The LINNEAN SOCIETY of London ZOOLOGICAL Journal of the Linnean Society

Macroevolutionary ecomorphology of the Carnivora skull: adaptations and constraints in the extant species

Journal:	*Zoological Journal of the Linnean Society*
Manuscript ID	ZOJ-04-2021-4570
Manuscript Type:	Original Article
Keywords:	skull < Anatomy, adaptation < Evolution, functional morphology < Anatomy, mandible < Anatomy, Carnivora < Taxa, evolutionary rates < Evolution, morphometrics < Anatomy, cranium < Anatomy
Abstract:	The mammalian order Carnivora is characterised by a broad taxonomic and ecological diversity. By using a large sample of extant species, we formally evaluated the impact of ecological factors on carnivorans skull morphology taking advantage of a combined geometric morphometrics and comparative method approach. In doing this, we implemented several evolutionary models to account for different tempo and mode of evolution in skull size and shape data. These models validated the association between skull morphology and diet at interspecific scale. The functional distinction between pinnipeds (=aquatic) and fissipeds (=terrestrial) taxa was detectable only in mandible shape and cranial size while the impact of predaceous adaptations persisted in shape but not in the size component of the skull. High levels of morphological disparity and evolutionary rates were identified in specialised dietary groups and positive association between rates and disparity was found for skull size. Within the carnivoran skull, cranium and mandible showed consistent patterns of covariation that reflects constrained functional processes stabilising macroevolutionary processes. Aquatic adaptations allowed carnivorans to invade and persist within novel regions of the mandibular morphospace while the ability to catch and kill a prey provided opportunities for size and shape diversification related to different hunting modes.

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ADDITIONAL KEYWORDS: Geometric morphometrics – cranium – mandible – shape – comparative methods – Phylogenetic Generalised Least Squares – diet – predation – pinnipeds.

INTRODUCTION

Patterns of variation above species level elucidate the mechanisms of evolutionary processes that occur over a large temporal scale. Investigations seeking to identify such patterns allow building the macroevolutionary theory (Jablonski, 2017). Ecological adaptation is inevitably linked to macroevolutionary patterns and processes. Association between phenotypic variation and ecological adaption have been formalised by ecomorphology (Wainwright, 1991). Ecomorphology proposes that any organismal structure evolved in relation to a function, which in turn helps defining its fundamental niche.

Association between morphology and ecological adaptations have been identified at different taxonomic scales with patterns at the family level being the commonest tested (i.e., Kappelman, 1988; Elton et al., 2016; Barr, 2018). Still a major caveat in ecomorphology relies on the implementation of phylogenetic comparative methods (PCMs) to test its intuitive assumption (Barr & Scott, 2014; Scott & Barr, 2014). This is because morphological traits generally do not vary randomly between species (i.e., star-like phylogeny fits the data) but follow a hierarchical structure that allows to detect what is defined as the phylogenetic signal (=tendency for closely related species to resemble each other, Blomberg et al., 2003). The emergence of multivariate PCMs increasingly allowed the detection of phylogenetic signal (Adams, 2014a) and the implementation of ecomorphological comparative tests in a broad range of anatomical structures and clades (Harmon et al., 2005; Stuart-Fox & Mousalli, 2007; Barr, 2014; Sherratt et al., 2016; Serb et al., 2017).

The vertebrate skull received particular attention to test relationship between species variation and ecological adaptations (Westneat, 2005). With no doubt, vertebrate skulls (traditionally thought to be composed by two modules: the cranium and the mandible, Moss & Young, 1960; Cheverud, 1982) are designed for multiple functions. Mammals, in particular, provide a compelling evidence for trade-offs in the skull form and function. On the one side, biomechanical and developmental processes constrain mammalian skull variation at interspecific scale so that similar patterns are observed between clades (e.g. cranial evolutionary allometry, Cardini & Polly, 2013). On the other side, broad dietary adaptations at the level of entire mammalian clades (Price et al., 2012) evidently resulted in a wide diversification of forms (Janis, 1990; Pineda-Munoz et al., 2016).

Since the earliest biometric studies, Carnivora were the focus of macroevolutionary investigations due to the broad ecological adaptations exhibited by living members of this clade and to its rich taxonomic diversity (Crusafont-Pairó & Truyols-Santonja, 1956, 1957; Ewer 1973; Gittleman 1985). In spite of a large number of studies, we lack a fully comprehensive comparative framework to interpret phenotypic variation in the entire clade. Studies by Radinsky (1981), Meloro & O'Higgins (2011), Figueirido et al. (2011), Prevosti et al. (2012), Michaud et al. (2018), Slater & Friscia (2019) covered skull ecomorphological adaptation in terrestrial forms (named fissipeds), while Bininda-Emonds et al. (2000), Echarri & Prevosti (2015), Jones et al. (2015) and Machado et al. (2018, 2019) attempted to explore living Carnivora including also the aquatic subclade of pinnipeds. As monophyletic group, pinnipeds are part of the arctoid clade and their diversification coincide with the acquisition of extreme phenotypic adaptations towards a semi-aquatic lifestyle (i.e., the pinniped ankle, Polly, 2008). Since the aquatic environment provides novel challenges to locomotory and feeding adaptations (Estes ,1989; Adam & Berta, 2002; Botton-Divet et al., 2017, 2018), we expect morphological diversification in the carnivoran skull to burst when clades invaded the aquatic niche, however this was not found by Jones et al. (2015) on a sample of representative crania. If this theory might apply to the morphological evolution of the mandible is still not known. Another factor that could have influenced skull morphological evolution in Carnivora is the mode of food acquisition. Meloro et al. (2011) proposed predation to be a strong selective adaptation imposed by catching and holding of live prey on the carnivoran mandible. Yet this hypothesis remains to be tested in the cranium.

Using a large sample of carnivoran species (64% of the extant diversity) we tested the impact of dietary, aquatic and predatory adaptations on skull size and shape. By looking at crania and mandibles separately we also expect to identify patterns of macroevolutionary covariation to differ in relation to ecological adaptations (Figueirido et al., 2013; Segura et al., 2020). Because Carnivora skull and dental morphology do not consistently evolve under Brownian motion mode of evolution (Meloro & Raia, 2010; Slater & Friscia, 2019), we implemented within a geometric morphometrics (GMM) framework a way to allow comparisons of size and shape data as well as disparity and evolutionary rates under a selection of different evolutionary models. Dietary adaptations should impact strongly skull size and shape, while level of morphological disparity and evolutionary rates are expected to vary among the diet categories depending on how functionally demanding they are (Meloro et al., 2015a; Felice et al., 2019). Specializations towards a predaceous or aquatic life-style should equally influence interspecific variation in the skull of Carnivora and level of covariation between the cranium and the mandible.

MATERIAL AND METHODS

SPECIMENS AND LANDMARK DATA

Two dimensional landmark coordinates were collected on a sample of 529 crania (in ventral view) and 554 mandibles (lateral view), representative of 188 out of 295 Carnivora species. Specimens were housed at several institutions including: Royal Museum for Central Africa (Tervuren), Kenya National Museums (Nairobi), Natural History Museum (London), World Museum (Liverpool), Elephant Seal Research Group (Falkland Islands) and National Museums of Scotland (Edinburgh) (for a full list see Archived Data and Supporting Information, Table S1). Each photographed specimen was adult, as indicated by complete dentition and/or high degree of cranial suture closure. For each species, at least one mandible and one cranium were sampled, however an individual for each sex was included whenever possible.

Pictures were taken on the cranium (ventral view) and the mandible (lateral view) using a manfrotto tripod and a Nikon D40 (Nikkor lens 55-200 mm, focus set at 100 mm) positioned at least one meter height from the specimen to minimise distortion due to camera lens.

Landmarks (cranium=30, mandible=10) were digitised using tpsDig 2 (Rohlf 2015) to cover general aspects of skull geometry and to ensure homology without particular references to the postcanine dentition since in pinnipeds premolars and molars are indistinguishable (Fig. 1, Supporting Information, Table S2).

Size and shape data were obtained from Cartesian coordinates (x, y) of landmarks using the Generalised Procrustes Analysis (GPA, Rohlf & Slice, 1990) following three steps: 1) the standardization of size (division of the landmark coordinates of each specimen by its centroid size CS, the square root of the sum of squared distances of landmarks from their barycentre), 2) the removal of translational variation (barycentres from all specimens are superimposed), and 3) the minimization of rotational differences (least-square minimization of the sum of squared distances of corresponding landmarks in a sample). GPA was separately applied to the cranium and the mandible. Data obtained for each specimen were averaged by species for all the subsequent analyses. Sensitivity analyses on a subsample of 50 species with sufficient sexed individuals ensured negligible impact of landmark digitisation error, asymmetry and sexual dimorphism on interspecific size and shape variation.

ECOLOGICAL CATEGORISATIONS

Different dietary classifications have been applied to Carnivora in relation to food type and mode of consumption (Van Valkenburgh, 1989). We followed Christiansen & Wroe (2007) that account for food type but also relative prey size. These categories were implemented for the pinnipeds, following Jones et al. (2013) to discriminate piscivores from molluscivores and crustacivores.

Whenever the attribution of a species included in our sample was not provided in the studies that originally proposed the categorisations or was uncertain, we assessed it relying on the information available in the *Handbook of the Mammals of the World - Volumes 1* and *4* (Wilson & Mittermeier, 2009, 2014 and references therein). Additionally, two broad categories were applied to test the strength of selective pressure imposed by the aquatic environment and predaceous lifestyle: 1. fissiped / pinniped; 2. predators / non-predators. The first categorisation is phylogenetic but also functional because pinnipeds show a distinct locomotory pattern than the other terrestrial carnivorans; the second category follows Meloro et al. (2011) defining 'predaceous' all the species whose diets are primarily composed of vertebrates (including fish), whereas taxa with predominantly omnivorous, insectivorous and frugivorous diets are 'non-predaceous' (Supporting Information, Table S1).

COMPARATIVE ANALYSES: THE BROWNIAN MOTION MODEL

A molecular phylogeny inclusive of the 188 sampled species was generated using the 10K tree project (Arnold et al., 2010). This phylogeny is based on 14 mitochondrial genes, 14 autosomal genes and one gene from the Y-chromosome, all available on GenBank. For the tree inference, the authors used MrBayes (v. 3.2 - Ronquist and Huelsenbeck 2003) and node ages were inferred using 16 fossil calibration points, extracted from the Paleobiology Database (http://paleodb.org).

The phylogeny (Supporting Information, Fig. S1) was employed to apply comparative methods (Harvey & Purvis, 1991) on size and shape data in order to: 1) assess the degree of phylogenetic signal in the Carnivora skull measured by the K statistics and its multivariate extension K_{multiv} (to quantify how much the phylogeny fit the data, Adams, 2014a); 2) test for the impact of ecological categorisations on skull size and shape (using the distance based method Procrustes ANOVA and its phylogenetic equivalent *D-PGLS* whose statistical significance is assessed via permutations, Adams & Collyer 2015); 3) assess differences in morphological disparity (=MD, the variance in size and shape; this was phylogenetically corrected using residuals of PGLS models, Michaud et al. 2018) and evolutionary rates (estimated using the σ^2 statistic that quantifies the rate of variance accumulation in traits over time while accounting for phylogenetic relationships, Adams, 2014b) between ecological categories; 4) test the degree of covariation between cranium and mandible at macroevolutionary scale using Partial Least Squares (PLS, Rohlf & Corti, 2002) and its phylogenetic equivalent (Adams & Felice, 2014). This test was also repeated within the broad ecological categorisations using the "effect size" metric (Adams & Collyer, 2016) to quantify the strength of morphological integration. Since masticatory constraints are assumed to differ in ecological groups, we expect different patterns of macroevolutionary covariation in these components of the skull (Linde Medina et al., 2016).

All these analyses were performed using the R package geomorph (Adams & Otarola-Castillo, 2013) which assumes morphological data to follow Brownian motion mode of evolution that is: the amount of evolutionary change in a given phenotypic trait is proportional to branch lengths (i.e., time if the phylogeny is a chronogram, Garland et al., 1992).

COMPARATIVE ANALYSES: BEYOND BROWNIAN

Alternative models of trait evolution have been tested on Carnivora skull and dentition including delta, kappa, lambda, Ornstein-Uhlenbeck (OU), and Early Burst (EB) (Meloro & Raia, 2010; Slater & Friscia, 2019). OU takes into account evolutionary phenomena like stabilizing/divergent selection and stasis so that traits can evolve towards a single or multiple optima (Hansen, 1997; Butler & King, 2004; Beaulieu et al., 2012). Delta, kappa and lambda models are branch length transformations that stretch basal or terminal nodes approximating respectively gradual accelerations/slowdowns in the rate of trait evolution through time, gradualism or punctuated equilibrium conditions, or different levels of phylogenic signal (Pagel, 1997, 1999a, 1999b). Finally, EB assumes exponentially reducing diversification rates through time, typical of adaptive radiations (Harmon et al., 2010; Ingram et al., 2012). These models were tested on both skull size and shape data using the function transformPhylo.ML in the package motmot (Thomas & Freckleton, 2012). To identify the ability of maximum likelihood in detecting the best mode of evolution for shape data, we simulated multivariate Brownian motion datasets with the dimensionality introduced by our shape data (20 procrustes coordinates for the mandible and 60 for the cranium). We run the simulations 100 times to detect how often Brownian was misidentified by the other models of evolution using log.likelihood, following the same recommendation of Adams & Collyer (2018) with the packages Geiger (Harmon et al., 2008) and motmot (Thomas & Freckleton, 2012). For the OU model, we tested only how BM compared with OU1 (often mentioned as "single stationary peak") following Cooper et al. (2016) that already identified high rates of model misspecification with single traits for phylogenies smaller than 200 taxa.

To implement the best mode of evolution into PGLS models, disparity and evolutionary rates, residuals of each PGLS that assumed BM were tested against the evolutionary models that exhibited the lowest misspecification rates using the function "transform.Phylo.ML". The branch lengths of the original phylogeny were subsequently transformed according to the model parameter exhibiting the highest maximum likelihood. The PGLS was run again with the new transformed phylogeny and residuals re-checked for BM (see Zelditch et al., 2017). For PLS, both matrixes of shape data (=Procrustes coordinates of cranium and mandible) were combined using the function 'cbind' (Meloro et al., 2017) and tested for mode of evolution with "transform.Phylo.ML". Branch lengths of the phylogeny were transformed accordingly and the new resulted tree was implemented into the function "phylo.integration".

RESULTS

SIZE AND SHAPE VARIATION

Phylomorphospace shows in both cranial and mandibular shape variation a strong influence of phylogeny with species clustering in the morphospace according to their family (Fig. 2). For the cranium, PC1 (47.09% var.) describes the elongation of the rostrum relative to the braincase with canids homogenously occupying positive scores while felids and mustelids negative ones (Fig. 2A). The second PC (20.1% var.) relates to changes in the braincase and zygomatic region with species at the most negative extreme (e.g. *Mustela nivalis* and *Herspestes* spp.) showing a relative elongation of the braincase and a shortening of the zygomatic arches while on the positive extreme felids are characterised by wider zygoma and rostrum but short braincase (Fig. 2A-B). The third PC (9.7% var.) best separates fissipeds from pinnipeds since it relates to the palatal relative width (wider in fissipeds than in pinnipeds) as well as the relative elongation of the zygoma (Fig. 2B).

For the mandible, PC1 (51.5% var.) separates Otariidae, Phocidae and Odobenidae from the other Carnivora due to their shorter ramus relative to the corpus (Fig. 2C-D). On PC2 (shape changes occur mostly for the corpus region that is thicker in procyonids and ursids (negative scores) rather than pinnipeds and herpestids/canids (positive scores). PC3 (10.9% var.) encompasses changes in the diastema between lower canine and premolar/molar raw and separates felids, phocids and Malagasy carnivorans from the other groups (Fig. 2D). A strong and significant phylogenetic signal ($P < 0.001$) is confirmed for cranium and mandible shape ($K_{multiv} = 0.57$ in both cases) as well as size (cranium $K = 0.70$, mandible $K = 0.72$).

Procrustes ANOVA models (Table 1) identify in cranial and mandibular shape a significant impact of diet, which explains the highest percentage of variation followed by fissiped – pinniped then predatory functional categorisation. This latter factor is non-significant in mandible shape. Models for size mirrors shape data with predatory function being non-significant in all cases. When phylogeny is accounted for assuming Brownian, results are congruent except for fissiped/pinniped distinction that is non-significant for cranio-mandibular size and cranium shape (Table 1). Evolutionary allometry significantly impacts cranial (c.ca 9% after phylogenetic correction), more than mandibular shape variation however it did not affect significance of the ecological models (table S2).

ECOMORPHOLOGICAL MODELS BEYOND BROWNIAN

The BM simulated datasets are consistently detected by lambda (min λ = 0.999857 and all upper CI = 1), EB (> 95% of cases the ACDC parameters approach 0.00=BM) and to lesser extent kappa (κ > 0.88 in every simulation and κ > 0.94 in 95% cases). OU1 is rarely approaching alpha parameters equal to 0.0 -which is expected by BM- and the same applies for delta that is expected to be 1.00. The distribution of Likelihood differences between each model and BM confirms high rates of misspecification for OU1 and delta (Supplementary Information, Figs. S2-S4).

For the Carnivora skull shape data, lambda is detected as the best mode of evolution showing similar parameters for the cranium (λ=0.85) and the mandible (λ=0.84). Size data instead are fitted by kappa, a result congruent with the function 'fit.continuous' (Revell, 2012). Cranium and mandible again exhibit similar kappa (0.57, and 0.59, respectively, Supplementary Information, Table S2).

The implementation of different evolutionary models does not alter much the ecomorphological patterns observed. In all cases, lambda model provides a fit better than Brownian for shape data (with parameters varying around 0.56-0.84) while kappa transformation (values between 0.54 – 0.84) is preferred for size (Table 1, Supplementary Information, Fig. S5). For cranial shape, fissiped/pinniped is still a non-significant factor while it explains more variance than predatory function in the mandible (4.2% vs 2.1%). Skull size is significantly impacted by diet only, and its association with shape still holds after implementing lambda but it is much weaker in the mandible (1.9% var.) than in the cranium (9.7% var.) (Table 1).

DISPARITY AND EVOLUTIONARY RATES

Morphological disparity does not consistently change between fissiped and pinniped for cranial and mandibular shape no matter if Brownian or lambda models are implemented, while size disparities are significantly higher in fissipeds (Table 2). Predaceous carnivorans equally show higher disparities than non-predaceous taxa in shape, but not in size. Evolutionary rates (after lambda model implementation) are higher in the cranio-manidbular shape of pinnipeds as well as non-predaceous species. For size no changes in rates are detectable (Table 2).

The interpretation of disparities and evolutionary rates between diet categories is better simplified by a scatter plot (Felice et al., 2018) showing the values corrected following lambda and kappa models for shape and size data, respectively (for values based on BM see Supplementary Information, Fig. S5). When shape is concerned, specialised form of diet such as molluscivory exhibits a considerably high disparity and evolutionary rate (Fig. 3). The lowest shape disparity is found in the herbivores/frugivore group while high disparities are equally detectable for piscivores and crustacivores. In size, a significant and positive association is detected between morphological disparity and evolutionary rates following a "carnivory" gradient with herbivores/frugivores still showing the lowest disparities and rates that are gradually increasing in small, medium and large prey specialists (Fig. 2). Molluscivores are outliers due to their relatively lower disparity values for high evolutionary rates in size.

MACROEVOLUTIONARY COVARIATION

The PLS models identify in all cases significant levels of covariation between cranium and mandible shape (Table 4). In Carnivora as whole the covariation is partially driven by changes in relative rostrum elongation coinciding with changes in relative corpus length (Fig. 3). Pinnipeds homogeneously occupy negative PLS scores being characterised by short rostrum, wider zygoma, short mandibular corpus and wider ramus region. This trend could also be identified in predaceous species, while covariation in pinnipeds is strongly influenced by the unusual morphology of the walrus *Obobenus* with a broad rostral region (due to the presence of highly developed tusks) and tick and short mandibular corpus (Fig. 3). Phocids that occupy negative scores are characterised by a narrower rostrum, broader braincase, wider ramus and relatively slender corpus. The implementation of Brownian or lambda models (those are fitted on lower dimensional matrix of 44 PC scores whose simulations proved to be identical to the procrustes raw shape data, Supplementary Information, Fig. S6) significantly decreases the effect size in the whole sample and confirms no differences in the strength of covariation between predaceous vs non-predaceous taxa. Fissipeds, although have a relatively lower correlation coefficient in PLS1 vectors, show greater effect size than pinnipeds (Table 4).

DISCUSSION

Cranial and mandibular morphologies within Carnivora are clearly partitioned at family level. Since early morphometric studies, this pattern was apparent in both size and shape components of the skull, while the detection of ecological adaptations is more subtle (Crusafont-Pairo & Truyols Santonja, 1956, 1957; Radinsky 1981; Meloro et al., 2008, 2011; Figueirido et al,. 2011; Prevosti et al. 2012). We were able to identify a contained impact of ecological functional groups that persist to some extent after Brownian motion or other alternative modes of evolution are accounted for (Table 1). More specifically, diet is consistently linked with all aspects of cranial and mandibular morphology explaining higher level of variation in size rather than shape. Diet generally account for c.ca 10% in shape variance, which was similarly found in other mammalian and vertebrate groups (e.g., primates, Meloro et al., 2015b; birds, Felice et al., 2019). Broader categorisations related to aquatic or predatory adaptations are even less relevant but identified significantly distinct patterns in the cranium and the mandible. For the cranium the invasion of aquatic niches did not impact shape but affected size, being pinnipeds consistently larger than terrestrial carnivorans due to thermoregulation, basal metabolic costs and food intake functions imposed by the aquatic environment (Gearty et al., 2018). In the mandible we found quite the opposite with shape differences becoming apparent on PC3 axis, which describes a coronoid process close to the condyle indicative of a short temporalis attachment area. Taken to the extreme, such variation might lead to the reductions in the ramus observed in cetaceans (Berta et al. 2015). Ito and Endo (2016) reported for *Phoca larga* muscles masses comparatively much smaller (almost 50% in the temporalis) than those of a similar sized fissiped (*Puma concolor*) and Laakkonen & Jernvall (2020) have recently reported the same pattern for two species of ringed seals (*Pusa* spp.). This is consistent with the hypothesis of Jones et al. (2013) that masticatory muscles in pinnipeds might be comparatively weaker than in fissiped due to their necessity to produce high bite force in combat rather than chewing. Masticatory muscles arrangement explains to some extent also the variance associated to a predaceous life style that requires delivering stronger bite forces (Christiansen & Wroe, 2007; Meloro et al., 2011). These ecological factors altogether are modulated by evolutionary allometry that impact more the cranium (as expected by the CREA hypothesis, Cardini & Polly, 2013) than the mandible (Meloro et al., 2015a).

The implementation of different evolutionary models corroborates these hypotheses with consistent results occurring assuming Brownian motion or alternative modes of evolution. For cranial and mandibular size we detected kappa parameters remarkably similar to those found by Meloro & Raia (2010) on the first lower molar (=carnassial) length of living and fossil fissipeds, ranging between 0.53-057. Similarly for skull shape, lambda was identified as the best transformation following Meloro & Raia (2010) findings on lower carnassial angular height (a proxy for degree of hypo – hyper carnivory). Lambda is a way to incorporate different levels of phylogenetic signal (similarity between the phenotypic traits due to common ancestry) and is quite effective in phylogenetic regression of univariate traits (Revell, 2010). The recent work of Slater &

Friscia (2019) suggests that the lower slicing vs grinding area of Carnivora possibly evolved following Early Burst model however, their dataset did not include pinnipeds, but incorporated fossils. This suggests that the ecological arguments to support carnivorans diversification applies at different hierarchical taxonomic scales. Pinnipeds represent an important "taxonomic" component of Carnivora that "escaped" functional constrains dictated by carnassial morphology evolving different feeding strategies including suction, grip and tear (Hocking et al., 2017).

Our models led to further macroevolutionary interpretations related to morphological disparities and evolutionary rates. We found no differences in disparity values between fissiped and pinniped taxa confirming Jones et al. (2015). That is: aquatic adaptations provided Carnivora to similar ecomorphological opportunities of diversification although in a consistently different region of the morphospace [particularly for the mandible, see Polly, 2008]. This phenomenon occurred relatively quickly as detectable in the high evolutionary rate of pinnipeds, at least if the lambda models is assumed for shape evolution. Predaceous Carnivora instead exhibit wider disparity in shape but not faster rates. Indeed, Carnivora evolved multiple predatory modes (e.g. stalker, cursorial) some of which already constrained mandibular shape convergent patterns (Meloro et al., 2015a). The discrepancy observed for predaceous taxa between shape disparity and evolutionary rate can be to some extent generalised also when diet categories are scrutinised. Highly demanding feeding imposed by the consumption of molluscs resulted into exceptionally high disparity and evolutionary rate for both cranial and mandibular shape. This category was identified for *Enhydra lutris* as well as the two pinnipeds: *Erignatus barbatus* and *Odobenus rosmarus*. The consumption of molluscs by these species is achieved with different behaviours affected by the morphology: *Enhydra* use bunondont molars to crash molluscs, while *Odobenus* tusks greatly affect its cranial and mandibular morphology. The other aquatic diets equally showed higher level of disparities but relatively slower rates. This pattern can be justified by the presence of disparate fissipeds (i.e., otters as well as the small cat *Prionailurus planiceps*) and pinniped taxa whose cranio-mandibular shape are quite distinct due to differences in dental morphologies and mastication. On the other hand, size disparities and rates follow a positive association. A strict linear association is expected under neutral evolution (Felsenstein, 1985) although in our case the best fitting function is exponential. This trend evidently relates with the nature of our ecological diet categorisation that account for a size gradient into feeding function. Groups showing lower size disparity are characterised by a diet not energetically demanding (e.g. herbivores and fruit) while increasing level of specialisations towards large prey provides more opportunity for size variation. Carbone et al. (1999) identified the size constraint beyond large prey specialisation that fit into the pattern we observed here. Lack of positive association between disparities and rates in shape is common in vertebrate skulls and was equally not detected by Michaud et al. (2018) in Carnivora. Within this context, the framework proposed by Felice et al. (2018) suggests that level of integration among structures perhaps provides constraints that are not favouring neutral evolutionary processes. To some extent we explored this issue by looking at the level of functional covariation between the cranium and the mandible. This was consistently detected in the whole sample and subsample as expected by biomechanical efficiency. Fissipeds exhibit higher effect size than pinnipeds corroborating the hypothesis that aquatic specialisations provided novel ecomorphological opportunities by relaxing dental (i.e. pinnipeds have lost the carnassials functionality) and muscular constraints associated with food mastication. On the opposite side, predaceous species do not show stronger level of covariation between the cranium and the mandible even if their effect size is much larger than non-predaceous species. Michaud et al. (2020) equally found similar results in feliform Carnivora suggesting that the cranio-mandibular shape covariation pattern is quite conservative within broad ecological categorisations.

CONCLUSION

The cranio-mandibular complex of living Carnivora showed weak but consistent association between size, shape and dietary specialisations. The invasion of more aquatic lifestyle experienced by pinnipeds identified for the mandible shape novel opportunities of morphospace invasion related to the relaxation of chewing constraints and masticatory muscles (as proposed in Jones et al., 2015). On the other hand, predatory adaptations impacted only to a limited extent shape variation but not level of macroevolutionary covariation between cranium and mandible. Molluscivory has been identified as the diet category with the highest level of disparity and evolutionary rate in shape due to its quite specific functional demand. The subtle impact of diet perhaps relates with the inadequacy of categorising ecological specialisation that in Carnivora are rarely devoted to one food type only. Selective processes are channelized at broad taxonomic scale as supported by Michaud et al. (2018) that identified strong association between morphological disparities and ecological specialisations at family level. Covariation patterns at macroevolutionary scale reflect morphological stability necessary for the correct function of the cranio-mandibular complex.

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ARCHIVED DATA

The data underlying this article are available in the Dryad Digital Repository, at https://datadryad.org/stash/share/6s2IZtvxBkoCSegpISRwoD4eklFUsuTzm580RgCTT1s

TABLES

Table 1. Summary statistics for Procrustes ANOVA models computed to test the influence of pinniped vs fissiped categorisation (=PInn/Fiss), diet and locomotion on cranial and mandibular size and shape. Non-significant P values are highlighted in bold

				OLS				**PGLS (BM)**				**PGLS (model fit)**				
		df1	**df2**	**R^2**	**F**	**Z**	**P**	**R^2**	**F**	**Z**	**P**	**Param**	**R^2**	**F**	**Z**	**P**
Cranium Shape	Diet	8	179	0.179	4.875	5.984	0.001	0.062	1.487	2.154	0.012	λ:0.867	0.070	1.690	2.727	0.001
	Fiss/Pinn	1	186	0.091	18.608	4.507	0.001	0.004	0.686	-0.493	**0.669**	λ:0.523	0.010	1.916	1.463	**0.076**
	Pred/NoPred	1	186	0.015	2.791	1.888	0.025	0.017	3.273	2.492	0.004	λ:0.859	0.022	4.125	3.048	0.001
Mandible Shape	Diet	8	179	0.310	10.069	8.197	0.001	0.088	2.150	3.726	0.001	λ:0.855	0.094	2.311	4.130	0.001
	Fiss/Pinn	1	186	0.336	93.917	6.380	0.001	0.013	2.480	1.962	0.015	λ:0.568	0.042	8.160	3.994	0.001
	Pred/NoPred	1	186	0.012	2.242	1.451	**0.071**	0.028	5.340	3.138	0.001	λ:0.867	0.021	4.077	2.678	0.001
Cranium Size	Diet	8	179	0.284	8.878	4.217	0.001	0.120	3.054	2.215	0.003	K 0.558	0.123	3.126	2.239	0.002
	Fiss/Pinn	1	186	0.323	88.607	2.577	0.001	0.016	3.020	1.072	**0.078**	K 0.839	0.029	5.535	1.346	**0.027**
	Pred/NoPred	1	186	0.011	2.1663	0.896	**0.154**	0.002	0.356	0.160	**0.528**	K 0.574	0.002	0.467	0.297	**0.473**
Mandible Size	Diet	8	179	0.220	6.301	3.607	0.001	0.085	2.073	1.544	0.040	K 0.544	0.100	2.481	1.838	0.018
	Fiss/Pinn	1	186	0.257	64.276	2.445	0.001	0.011	2.103	0.895	**0.149**	K 0.814	0.018	3.343	1.113	**0.061**
	Pred/NoPred	1	186	0.007	1.246	0.610	**0.269**	0.001	0.032	-0.782	**0.528**	K 0.596	0.001	0.007	-1.352	**0.901**
Cranium	Allometry	1	186	0.093	19.168	4.524	0.001	0.093	19.086	6.279	0.001	λ:0.856	0.097	19.99	6.227	0.001
Mandible		1	186	0.113	23.630	4.474	0.001	0.014	2.713	2.143	0.013	λ:0.848	0.019	3.593	2.477	0.001

Table 2. Morphological disparity (MD) and evolutionary rates (EvolRates) parameters and p-values (in **bold** if significant) computed for fissipeds and pinnipeds in cranium (Cra) and mandible (Mand) shape and size. Additional abbreviations: Shape = SH, lnCS = natural logarithm of centroid size.

				MD	P-value	EvolRates	P-value
Brownian	SH	Cra	Pinniped	0.420	0.748	6.69E-06	**0.001**
			Fissiped	0.447		4.12E-06	
			Predator	0.011	**0.001**	9.63E-06	0.970
			No-Pred	0.007		9.69E-06	
		Mand	Pinniped	0.407	0.639	1.77E-05	0.76
			Fissiped	0.439		1.72E-05	
			Predator	0.015	**0.002**	2.05E-05	0.226
			No-Pred	0.009		2.53E-.05	
	lnCS	Cra	Pinniped	4.934	**0.022**	0.004	0.185
			Fissiped	9.238		0.005	
			Predator	0.227	0.252	0.005	0.244
			No-Pred	0.282		0.004	
		Mand	Pinniped	5.585	**0.021**	0.004	0.124
			Fissiped	11.526		0.006	
			Predator	0.272	0.501	0.006	0.102
			No-Pred	0.312		0.004	
Model fit	SH	Cra	Pinniped	0.383	0.603	5.66E-06	**0.001**
			Fissiped	0.417		3.42E-06	
			Predator	0.011	**0.001**	3.66E-06	**0.03**
			No-Pred	0.007		4.94E-06	
		Mand	Pinniped	0.363	0.492	1.02E-05	**0.002**
			Fissiped	0.402		7.71E-06	
			Predator	0.015	**0.002**	8.00E-06	**0.002**
			No-Pred	0.009		1.33E-05	
	lnCS	Cra	Pinniped	2.519	**0.055**	0.008	0.341
			Fissiped	4.536		0.011	
			Predator	0.227	0.286	0.010	0.643
			No-Pred	0.277		0.009	
		Mand	Pinniped	2.976	**0.044**	0.008	0.198
			Fissiped	5.983		0.012	
			Predator	0.273	0.545	0.011	0.288
			No-Pred	0.309		0.009	

Table 3. Correlation coefficient (r) and effect size (ES) showed for Partial Least Squares models performed without phylogenetic correction, after assuming Brownian or Lambda transformation. Symbols denote significantly different effect size

		Carnivora	**Fissiped**	**Pinniped**	**Predaceous**	**Non-Predaceous**
PLS	r	0.724	0.81	0.86	0.725	0.826
	ES	13.292*	12.725^	4.61^	12.035**	5.187**
PLS-BM	r	0.679	0.629	0.835	0.696	0.825
	ES	11.015*	8.269	3.429	9.1907	5.3885
PLS - Lambda	r	0.719	0.7	0.836	0.686	0.832
	ES	12.13*	10.669^	3.487^	10.062	5.5039
	λ	0.812	0.765	0.935	0.835	0.852

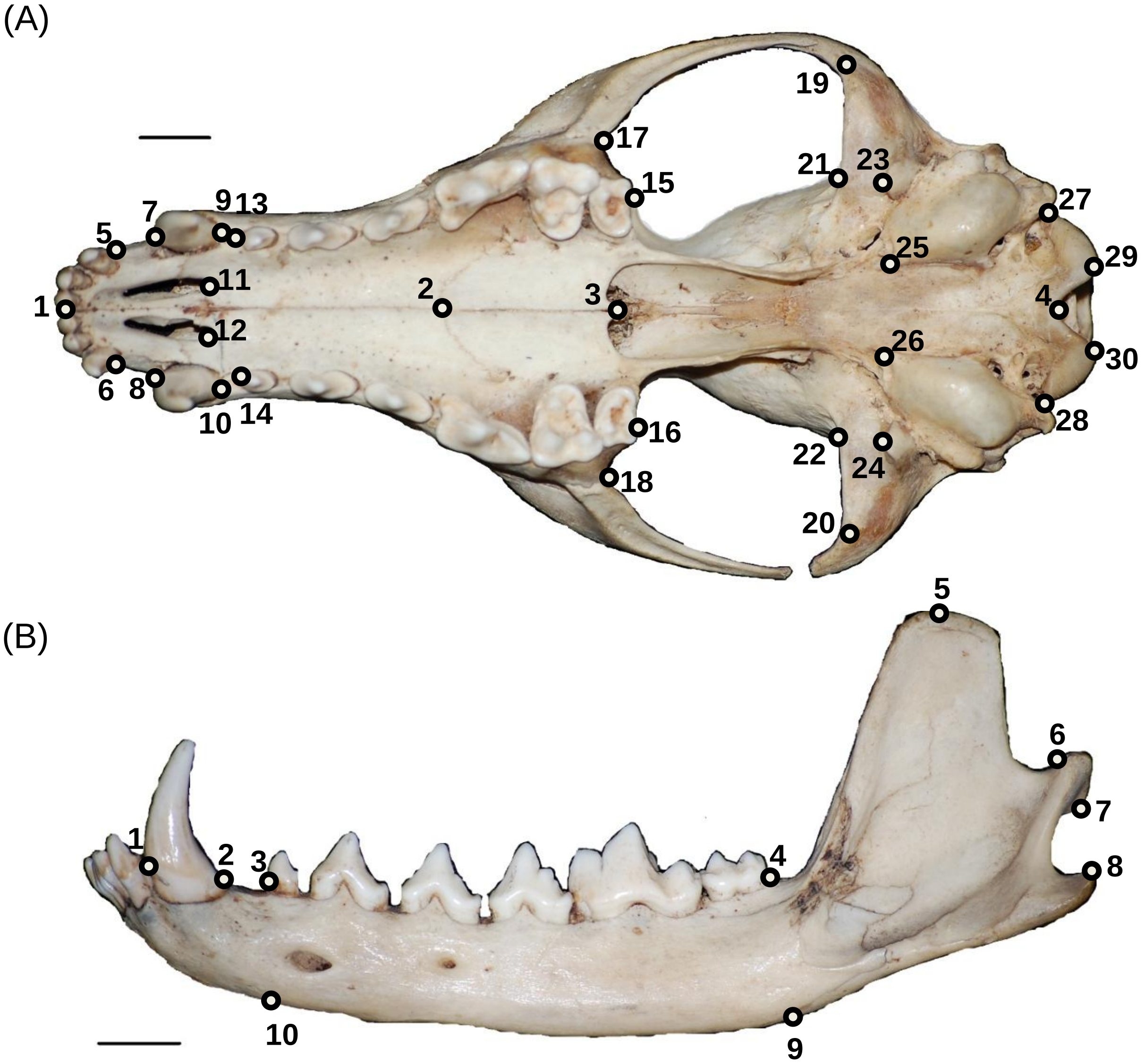
Figure captions

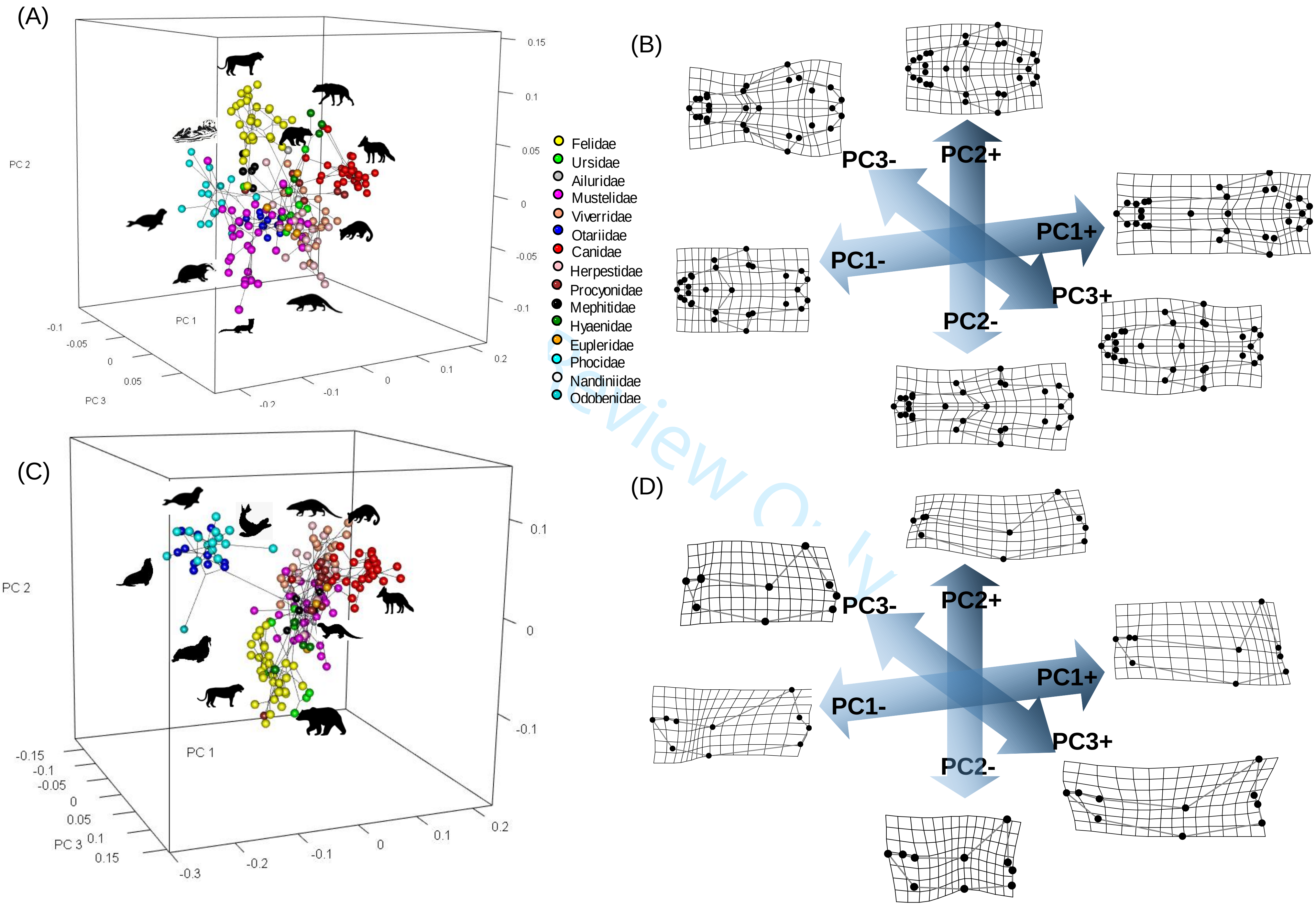
Figure 1. Landmark configuration on cranium (A) and mandible (B) of red fox (*Vulpes vulpes*). Scale bar is 1 cm.

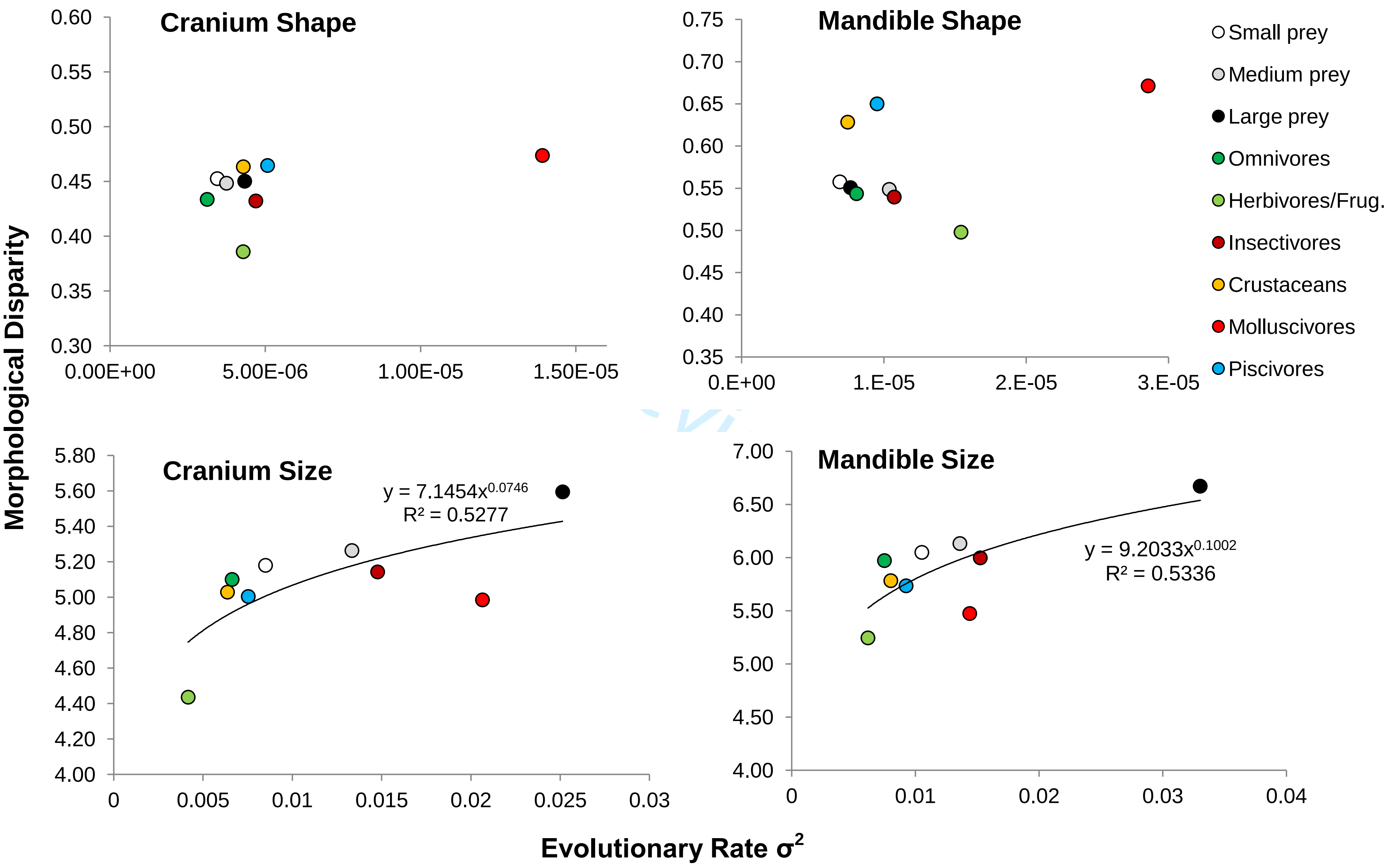
Figure 2. Phylomorphospaces for the cranium (A) and the mandible (C) with respective thin plate spline deformations (B, D). Families are colour coded and animal silhouette are provided for the main taxonomic groups.

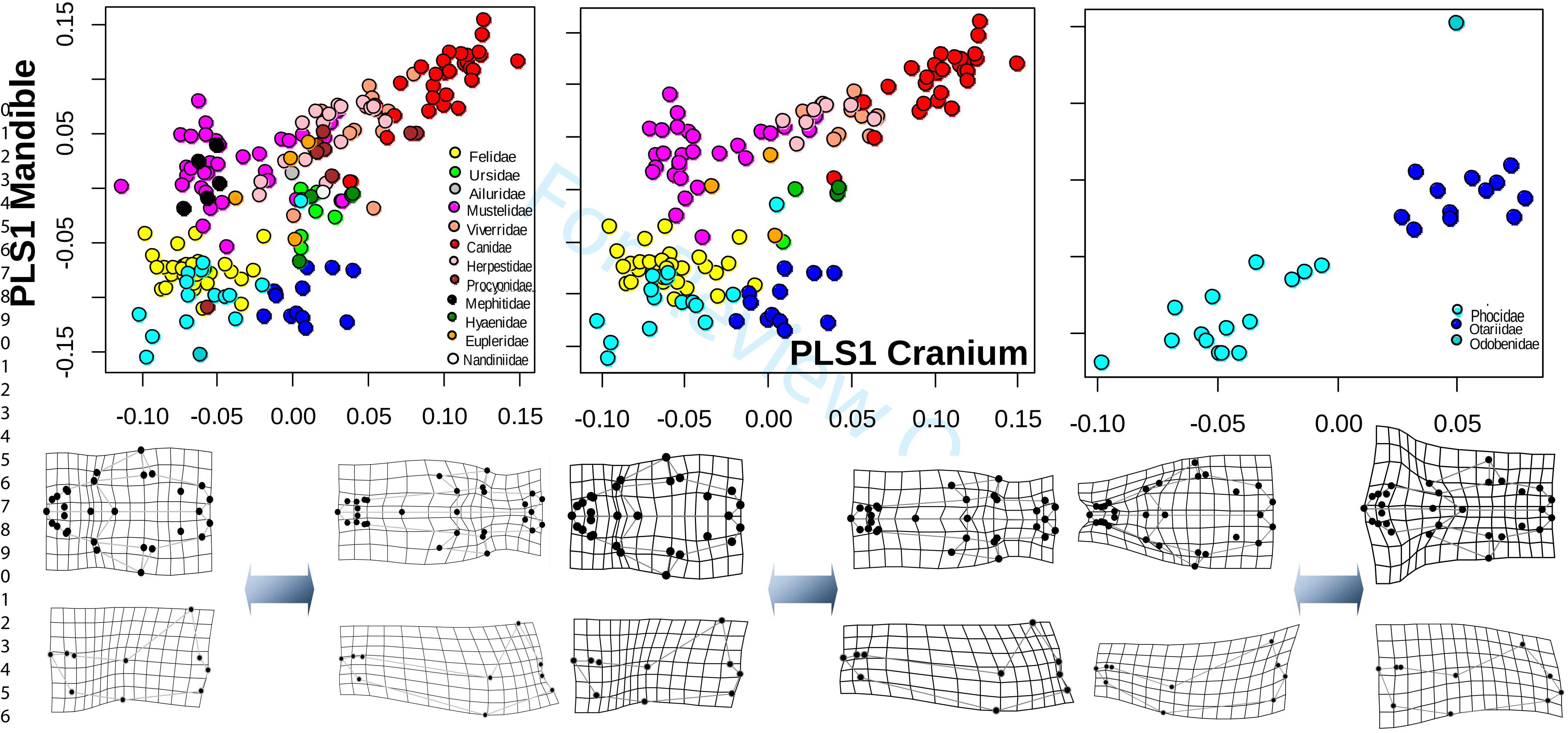
Figure 3. Scatterplot of evolutionary rates vs morphological disparity after phylogenetic correction following lambda (for shape) or kappa (for size) mode of evolution. Line of best fit is shown when association between the two variables was tested as statistically significant ($P < 0.05$).

Figure 4. Partial Least Squares of cranium vs mandible shape without phylogenetic correction to show taxonomic distribution and the respective thin plate spline PLS vector deformations on the total sample (left), subsample of predators (middle) and subsample of pinnipeds (right).


(A)
19
17
21
23
15
27
9
13
7
5
25
29
11
1
2
3
4
12
26
30
6
8
10
14
28
16
22
24
18
20
(B)
5
6
7
1
2
3
4
8
10
9


(A)
PC 2
PC 1
PC 3
0.15
0.1
0.05
0
-0.05
-0.1
-0.1
-0.05
0
0.05
-0.2
-0.1
0
0.1
0.2
Felidae
Ursidae
Ailuridae
Mustelidae
Viverridae
Otariidae
Canidae
Herpestidae
Procyonidae
Mephitidae
Hyaenidae
Eupleridae
Phocidae
Nandiniidae
Odobenidae
(B)
PC3-
PC2+
PC1+
PC1-
PC3+
PC2-
(C)
PC 2
PC 1
PC 3
0.1
0
-0.1
-0.15
-0.1
-0.05
0
0.05
0.1
0.15
-0.3
-0.2
-0.1
0
0.1
0.2
(D)
PC3-
PC2+
PC1+
PC1-
PC3+
PC2-


Cranium Shape
0.60
0.55
0.50
0.45
0.40
0.35
0.30
0.00E+00
5.00E-06
1.00E-05
1.50E-05
Mandible Shape
0.75
0.70
0.65
0.60
0.55
0.50
0.45
0.40
0.35
0.E+00
1.E-05
2.E-05
3.E-05
○ Small prey
○ Medium prey
● Large prey
● Omnivores
● Herbivores/Frug.
● Insectivores
● Crustaceans
● Molluscivores
● Piscivores
Morphological Disparity
Cranium Size
y = 7.1454x^0.0746
R² = 0.5277
5.80
5.60
5.40
5.20
5.00
4.80
4.60
4.40
4.20
4.00
0
0.005
0.01
0.015
0.02
0.025
0.03
Mandible Size
y = 9.2033x^0.1002
R² = 0.5336
7.00
6.50
6.00
5.50
5.00
4.50
4.00
0
0.01
0.02
0.03
0.04
Evolutionary Rate σ²


PLS1 Mandible
0.15
0.05
-0.05
-0.15
Felidae
Ursidae
Ailuridae
Mustelidae
Viverridae
Canidae
Herpestidae
Procyonidae
Mephitidae
Hyaenidae
Eupleridae
Nandiniidae
-0.10
-0.05
0.00
0.05
0.10
0.15
PLS1 Cranium
Phocidae
Otariidae
Odobenidae