al. 2012; Joeckel 1998; Stefen 1999, 2001; Stefen and Rensberger 2002; Tanner et al. 2008; Tseng 2009). All of these morphological traits have been interpreted as adaptations to exert extremely high bite forces for chewing and biting on hard materials (Fig. 1C) and dissipate the stresses generated (Sacco and Van Valkenburgh 2004; Christiansen and Adolfssen 2005; Christiansen and Wroe 2007; Figueirido and Soibelzon 2010; Figueirido et al. 2010a, 2010b, 2011a, 2011b, 2012; Oldfield et al. 2012). However, several functional differences between bamboo feeders and bone-crackers also exist. For example, bamboo-feeders have a higher position of the condylar process of the mandible (Fig. 2) relative to the tooth row than bone-crackers which allow the former to have a slight translation movement of the lower jaw. However, although this action is an important movement for chewing and processing the fibrous bamboo leaves, the translation movement in the giant panda is very limited (only 5.4mm of translation) as a consequence of having a transverse cylindrical mandibular articulation forcing the jaw action mainly to a simple hinge movement vertically (Davis 1964).

Another morpho-functional difference between both groups of canivorans is that although both have an exceptional ability for exerting large bite forces (Fig. 1C) they could be using this ability in a different way. In fact, while bone-crackers are particularly adapted to exert high peak forces to cracking bones during punctual periods of time and to resist the stresses generated, bamboo-feeders could be adapted to resist fatigue as a result of constant chewing applying sub maximal forces over protracted periods. However, the fact that the giant panda torn off the stripped outer layer of bamboo trunks by means of a twisting movement of the fore foot coupled with a lateral turning of the head by an active bite (Davis 1964) indicates that most probably giant pandas are adapted to resist both: high peak forces during punctual periods of time and fatigue during constant chewing. In fact, although both pandas invest more time chewing on bamboo leaves and stalks than cracking bamboo trunks (at least the red panda), hyenas also feed on flesh on a regular basis and fracture limb bones less frequently for accessing their medullary contents (e.g., Kruk 1972; Ewer 1973; Palmqvist et al. 1999, 2011). From a biomechanical point of view, in both cases what matters is the force that is exerted during those activities that demand a greater resistance of the skull against the stresses generated by elevated loads (i.e., as those produced during bamboo/bone-cracking). In other words, although these loads are only exerted occasionally, there is safety factor which implies that the skulls of pandas and hyenas must be adapted for withstanding the maximal loads exerted during chewing and biting.

In sum, bone-crackers and bamboo-feeders feed regularly on extremely hard and tough materials (Fig. 1A,B). Accordingly, both groups of carnivorans seem to share a set of skull traits related with the ability for exerting exceptionally large bite forces (Fig. 1C) and to dissipate the stresses generated. As a consequence, these shared traits between both groups of carnivorans could be interpreted as potential adaptations towards durophagy. However, in spite of this morphological resemblance and presumed functional similarity between bone-crackers and bamboo feeders there is a lack of ecomorphological studies of skull shape evolution towards durophagy in a comprehensive way. This is particularly the main objective of this article.

MATERIAL AND METHODS

Data collection and geometric morphometrics

We collected 299 mandibles and 322 crania of adult individuals belonging to 57 species –45 living and 12 extinct (†)– of all living terrestrial families of the order Carnivora plus the extinct family Percrocutidae (see Table 1). We collected data from only adult individuals –as indicated by closed basilar synchondroses and complete tooth eruption. Mandible and cranial shapes were recovered with a set of landmarks representing functional key features in the carnivoran skull (Fig. 2). Landmarks were digitized into two-dimensional Cartesian coordinates (x,y) on high-resolution digital images using TPSdig V. 211 (Rohlf 2008). Digital images were collected using a tripod and following a standardized protocol for avoiding lens distortion and parallax. Later, interlandmark distances were modeled by means of an outline, in order to obtain clearer shape transformation models in subsequent multivariate analysis. All the specimens were aligned using Procrustes superimposition procedure and projected onto the tangent space (Dryden and Mardia 1998).

Testing the influence of phylogeny and allometry in skull shape

In order to test the presence of phylogenetic signal in our data and to assess for phylogenetic patterning in multivariate analyses, a phylogenetic consensus tree was assembled with Mesquite (Maddison and Maddison 1997) using published sources (see Fig. 3).

We used a permutation approach developed by Laurin (2004), extended for multivariate analysis by Klingenberg and Gidaszewski (2010) and applied to shape data by Gidaszeswski et al. (2009), Figueirido et al. (2010) and Klingenberg et al. (2012) to simulate the null hypothesis of complete absence of phylogenetic signal in mandible and cranial shapes. The 56 observed mean species shapes were randomly distributed as the tips of the phylogeny in 10,000 permutations. For each permutation, tree length (i.e., the sum of the squared Procrustes distances between ancestral and descendant shapes for all branches) was computed. If the resulting tree length computed for each permutation was greater than the one obtained with the original data, the null hypothesis of absence of phylogenetic structure in our data was rejected. A *P*-value was used for assessing the presence of phylogenetic signal in shape (Klingenberg and Gidaszewski 2010).

A multivariate regression analysis (Monteiro 1999) of shape (i.e., using Procrustes coordinates-Pco) on size (i.e., using Centroid size-Cs) was performed for testing the influence of allometry. Independent contrast analysis (Felsenstein 1985) was applied to take into account the phylogenetic relationships of the species under study (e.g., Harvey and Pagel 1991; MacLeod 2001). Therefore, the contrast for shape (Pco) was regressed on the contrast for size (Cs). The statistical significance was tested with a permutation test against the null hypothesis of complete independence of shape on size (Drake and Klingenberg 2008).

The phenotypic spaces and their histories of phylogenetic occupation

The distribution of durophages in the phenotypic space was explored by Principal Components Analysis (PCA) using the covariance matrix. As PCA finds orthogonal axis of maximal variance, it is therefore a suitable method for exploring the phenotypic variation of mandible and cranium shapes.

To investigate the phylogenetic history of the phenotypic space occupation, we first reconstructed the ancestral states of cranium and mandible shapes using the squared-change parsimony method (Maddison 1991) weighted by branch lengths (see Fig. 3). Subsequently, these shapes were plotted on the original phenotypic spaces and the branches of tree were connected (Klingenberg and Ekau 1996; Rholf 2002; Polly et al. 2008; Gidazweski et al. 2009; Klingenberg and Gidaszewski 2010; Figueirido et al. 2010; Klingenberg 2012) to obtain mandible and cranium "phylomorphospaces". This approach provided us a unique opportunity to explore the history of phylogenetic occupation of phenotypic spaces. Furthermore, we explored the evolutionary trajectories of shape transformation towards durophagy by investigating the shape changes from ancestral state reconstructions to the tips of the phylogeny in durophagous taxa.

Exploring shared morphological traits in the skull of durophagous carnivores

Given that PC axes reflect the greatest variance in the whole dataset and the specimens are ordered on these axes according to the major patterns of shape variation, PCA is not an appropriate method for discriminating a priori defined groups of specimens. In order to separate durophages from other carnivores included in the sample, we computed a linear discriminant analysis (DA) from cranium and mandible shapes. Similarly, the morphological differences between bone-crackers and bamboo-feeders were also explored using DA. The reliability of the discrimination was assessed by the "leave-one-out" cross-validation method (e.g., Timm 2002) given the high dimensionality of our data. Subsequently, the statistical significance of pairwise differences in mean shapes was assessed with a permutation test (10,000 in our case) using the Mahalanobis distances (MD) between groups.

Investigating patterns of covariation between mandible and cranium shapes in durophagous carnivorans

Patterns of covariation between cranium and mandible shapes were explored using two-block partial least squares (2B-PLS) analysis (Rohlf and Corti 2000; Zelditch et al. 2004; MacLeod 2006). Separate Procrustes fits for each block –i.e., mandible and cranium shapes– were performed for analyzing the shape of the two configurations of landmarks (Klingenberg 2009). Also, the *RV* coefficient of Escoufier (1973) was computed as a scalar measure of the strength of the association between mandible and cranium shapes. Statistical significance was tested with a permutation test against the null hypothesis of complete absence of covariation between blocks (Klingenberg 2009). In addition, the *RV* coefficient of a second PLS analysis from the contrasts for both blocks of variables was computed for exploring if covariation between mandible and cranium shapes was due to phylogenetic patterning. Statistical significance of the *RV* coefficient was tested by a permutation test (10,000 in our case) against the null hypothesis of independence between both block of variables.

All the morphometric procedures, including multivariate analyses, were performed with MorphoJ software package (Klingenberg 2011).

RESULTS

The influence of phylogeny and allometry on skull shape

The permutation test indicated a strong phylogenetic signal in both cranium size and shape (LogCs: *Tree length* = 2.39619, $P < 0.0001$; Pco: *Tree length* = 0.2144, $P<0.0001$) and mandible size and shape (LogCs: *Tree length* = 2.76301, $P<0.0001$; Pco: *Tree length* = 0.25306, $P<0.0001$).

The multivariate regression of Pco on LogCs was statistically significant for both crania and mandibles ($n= 322$; cranium: $P < 0.0001$; $n= 299$; mandible: $P = 0.001$), with a percentage of shape explained for by size differences of 8.609% for the crania and 1.557 % for the mandible. The contrast for shape (Pco) against the contrast for size (LogCs) yielded a clear significant association for both the cranium ($n= 56$; $P = 0.001$) and the mandible ($n= 55$; $P = 0.010$), with percentages of shape explained for by size differences of 14.666% and 5.562%, respectively. Therefore, since allometry is a significant source of shape variation in our sample, the regression residuals of shape on size were computed to eliminate the predicted component of shape variation due to size differences (Klingenberg 2009). These regression residuals were used as strict shape variables free of allometric effects in all subsequent multivariate analyses. It is worth noting that it would be ideal to compute a pooled-within species regression analysis rather than an conventional multivariate regression (at least in those cases were all the species share the same regression slopes). However, the fact that some species in our sample are only represented by one or two individuals, particularly in the case of fossil taxa, precludes us from performing the pooled within-species regression analysis. Furthermore, the slopes within species were different which also precludes us from obtaining residuals from this regression analysis.

The phenotypic spaces

The phenotypic spaces derived from the PCA of the covariance matrix for the residuals of the 322 crania are shown in Figures 4A, B. Given that the first three Principal Components (PCs) represent a reasonable amount of the total shape variation (>72% of variance explained), we only present here these three axes. The first PC (Fig. 4A) differentiates clearly the dolichochepahlic crania of the family Canidae –with negative scores– from the crania of the other species included in the sample –scoring positively (Fig. 4C). In contrast, the second PC (Fig. 4A) describes a shape gradient that goes from the crania of the family Felidae –with positive scores– to the crania of the other specimens included in the sample –scoring negatively– according with those morphologies showed in Figure 4D. The third PC (Fig. 4B) accounts for shape changes from the cranium of durophages –taking positive scores– to crania of other species –with negative scores (Fig. 4E).

The PCA computed from the covariance matrix for the residuals of the 299 mandibles included in the sample yielded 20 PCs. Again, the first three axes explained >70% of the original variance, and therefore, we only show here the results derived from them. The first PC (Fig. 4F) accounts for the shape changes that take place from the mandibles of the kinkajou (*P. flavus*) –with positive scores– to those of other species –with extreme negative scores some representatives of the family Canidae (Fig. 4H). Conversely, the second PC (Fig. 4F) relates mainly with a morphological gradient that goes from the mandibles of caniform carnivorans –with extreme negative scores for the mandibles of Ailurudae and Ursidae– to the ones of feliforms, showing extreme positive scores, with those shapes depicted in Figure 4I. Finally, the third PC accounts for shape changes from the mandible of durophagous carnivorans, taking negative scores in this third axis (Fig. 4G), to those of other carnivores –scoring positively– with the morphological traits shown in Figure 4J.

The phylomorphospaces and the inferred evolutionary pathways towards durophagy

The phylogenetic history of the phenotypic space occupation depicted from the first and second PCs of both crania and mandibles (Figs. 4A, F) resulted in the phylomorphospaces shown in Figures 5A, C. In general, many terminal branches of the tree are relatively short whereas the internal branches appear to be long. This indicates that closely related species possess similar cranial shapes (Gidaszewski et al. 2009). Furthermore, branches tended to be quite uncrossed in these phylomorphospaces, which indicates a low degree of convergence in the shapes recovered by the first two eigenvectors. Therefore, since the shapes of the species belonging to the same family were often found in the same areas of these morphospaces, a high degree of phylogenetic structure is implied. However, the phylogenetic history of the phenotypic space occupation depicted from the second and third PCs (Fig. 4B, G) of both anatomical structures (Fig. 5B, D) indicates the presence of evolutionary convergence. In fact, a visual inspection of these graphs allows appreciating that the internal branches of the tree are relatively short compared to the terminal ones. This suggests that some closely related species showed clearly different cranial and mandibular shapes (Gidaszewski et al. 2009). Moreover, in both plots there are many sharp changes of direction in the evolutionary trajectories, with many crossed branches leading to a “messy” appearance (Fig. 5B, D).

It is worth noting that the reconstructed evolutionary trajectories of skull shape transformation are different depending on the family that which durophages belong (Fig. 5E). However, as revealed by the phenotypic spaces (Fig. 4B,G) and their respective phylomorphospaces (Fig. 5B, D), durophages have attained similar morphological traits, which suggests their convergent adaptation to feeding on hard/tough tissues (i.e., bone and bamboo). In contrast, other morphological traits have evolved independently as specific features of bone-crackers and bamboo-feeders (Fig. 5E).

The morphological traits of the skull shared by durophages

In order to quantify those traits shared by durophages that were identified in the phenotypic spaces, a DA was computed to identify those morphological traits that best distinguish between durophages and other carnivores. The discrimination of both groups, using cranium shape, was highly significant (MD = 4.7468; $P < 0.0001$; >95% of correct classifications [CC]; Fig. 6A). Durophages are characterized by having a deep cranium with a large sagittal crest, downward positioned orbits, a short and deep snout, and reinforced postgelonoid processes (Fig. 6C; see also Fig. 2D). The discrimination between both groups using mandible shape was also significant (MD = 3.1686; $P < 0.0001$; ~ 90% CC; Fig. 6E) indicating that, compared to other carnivores, the mandible of durophages has a large coronoid, a more dorsally positioned condyle, and a more concave and deeper corpus (Fig. 6G).

In order to identify those morphological traits that best distinguish between bamboo-feeding and bone-cracking carnivorans, a second DA was computed between both groups. The discrimination between bone-crackers and bamboo-feeders using cranium shape was significant [MD = 13.9643; $P< 0.0001$; >95% CC; Fig. 6B], which allows recognition of a set of cranial traits indicative of these specific feeding behaviors (Fig. 6D). Specifically, bamboo-feeders have a more developed occiput anteriorly, larger post-carnassial molars, more horizontal zygomatic arches, more anteriorly placed orbits and a larger postglenoid process relative to bone-cracker carnivores (see Fig. 2). In contrast, bone-crackers are characterized by having well developed carnassials and pre-carnassial molars, as well as more frontalized orbits and a posteriorly developed occiput (Fig. 6D). Similarly, the discrimination between both feeding groups using mandible shape was highly significant (MD = 9.8617; $P < 0.0001$; 100% CC; Fig. 6F). The results obtained show that the mandibles of bamboo-feeders are larger and with a more anteriorly oriented coronoid, a more dorsally positioned condyle, are deeper below the postcarnassial molars and shows a more developed grinding dentition relative to bone-crackers. In contrast, bone cracking carnivores are characterized by having a well developed anterior dentition (i.e., premolars) (Fig. 6H).

Patterns of covariation between cranium and mandible shape in durophages

The 2B-PLS analysis performed for testing the covariance between crania and mandibles is shown in Figure 7. The morphological covariation between cranium and mandible shape was statistically significant ($RV = 0.663$; $P < 0.0001$). Similarly, the 2B-PLS computed from the contrast of mandible and cranium shapes provided statistically significant results ($RV = 0.599$; $P < 0.0001$).

From a total of nine significant pairs of PLS axes, we only show here the results of the first three, because they jointly account for >98% of the total shape covariance. The first pair of axes (85.9 % of the total covariance) mainly explained changes from dolichocephalic crania and mandibles to brachycephalic ones (Figs. 7A, B). The second pair of axes (9.1% of explained covariance) was also significant ($P < 0.0001$) and they mainly explain changes related to the shape of the neurocranium and zygomatic arches (among the cranium) plus the orientation of the coronoid process and the corpus (among the mandible) (Figs. 7C, D). Finally, the third pair of PLS axes, although it explains a low proportion of the total covariance (only 3.5%), is still significant ($P < 0.0001$) and mainly separates the skull of durophagous carnivorans from those of other species included in the sample (Fig. 7E, F).

DISCUSSION

Durophagous carnivorans are confined in the phenotypic space

Our results demonstrate that despite the different resources consumed by durophagous carnivores, bone-crackers and bamboo-feeders share the same regions of phenotypic skull space (Figs. 4B, G). This demonstrates that both groups of carnivorans share a set of anatomical traits in their skulls (Figs. 4E, J), which leads us to hypothesize that they could represent morphological adaptations towards "durophagy". However, we obtained a significant phylogenetic signal in both mandible and cranium shapes, which casts doubt on considering these traits as solely the outcome of natural selection. The study of phylomorphospaces and the inferred evolutionary trajectories provide interesting clues on the role of natural selection in shaping these traits.

The evolutionary routes to reach adaptations towards durophagy

Both the reconstructed phylomorphospaces and the inferred hypothetical evolutionary pathways of skull shape transformation towards durophagy indicate that natural selection is not sufficient for explaining the shared anatomical traits among bone-crackers and bamboo-feeders. In fact, although durophages reached similar –but not identical– skull morphologies (Fig. 5E) and show similar deviations from their sister groups, their evolutionary pathways differed depending on the phylogenetic legacy of each particular family. In sum, the results of PCA indicate that the traits shared between both carnivoran groups are strongly influenced by both phylogenetic inheritance (including here different types of constraints; Schwenk 2003) and natural selection. However, further investigation based in Bayesian approaches (e.g., Slater et al. 2012) could clarify more finely to which model of evolution fits the evolutionary patterns described here.

Morphological adaptations of durophagous carnivorans

Given that the groups of “durophagous” carnivores and “other taxa” are both represented by different families belonging to two different suborders, the results obtained in DA allow us to identify a shared suite of morphological features among durophages that are relatively independent of the phylogenetic legacy of each particular family. Such features could be *a priori* considered as potential adaptations towards durophagy. However, convergence *per se* is not indicative of adaptation (Stayton 2008; Losos 2011). In fact, evolutionary convergence of traits can occur without the implicit action of natural selection favoring them within a particular selective environment (see Losos [2011] and references therein). Therefore, since phenotypes may evolve convergently in similar environments, even if not directly favored by natural selection, independent arguments are necessary for testing the adaptative nature of the traits shared by durophages.

Functional studies of trait evolution could give clues to test our adaptation hypothesis, as selection operates on the functional consequences of traits (Arnold 1983). There is compelling evidence from skull biomechanics in mammals (Fig. 2B) that all these traits enhance the ability to produce the large bite forces required for feeding on haed/tough foods and for resisting the high compressive loads generated during chewing and biting (e.g., Ewer 1973). For example, a well developed sagittal crest (Fig. 2D) indicates a large area of attachment for the temporalis muscle (e.g., Ewer 1973) and temporalis volume correlates well with bite force (e.g., Christiansen and Adolfsen 2005; Christiansen and Wroe 2007; Wroe et al. 2005). Similarly, large distances between the condyle and both the coronoid –i.e., insertion area of the temporalis– and angular –i.e., insertion area of the masseter– processes of the mandible (Fig. 2D) enhance the input levers of the temporalis and masseter muscles, respectively (Fig. 2B), which increases mechanical advantage and bite force (Biknevicius and Van Valeknburgh 1996). Similarly, a shortened facial skeleton (Fig. 2D) diminishes the output moment arms at different points of the dentition (Fig. 2B) and also increases bite force (Turnbull 1976; Biknevicious and Van Valkenburgh 1996; Christiansen and Wroe 2007). Enlarged postglenoid processes result in a deep glenoid fossa (Fig. 2D), which precludes dislocating the lower jaw when large bite forces are exerted at closing angles (Fig. 2A) (Ewer 1973, Werdelin, 1989). A deep frontal region of the skull is the consequence of having large paranasal sinuses, which are involved in dissipating the high compressive loads generated during chewing (dotted lines in Fig. 2B) (Werdelin 1989; Joeckel 1998; Tanner et al. 2008). Similarly, a deep mandibular corpus correlates to a large proportion of cortical bone, which is responsible for dissipating compressive forces (Biknevicious and Ruff 1992). Therefore, since these anatomical features of the skull enhance the biomechanical performance required to feed on hard/tough foods, it seems reasonable that these phenotypes represent convergent adaptations towards durophagy.

The cranium of durophages reflects the "nature" of the resources consumed and their mandible the "type" of food

Although the DA performed for separating durophagous carnivores from other taxa provided significant results using both the cranium and the mandible, the discrimination using cranial shape was better than the one with mandible shape (compare the overlapping areas –in grey– of the histograms depicted in Figs. 6A, E). The crania of bone-crackers and bamboo-feeders are more similar in shape than their mandible. In fact, this was already noted from the PCA (compare the areas occupied by durophages in Figs. 4B, G). This result was unexpected, as previous investigations indicated that lower jaw shape has more evolutionary plasticity towards particular feeding adaptations than cranial shape (Barone 1986). The reason is that while mandible morphology mainly reflects feeding behavior, cranium shape is more constrained by conflicting functional demands (e.g., feeding, olfaction, vision and brain processing; Figueirido and Soiblezon 2010; Figueirido et al. 2010a,b, 2011a,b). Furthermore, the cranium of carnivores is made up of a set of bones (i.e., ~33) but the mandible is only composed of the dentary bone. As a consequence, the lower jaw should be a structure easier to modify towards durophagy than the cranium (Figueirido et al. 2012). However, the results obtained here point to the opposite direction.

The second round of DA performed to discriminate between bamboo-feeders and bone-eaters gave clues about this counterintuitive result. Here, we obtained a better discrimination between both groups of durophages using mandible shape than using cranium shape (compare the histograms depicted in Figs. 6B, F). This result confirmed previous statements on the higher evolutionary plasticity of the carnivoran mandible compared to the cranium, as the latter seems to be more limited to evolve towards the particular feeding behavior of a durophage. As a result, while there are two different mandible solutions to be a durophage, depending upon the resources consumed –i.e., bamboo or bone– there is only one possible solution for the cranium. As a consequence, cranial shape reflects the nature of the resources consumed –i.e., hard or soft tissues– but mandible morphology more finely reflects the particular type of food –i.e., bone or bamboo. For this reason, durophagous carnivorans converge more in cranial shape than in lower jaw shape.

Durophagous carnivorans share patterns of covariation between the shapes of crania and mandibles

The fact that both structures reflect different aspects of feeding behavior in durophages opened the possibility to test if the cranium and the mandible were morphologically integrated. Furthermore, if cranial shape is more limited to evolve towards durophagy than mandible shape, we should expect a lower variation in their crania than in their mandibles. We analyzed patterns of covariation between cranium and mandible shape using PLS-analysis for exploring quantitatively this hypothesis.

In spite of the fact that the cranium and the mandible of durophages reflect different aspects of feeding behavior –i.e., nature and type of the resources consumed– our results clearly demonstrate that cranial and lower jaw shape are highly integrated in carnivores. This result was in part expected because other authors have identified the same two modules coordinating shape variability in the cranium –i.e., neurocranium and facial skull; Drake and Klingenberg (2010)– and in the mandible –i.e., ramus and corpus; Meloro et al. (2011). Furthermore, from a functional perspective this result was also expected, because the ramus is mainly connected with the neurocranium by the same main muscles involved in mastication and the corpus fits with the facial skeleton by the occlusion of upper and lower teeth.

Durophagous carnivorans also share patterns of covariation (Figs. 7E, F), most probably as a result of the functional demands to feed on tough foods. It is obviously inconceivable to have a “strong” cranium equipped to withstand high bite forces and a “weak” mandible without these biomechanical adaptations. Furthermore, for those morphological aspects recovered from the third pair of PLS-axes –which are those traits that best distinguish the pattern of durophagous covariation– cranial shape shows much less variation than lower jaw shape (Fig. 7E; *box-plots*), which confirms that the former has a more limited evolvability. However, this interpretation is mainly functional and again, the presence of a strong phylogenetic signal in cranium and mandible shape cast doubts on whether this pattern is exclusively an evidence of adaptation or reflects a constraint.

Teratological cats and dogs provide evidence that covariation in lower jaw and cranial shape is externally governed

The study of some cat –e.g., exotic short-hair cats– and dog –e.g., English bulldogs– breeds with a substantially longer lower jaw relative to the upper jaw (Fox 1963; Schlueter et al. 2009) constitutes a complementary approach to test if the pattern of covariation reported between cranial and lower jaw shape is externally or internally governed. These breeds were already considered as teratological phenotypes by Charles Darwin (1875), who identified the English bull-dog as a monstrosity fixed by man's selection. Experiments on artificial selection provide a valuable experimental test for assessing whether phenotypes not observed in nature are the result of selection or constraint (Losos 2011; Olson 2012), as they contribute information about which phenotypes can and cannot be produced by normal development (e.g., Alberch 1989; Galis et al. 2006; Olson 2012).

Brachycephalic breeds are known in the veterinary jargon as "undershot bite". The "undershot bite" or brachycephalic condition is considered the result of having a modified achondroplasic cranium with a extremely shorted snout and palatal region, which results in a wide face and causes the mandible to overhang beyond the maxilla (Stockard 1941; Fox 1963). All of these morphological traits are the breed standard in brachycephalic dogs (American Kennel Club 2006), which constitutes a documented record of the selection regime applied by breeders (Young and Bannasch 2006). The genetic cause of the brachycephalic condition –at least in dogs– is a mutation in the retro-gene coding for fibroblast growth factor 4 (*FGFR4*) (Parker et al. 2009), which causes an abnormal pattern in cartilage formation. In contrast, the opposite condition, the "overshot bite" or the "the parrot-mouth" seen in several dogs –e.g., in German Shepards (Fox 1963) and cattle have never been selected in any specific breed. In fact, this abnormal phenotype, when present, entails a set of injuries caused by the occlusion of the mandibular teeth in the soft tissues of the palatal region (Fox 1963). However, even although not being selected by breeders, this deformity seems to appear regularly in some dog breeds (see Stockard 1941; Fox 1963) and it is corrected, whenever possible, during the first months of individual's life.

Both abnormal conditions seen in domesticated animals indicate that these phenotypes are developmentally possible, which points to the hypothesis that phenotypes lacking integrated mandibles and crania are not the result of an internal constraint. In fact, this was already noted by Fox (1963) referring to Stockard (1941): "*By crossbreeding different types of dogs (dolicocephalic, mesocephalic, and brachycephalic) a wide spectrum of hybrid variations have been produced and it was concluded that the length of the upper jaw is inherited independently of the lower jaw and vice versa*".

Therefore, both phenotypes which do not have integrated mandibles and crania are ontogenetically possible. Consequently, there is no reason to invoke the presence of developmental constraints to shape the pattern of covariation between the shapes of the mandible and the cranium (Fig. 8). Thus, two possible evolutionary scenarios could explain the pattern of integration: *(i)* that this pattern is internally –developmentally– governed in wild species, but in the domestic ones the pleiotropic effects that integrate both structures have disappeared because artificial selection entailed both directional and stabilizing selection in lower jaw and cranial shapes, respectively (see Wagner, 1996; Wagner and Altenberg, 1996; Wagner et al., 2007); and *(ii)* that the observed pattern of integration is externally governed, and hence, it is only the outcome of natural selection. Under the latter scenario, both abnormal phenotypes of cats and dogs would be eliminated in the wild by natural selection at adult stages, as they result in several disorders in both dogs –e.g., dental anomalies, palatitis or otocephaly; Fox (1963)– and cats –e.g., abnormal dislocation of the ventral nasal concha, horizontally rotated upper canine teeth and steeply oriented nasolacrimal drainage system; Schlueter et al. (2009)– which makes their survivorship almost impossible without veterinary care. Distinguishing between these two hypotheses is a difficult task with the actual data. In any case, it is clear from the pattern of integration obtained here that the role of developmental constrains is absent or weak, and malleable by selection.

CONCLUSIONS

We have demonstrated that in spite of the extreme differences in the type of resources consumed by durophagous carnivorans, bone-crackers and bamboo-feeders share a set of unique traits. Furthermore, as these shared traits enhance the fitness of taxa under this environmental regime, we interpret them as adaptations to feed on tough/hard foods. Therefore, the external action of natural selection in shaping these traits is clear. However, the adaptations towards durophagy were reached independently in different carnivoran families that departed from quite different ancestral morphologies, which forced them to follow different evolutionary pathways to reach a similar phenotypic solution. Therefore, both the particular phylogenetic legacy of each durophagous family and the action of natural selection led to a pattern of incomplete convergence (Herrel 2004; Stayton 2008) in skull shape evolution towards durophagy. Furthermore, the cranium of carnivores is more limited to evolve towards durophagy than the mandible, perhaps because cranial morphology is a compromise between different functions while lower jaw shape is only involved in food acquisition and processing, or maybe because the cranium is composed of more bones than the mandible. In any case, this limitation is evidenced by the lower variation of the cranium compared to the mandible, and has led to a higher degree of evolutionary convergence in cranial shape than in lower jaw shape towards durophagy. While the mandible reflects the particular trophic adaptations of durophages –bamboo-feeding or bone-cracking– the cranium only reflects the nature of the items consumed –i.e., soft or hard tissues. In spite of the fact that cranial and lower jaw shape reflect different aspects of feeding behavior, both anatomical structures are highly integrated in the carnivoran skull. Previous studies of teratological cats and dogs subject to strong artificial selection indicated that non-integrated phenotypes are ontogenetically possible. This indicates that, if the pattern of integration between the shapes of the cranium and the mandible in carnivorans is the result of an internal constraint, it can be eliminated by strong artificial selection. The alternative explanation is that this constraint does not exist and the pattern of integration is merely due to natural selection. Therefore, we would expect an overlapping set of selective forces acting on both the cranium and the mandible, in addition to other non-masticatory demands on the cranium. Future analyses, for example the generation of biomechanical models that vary according to the major axes of morphological change highlighted in our morphometric analyses, will further clarify the functional basis not only for the differences in skull shape between durophages and other carnivorans, but also between bamboo and bone specialists.

The results obtained in this paper point to understanding evolutionary convergence as the combined result of natural selection and constraint. We do not expect evolutionary convergence of traits in the same environmental regime without the implicit action of natural selection (except those cases of chance, exaptations or correlations on another characters; see Losos [2011] and references therein), but its action has to be envisaged –in our view– upon a limited range of phenotypic variants imposed by different types of constraints –genetic, developmental, or structural. All of these potential constraints could be grouped under “phylogenetic constraints”. Although this term has a low operational value, it is a useful heuristic concept (Schwenk 1994). Therefore, we refer to phylogenetic constraints as those aspects derived from the early definition of body plans determined early in lineage phylogenies within determined biomaterials and under highly canalized developmental routes (e.g., Seilacher 1979; Maynard-Smith 1985; Gould and Lewontin 1979; Gould 1989; Wagner 1988; Schluter 1988; Ligon 1993; Thomas and Reif 1993; Schwenk 1995; Cheverud 1982, 1985; Wagner 1996), which strongly biases the production of future phenotypic variants.

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Table 1. Sample size of crania and mandibles used in this study. Species highlighted in light grey correspond to bone-crackers and those highlighted in dark grey correspond to bamboo-feeders. We considered among the bone-cracking specialists: *Dinocrocuta gigantea*† (family Percrocutidae; Werdelin and Solunias 1991) following Tseng (2009) and Tseng and Binder (2010); *Crocuta crocuta*, *Hyaena hyaena*, *Parahyaena brunea* and *Adcrocuta eximia*† (family Hyaenidae) following Nowak (1991) and Tseng and Wang (2011); *Borophagus secundus*†, *Epicyon saevus*† and *Aelurodon spp*. † (family Canidae, subfamily Borophaginae†) following Wang et al. (1999) and Tseng and Wang (2011). As bamboo-feeders we classified the red or lesser panda *A. fulgens* (family Ailuridae) and the giant panda *A. melanoleuca* (family Ursidae) following Johnson et al. (1988). Daggers denote extinct taxa.

FAMILY	SPECIES (Abbreviations)	N (mandible)	N (cranium)
URSIDAE	*Ailurpoda melanoleuca* (Ame)	13	15
URSIDAE	*Tremarctos ornatus* (To)	5	7
URSIDAE	*Ursus arctos* (Ua)	12	16
URSIDAE	*Ursus americanus* (Um)	5	8
FELIDAE	*Acinonyx jubatus* (Aju)	3	2
FELIDAE	*Felis serval* (Fser)	1	1
FELIDAE	*Felis temnicki* (Ftem)	1	1
FELIDAE	*Felis tigrina* (Ftig)	1	1
FELIDAE	*Lynx lynx* (Lly)	2	9
FELIDAE	*Neofelis nebulosa* (Nneb)	3	9
FELIDAE	*Puma concolor* (Pcon)	4	9
FELIDAE	*Panthera leo* (Pleo)	4	6
FELIDAE	*Panthera onca* (Ponc)	5	10
FELIDAE	*Panthera pardus* (Ppar)	5	3
FELIDAE	*Panthera tigris* (Ptig)	1	1
FELIDAE	*Panthera uncia* (Punc)	1	1
EUPLERIDAE	*Cryptoprocta ferox* (Cfer)	3	3
HERPESTIDAE	*Crossarcus obscurus* (Cros)	1	1
HERPESTIDAE	*Herpestes ichenumon* (Her)	3	4
VIVERRIDAE	*Genetta genetta* (Gen)	5	5
AILURIDAE	*Ailurus fulgens* (Aful)	12	12
PROCYONIDAE	*Bassaricyon medius* (Baa)	3	3
PROCYONIDAE	*Bassariscus sumichastri* (Bas)	3	3
PROCYONIDAE	*Procyon lotor* (Plot)	8	7

PROCYONIDAE	*Potos flavus* (Pfla)	10	10
MUSTELIDAE	*Eira barbara* (Eir)	8	8
MUSTELIDAE	*Gulo gulo* (Gul)	7	8
MUSTELIDAE	*Meles meles* (Mel)	6	9
MUSTELIDAE	*Mellivora capensis* (Mell)	5	5
MUSTELIDAE	*Taxidea taxus* (Tax)	5	5
HYAENIDAE	*Crocuta crocuta* (Ccr)	9	9
HYAENIDAE	*Hyaena hyaena* (Hhy)	11	8
HYAENIDAE	*Hyaena brunnea* (Hyb)	9	8
HYAENIDAE	*Ictitherium sp.* (Ict) †	1	3
HYAENIDAE	*Adcrocuta eximia* (Adc) †	-	3
HYAENIDAE	*Hyaenictitherium wongi* (Hyc) †	1	4
HYAENIDAE	*Dinocrocuta gigantea* (Din) †	1	2
CANIDAE	*Alopex lagopus* (Ala)	10	10
CANIDAE	*Cuon alpinus*(Cal)	11	8
CANIDAE	*Chrysocyon brachyurus* (Cbr)	5	1
CANIDAE	*Canis latrans* (Cla)	8	10
CANIDAE	*Canis lupus* (Clu)	12	10
CANIDAE	*Canis mesomelas* (Cme)	10	10
CANIDAE	*Canis aureus* (Cau)	8	9
CANIDAE	*Lycaon pictus* (Lpic)	9	10
CANIDAE	*Speothos venaticus* (Sve)	3	3
CANIDAE	*Vulpes corsac* (Vco)	4	10
CANIDAE	*Vulpes velox* (Vve)	8	1
CANIDAE	*Vulpes vulpes* (Vvul)	14	9
CANIDAE	*Borophagus secundus* (Bsec) †	1	4
CANIDAE	*Epicyon saevus* (Esa) †	1	1
CANIDAE	*Tomarctus hipophaga* (Tom) †	1	1
CANIDAE	*Aelurodon kilpatracki* (Akil) †	-	1
CANIDAE	*Aelurodon stirtoni* (Astir) †	1	1
CANIDAE	*Aelurodon ferox* (Afer) †	5	1
CANIDAE	*Desmocyon thompsoni* (Des) †	2	1
CANIDAE	*Carpocyon compressus* (Car) †	1	0

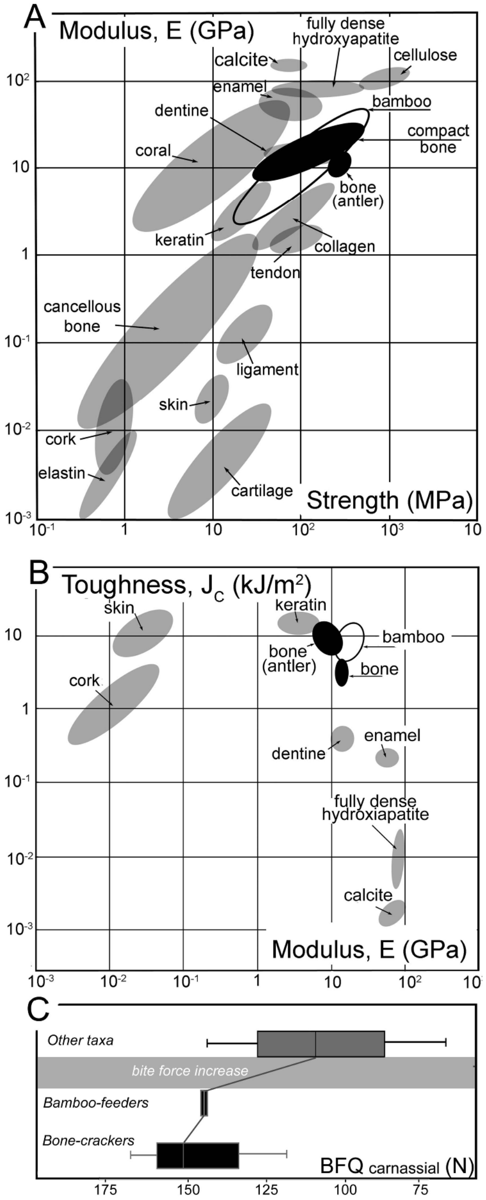

Figure 1. Material properties of bone and bamboo and bite force in bone-cracking and bamboo-feeding carnivorans. A, Bivariate plot showing Young's Modulus (E; measured in GPa) on the strength (σ; measured in MPa) of bone and bamboo relative to other natural materials (redrawn from Wegst and Ashby [2004]). B, Bivariate plot depicting the toughness of bone and bamboo (Jc; measured in KJ/m2) on Young's Modulus (E; measured in GPa) relative to other natural materials (redrawn from Wegst and Ashby [2004]). C, Box-plot showing the bite force quotient (bite force for each species in relation to its body mass) at the carnassials (BFQcarnassial) estimated by the dry skull method in the living bone-crackers, bamboo-feeders and other taxa included in our sample. The vertical line inside each box is the median. Box length is the interquartile range (IQR) and shows the difference between the 75th and 25th percentiles (data from Christiansen and Wroe 2007). Horizontal bars enclose values of 5–95%.

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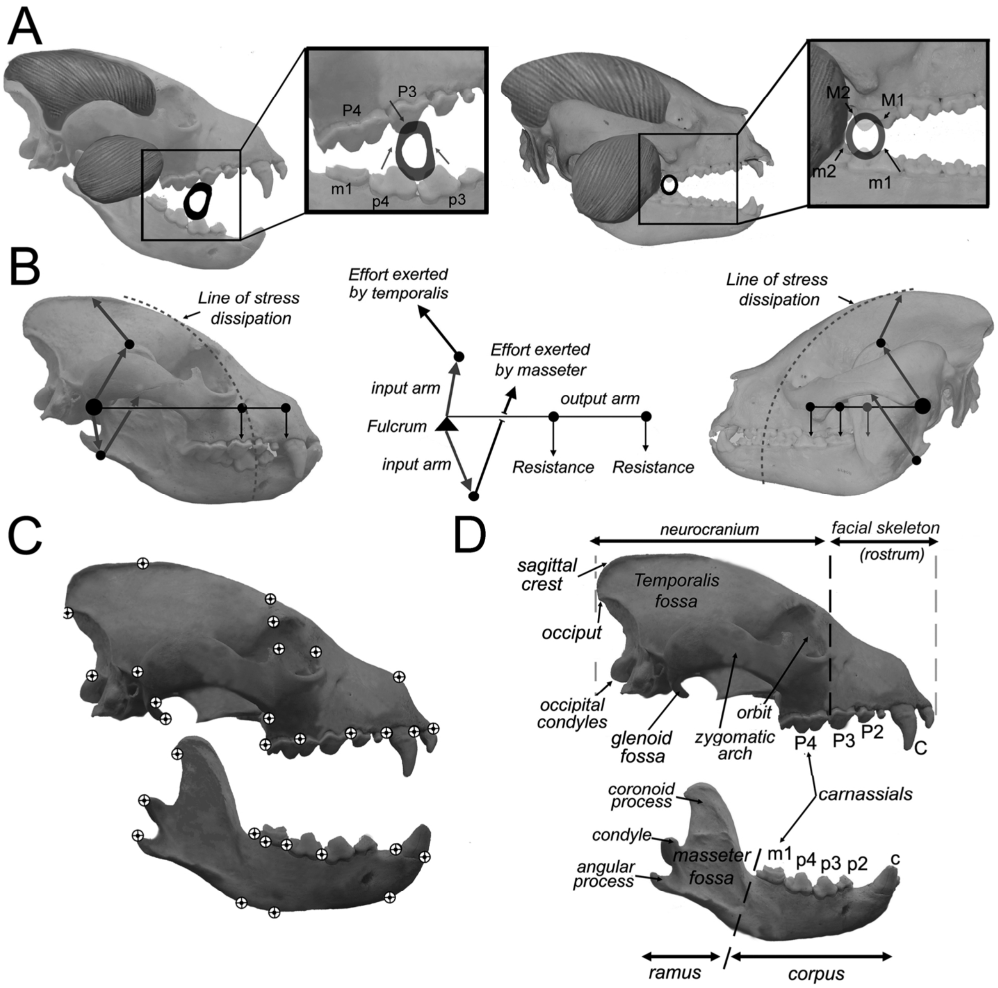

Figure 2. Skull biomechanics in durophagous carnivorans. A, Main muscles and dentition involved in the mastication practice, exemplified in a skull of spotted hyena (*C. crocuta*) and in a skull of giant panda (*A. melanoleuca*) with an hypothetical cross-section of a bone and bamboo stem, respectively. B, Masticatory apparatus modelled as a third class lever system showing the combined effort of the temporalis and masseter muscles as a function of their input arms, applied in a point between the fulcrum (temporomandibular joint) and the resistance exerted at the main teeth involved in processing food. The line of stress dissipation is a circle drawn with its centre at the fulcrum and with a radius of length from the fulcrum to P3 in the case of spotted hyaena and to M1 in the case of the giant panda (Werdelin 1989). C, Landmarks used in the morphometric analysis of skull function. D, Morphological key aspects in function recovered in the morphometric analyses. Abbreviations: C, upper canine; M, upper molar; P, upper premolar; c, lower canine; m, lower molar; p, lower premolar. The numbers indicate the position of each type of teeth. Skulls not to scale.
163x162mm (300 x 300 DPI)

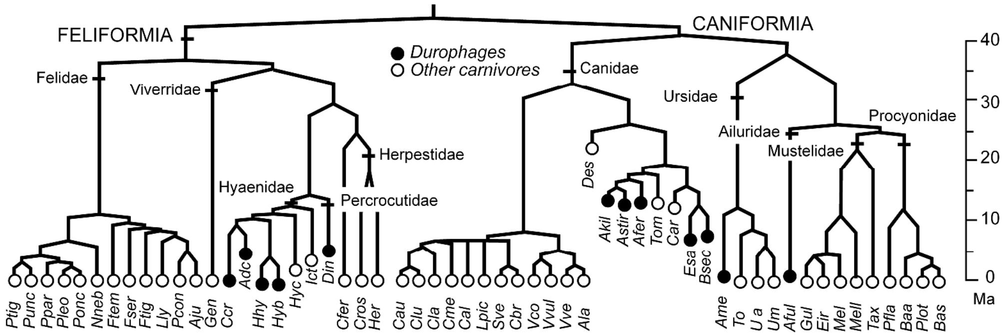

Figure 3. Phylogenetic tree used in this study. The main topology of the tree (i.e., interfamilial relationships) was arranged following Flynn et al. (2005), with the only exception of the unresolved polytomy for the family Viverridae. In this case, we follow Gaubert and Veron (2003), Finarelli and Flynn (2009) and Eizirik et al. (2010) and we considered the Viverridae (s.s.) as the stem group to Hyaenidae plus Herpestidae. To assess the intrafamilial relationships, we followed different published sources: Johnson et al. (2006) for the family Felidae; Koepfli et al. (2006) for Hyaenidae; Koepfli et al. (2007) for the family Procyonidae; Koepfli et al. (2008) for Mustelidae; Patou et al. (2009) for the relationships of Herpestidae; Krause et al. (2008) for Ursidae; and Bardeleben et al. (2005), Wang et al. (1999) and Tedford et al. (2009) for Canidae. The extinct family Percrocutidae was considered as a sister group of Hyaenidae following Werdelin and Solunias (1991) as were as the phylogenetic relationships of "stem" Hyaenidae (*Ictitherium, Hyaenictitherium, Adcrocuta*). We incorporated branch lengths as million years before present following the procedure described in Finarelli and Flynn (2006). See Table 1 for species abbreviations.
1257x416mm (96 x 96 DPI)

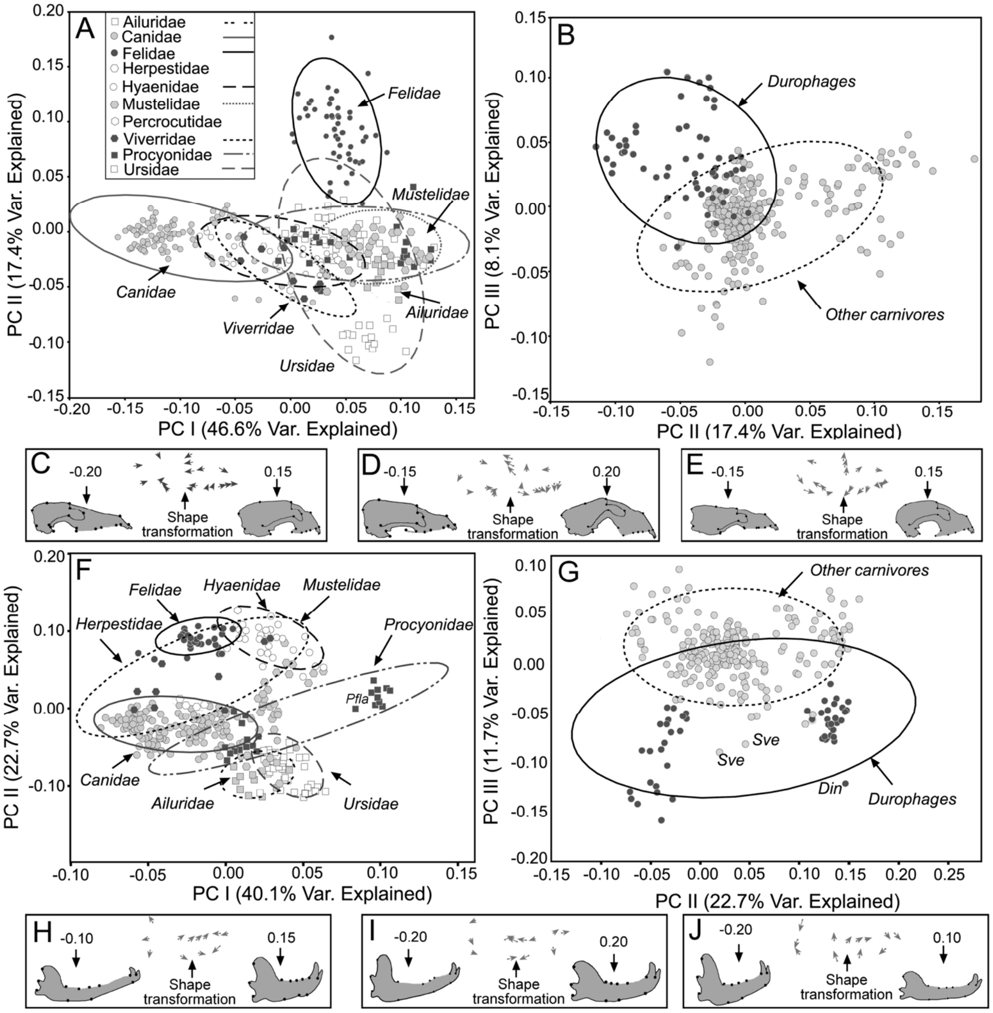

Figure 4. The phenotypic spaces derived from skull shape. A, Pairwise plot derived from the first two PCs of cranial analysis. B, Pairwise plot obtained from PCII and PCIII of cranial analysis. Shape variation accounted for by PCI (C), PCII (D) and PCIII (E) of cranial analysis. F, Pairwise plot depicted from the first two PCs of mandible analysis. D, Pairwise plot derived from PCII and PCIII of mandible analysis. Shape variation accounted for by PCI (H), PCII (I) and PCIII (J) of mandible analysis. The 95% confidence ellipses are also shown. For species abbreviations, see Table 1.
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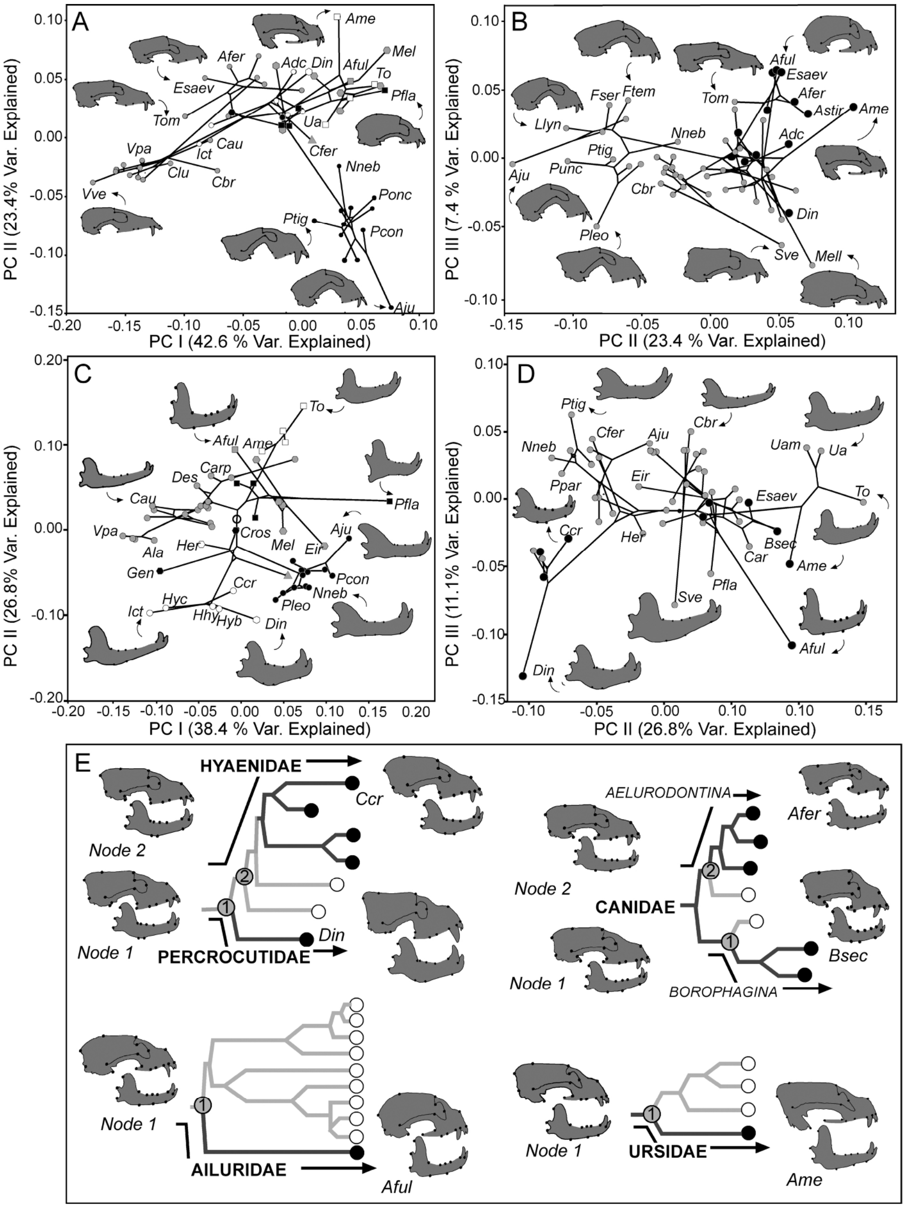

Figure 5. Phylomorphospaces and evolutionary trajectories of skull shape transformation. A, Projection of the phylogenetic tree topology onto the phenotypic space depicted from the first two PCs of cranial analysis. B, projection of the phylogenetic tree onto the phenotypic space depicted from PCII and PCIII of cranial analysis. C, Projection of the phylogenetic tree topology onto the phenotypic space depicted from the first two PCs of mandible analysis. D, projection of the phylogenetic tree onto the phenotypic space depicted from PCII and PCIII of mandible analysis. E, hypothetical evolutionary pathways followed by durophages, represented as the shape change from the reconstructed skull shape of the ancestors for each family to living species. Symbols as in Figure 4.
212x282mm (300 x 300 DPI)

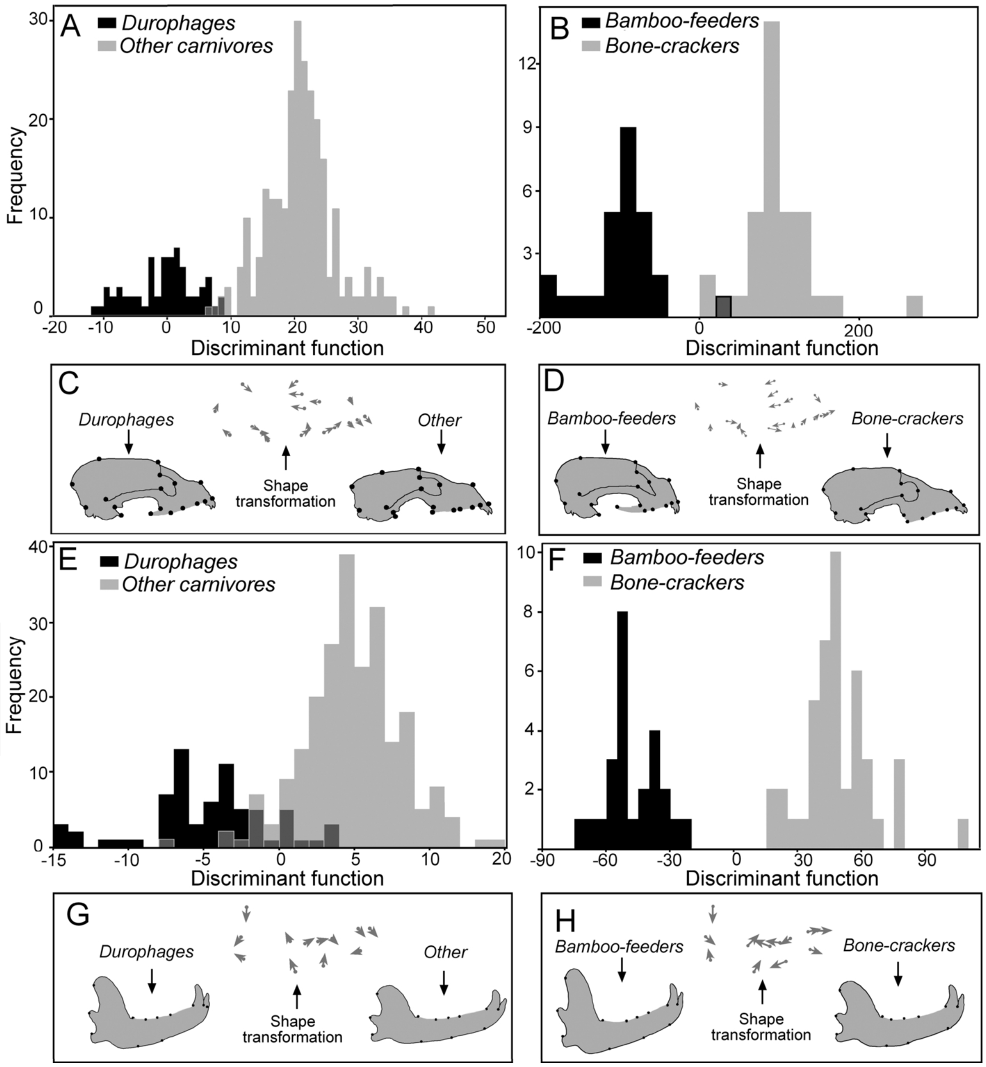

Figure 6.Discriminant analyses. A, Histogram showing the distribution of the specimens according to their scores on the discriminant function adjusted from cranial morphology to separate between durophages and other carnivorans. B, Histogram showing the distribution of the specimens according to their scores on the discriminant function adjusted from cranial morphology to separate between bone-crackers and bamboo-feeders. C, morphological variation accounted for by the discriminant function adjusted from cranial morphology to separate between durophages and other carnivorans. D, morphological variation accounted for by the discriminant function adjusted from cranial morphology to separate between bone-crackers and bamboo-feeders. E, Histogram showing the distribution of the specimens according to their scores on the discriminant function adjusted from mandible morphology to separate between durophages and other carnivorans. F, Histogram showing the distribution of the specimens according to their scores on the discriminant function adjusted from mandible morphology to separate between bone-crackers and bamboo-feeders. G, morphological variation accounted for by the discriminant function adjusted from mandible morphology to separate between durophages and other carnivorans. H, morphological variation accounted for by the discriminant function adjusted from mandible morphology to separate between bone-crackers and bamboo-feeders. Dark-grey bars represent the overlapping areas between groups.
164x174mm (300 x 300 DPI)

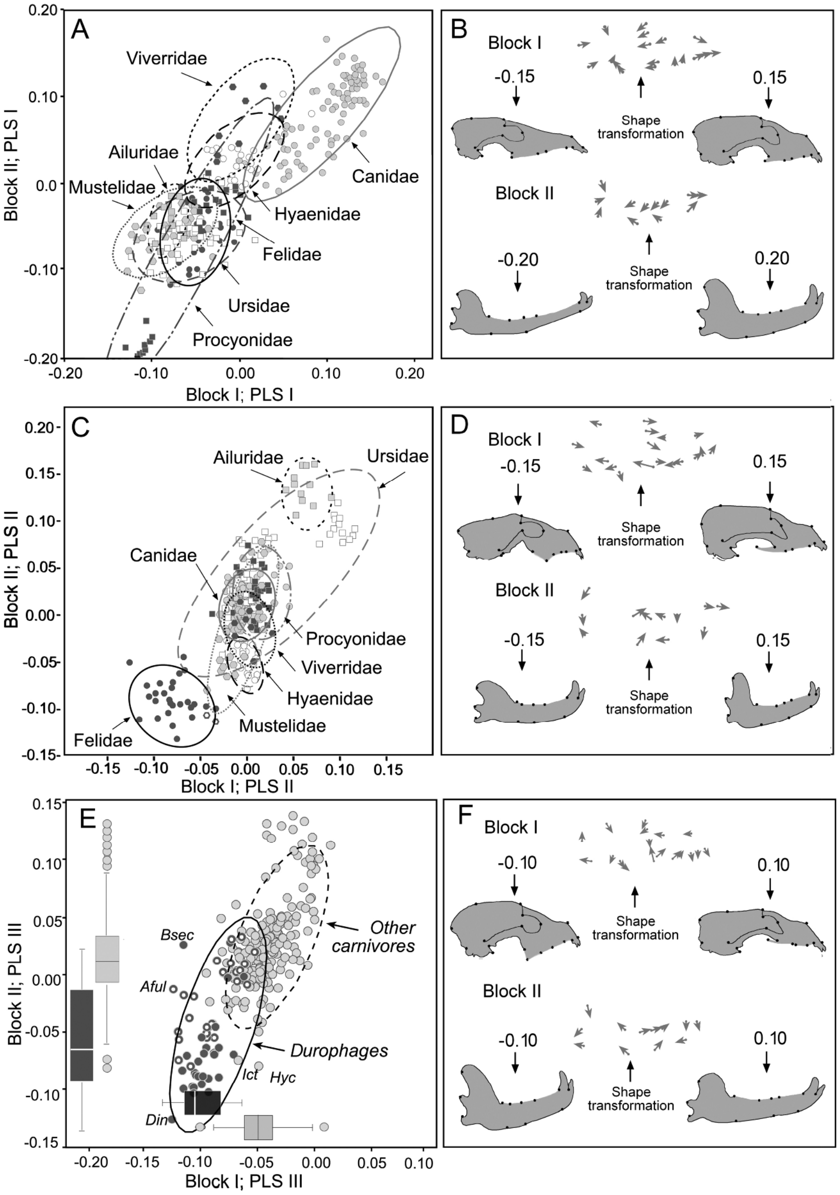

Figure 7. PLS-analysis performed between cranium (Block I) and mandible (Block II) shape. A, Pairwise plot derived from the first pair of PLS axes. B, Shape covariation between both blocks of variables accounted for by the first pair of PLS-axes. C, Pairwise plot derived from the second pair of PLS axes. D, Shape covariation between both blocks of variables accounted for by the second pair of PLS-axes. E, Pairwise plot derived from the third pair of PLS axes. Box-plots indicate the range variation of the species scores within this third of PLS axes in both blocks of variables. The vertical line inside each box is the median. Box length is the interquartile range (IQR) and shows the difference between the 75th and 25th percentiles. Horizontal bars enclose values of 5–95%. F, Shape covariation between both blocks of variables accounted for by the third pair of PLS-axes. Symbols as in Figure 4.
228x327mm (300 x 300 DPI)

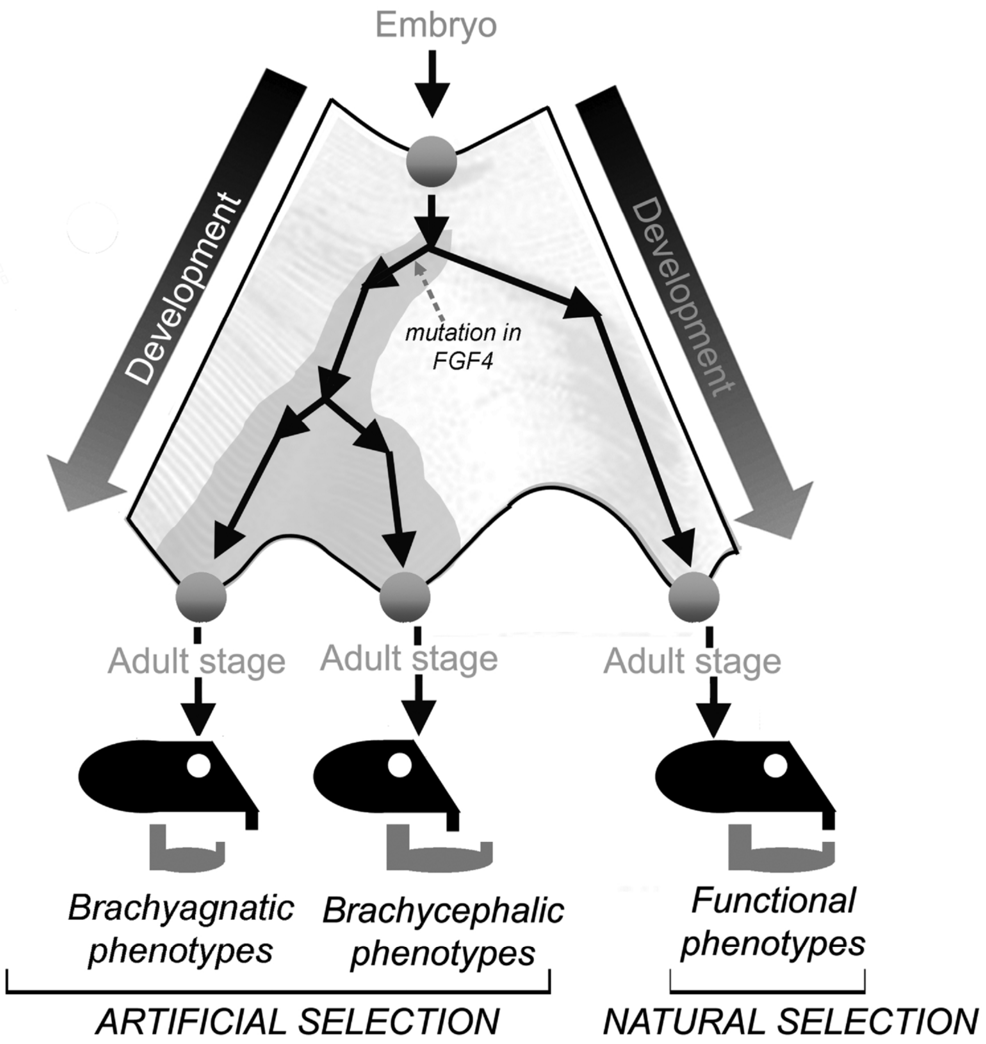

Figure 8. Hypothesis of ontogeny supported for the high integrated pattern of lower jaw and cranial shape depicted in the context of the epigenetic landscape of Waddington (1956). We propose here the mutation in the retro-gene coding for fibroblast growth factor 4 (FGFR4) as the factor that induces a change in the developmental pathway from functional to teratological phenotypes (see text for details) fixed by man's selection.
167x175mm (300 x 300 DPI)