Phylogeny and the Inference of Diet from Carnassial Shape across Carnivora

Alec J. Chiono*[1], Samantha S.B. Hopkins[2], and Samantha A. Price[1]
[1]Dept. of Evolution and Ecology, University of California, Davis
[2]Dept. of Geological Sciences, University of Oregon
*Presenter

© William Warby

© John Critchley

Abstract

The diet of carnivorans is commonly inferred from three linear measurements on the lower carnassial. Unfortunately, when phylogeny is taken into account, the dietary predictions made from these measurements lose significance. We therefore investigate an alternative method for inferring diet using geometric morphometrics. We identified 4 homologous landmarks on the occlusal view of both the upper and lower carnassial. Two axes of shape variation were found for each carnassial, all four displaying movements of landmarks that lead to the elongation of shearing surfaces. The phylogenetic signal within these traits is moderate across Carnivora but incredibly strong within the feliforms (cats and their relatives). Using phylogenetic discriminant function analysis to identify between hypercarnivores (meat), hypercarnivores (bone), mesocarnivores, and hypocarnivores, we found a high degree of dietary misclassification (32-50%), but the lower carnassial was better than the upper. Our results suggest different evolutionary trajectories for the two carnivoran suborders, with diet and phylogeny exceptionally tightly linked within feliforms. Moreover, these results suggest that current methods may not reliably estimate the diet of fossil carnivorans that are distantly related to extant groups. We are therefore investigating whether outlines of the lower carnassial will provide more reliable, phylogenetically-independent, estimates of diet.

Introduction

- Traditionally, to infer diet from carnassial morphology of carnivorans, three linear measurements of the lower carnassial have been used: the carnassial angle, the trigonid ratio, and the postcarnassial molar ratio. However, their explanatory power is greatly reduced when phylogeny is taken into account (Hopkins et al. in prep).

- Because phylogeny and ecology are tightly linked within the Carnivora, a reliable method for inferring diet in the absence of phylogenetic effects would be useful, especially when attempting to classify the diet of distantly related fossil species.

- Geometric morphometrics offers an alternative way to describe morphology, and has been successfully used to infer diet from mandibular shape of carnivorans (Meloro 2011). However, as individual fossil teeth are much more commonly found than complete jaws, we decided to investigate the ability to infer diet from geometric morphometric estimates of shape of the upper and lower carnassial.

Legend

	Hypercarnivore (meat)	Hypercarnivore (bone)	Mesocarnivore	Hypocarnivore	Symbol
Caniformia		No extant species			○
Feliformia					△

Methods

- We identified 4 homologous landmarks present across the Carnivora from the occlusal view of both the upper and lower carnassial, shown on the images to the right.
  - Upper: (1) protocone, (2) paracone, (3) metacone, (4) parastyle
  - Lower: (1) protoconid, (2) paraconid, (3) metaconid, (4) hypoconulid
- Photographs of 232 specimens of 125 extant terrestrial carnivorans were taken at the Museum of Vertebrate Zoology at UC Berkeley.
- Landmarks were digitized using tpsDig2 (Rohlf 2005) and aligned using Generalized Procrustes Analysis in the Geomorph package in R (Adams et al. 2013). The mean shape was calculated for each species with more than one specimen.
- Diet data was collected from the primary scientific literature, and if necessary from the secondary literature. Each species was classified into four dietary categories originally described by Van Valkenburgh (2007): hypercarnivore (meat), hypercarnivore (bone), mesocarnivore, hypocarnivore.
- Phylogenetic signal was estimated using the multivariate version of Blomberg's K (Adams et al. 2014) and the shape quantified using Principal Components Analysis.
- We estimated how well carnassial shape predicts diet using phylogenetic discriminant function analysis (Motani & Schmitz 2011).

Upper — lingual — posterior — anterior — buccal

Lower — buccal — anterior — posterior — lingual

Results & Discussion

Figure 1: Lower Carnassial Phylomorphospace
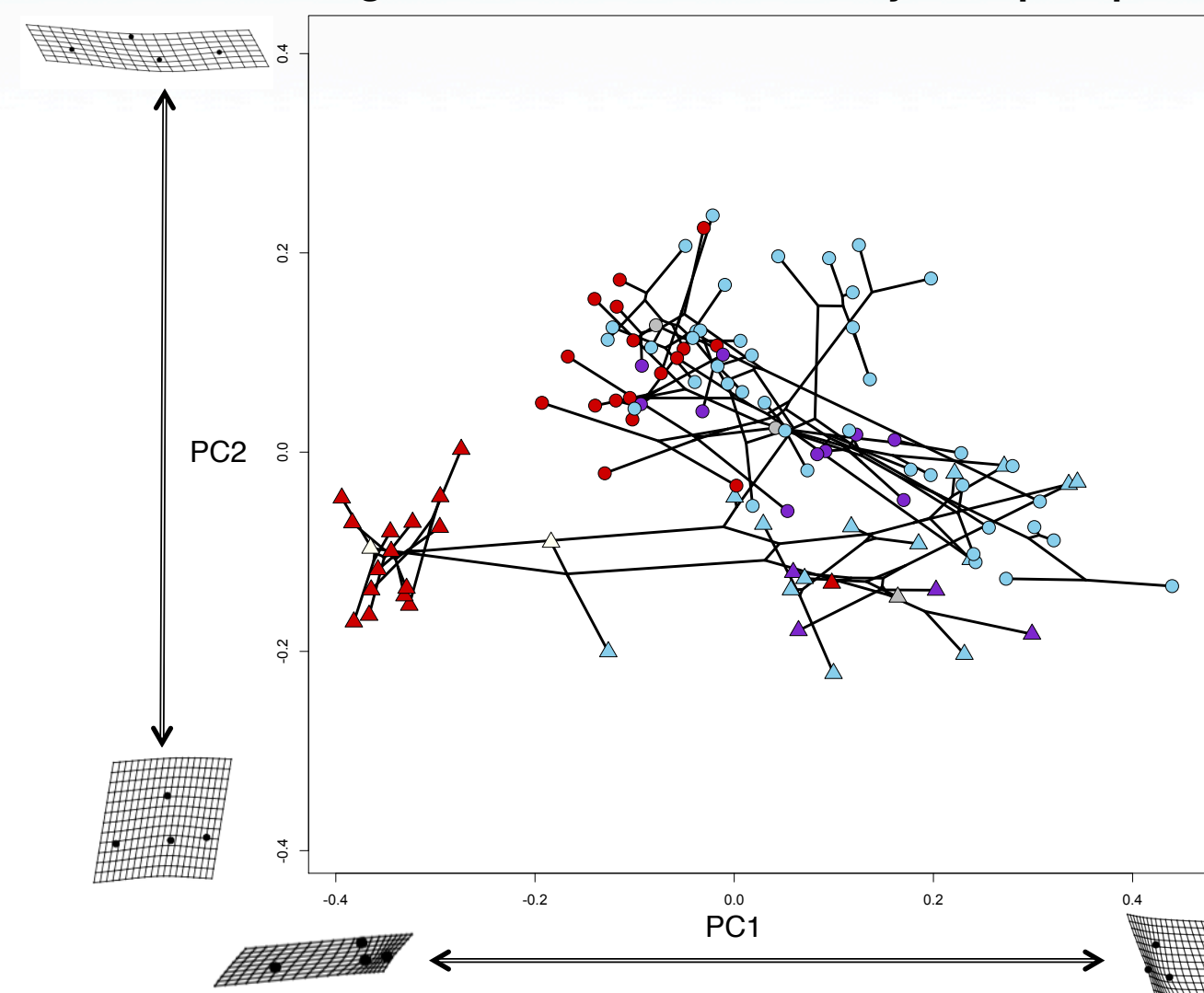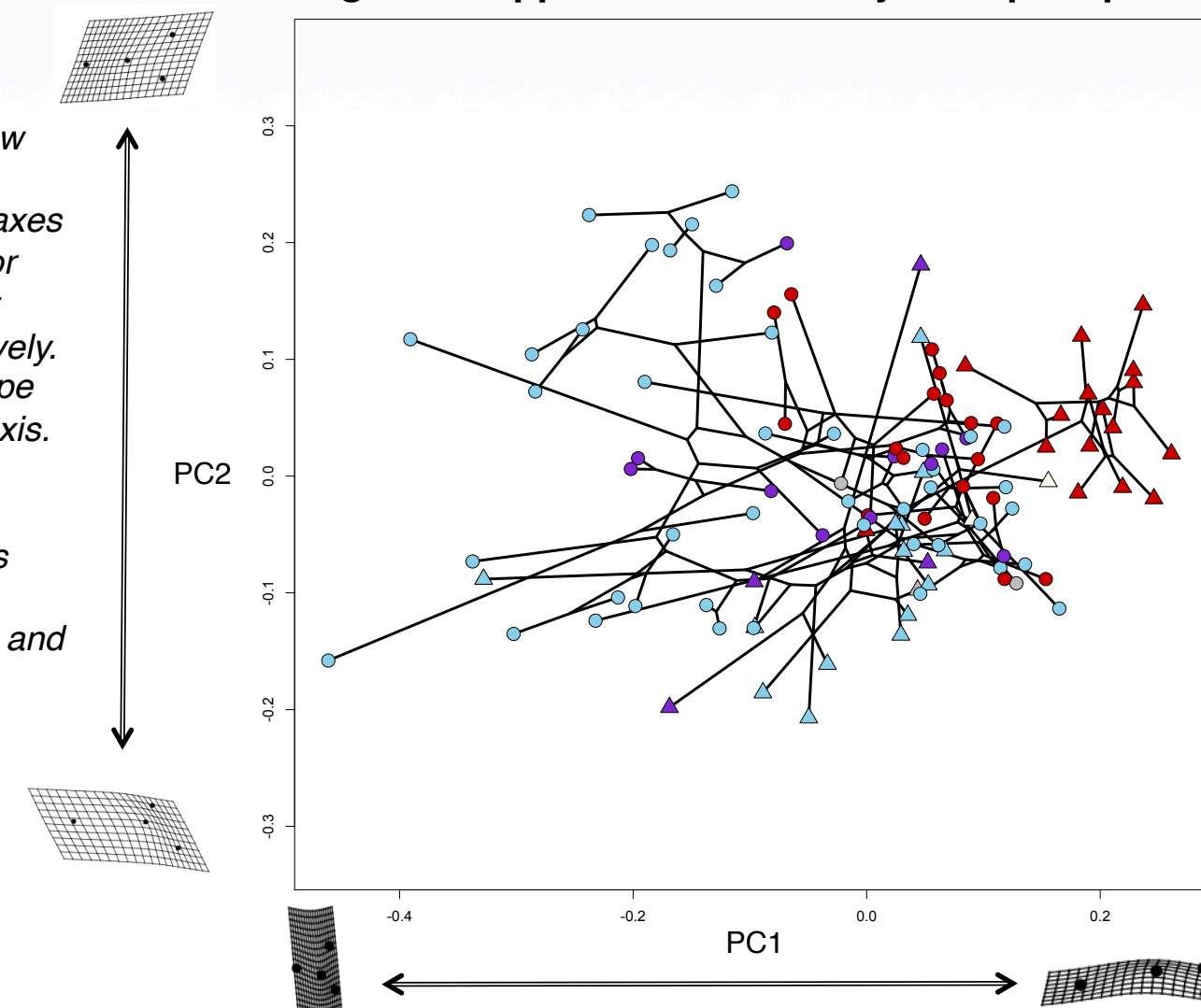

PC2 / PC1

Figure 2: Upper Carnassial Phylomorphospace

PC2 / PC1

Figures 1 and 2 show the distribution of species on the two axes of shape variation for the lower and upper carnassial, respectively. The changes in shape are given for each axis. Phylogenetic relationships are depicted by the lines connecting species. Color indicates diet, and shape indicates suborder.
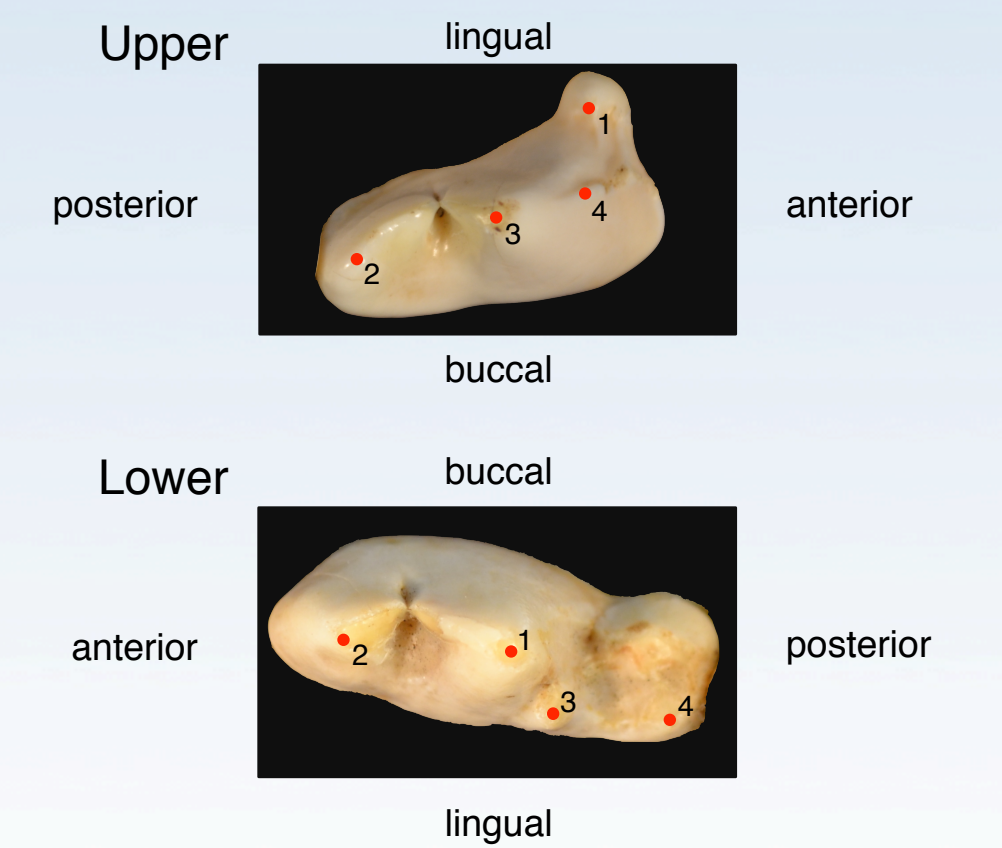
1. **Shape: we identified two axes of variation that lead to the elongation of shearing surfaces** in both the lower and upper carnassials (Fig. 1 & 2)
   - Lower: (PC1) reduction of the talonid and lengthening of the trigonid and (PC2) narrowing of the entire tooth. PC1 and PC2, together, account for 86% of shape variation.
   - Upper: (PC1) narrowing of the trigonid and lengthening of the talonid and (PC2) lengthening of the trigonid and shortening of the talonid. PC1 and PC2, together, account for 82% of shape variation.

   For the upper carnassial, both axes of shape variation explain changes in tooth morphology for feliforms and caniforms. However, for the lower carnassial, variation in the tooth morphology of feliforms is predominantly explained by PC1, while caniform variation is explained by PC1 and PC2.

2. **Phylogenetic signal: an intermediate but significant signal was present in carnassial shape across Carnivora.** Feliforms were found to have a much greater phylogenetic signal than caniforms and their lower carnassial exhibited a stronger phylogenetic signal than expected under Brownian motion (Table 1). Because of this difference in phylogenetic signals between the suborders, attempts at classifying diet may be more successful if the clades are analyzed separately.

Table 1: Multivariate Phylogenetic Signal

Group	Tooth	K (phylo. signal)	p-value
Carnivora	Upper	0.373	0.001
Carnivora	Lower	0.447	0.001
Caniformia	Upper	0.430	0.001
Caniformia	Lower	0.313	0.001
Feliformia	Upper	0.637	0.001
Feliformia	Lower	1.29	0.001

Estimated multivariate phylogenetic signal (K) (Adams et al. 2014) for both carnassials across Carnivora and the two suborders: Feliformia and Caniformia. Under Brownian motion K=1, therefore K<1 signifies that the tooth shape of closely related species are more different than expected under Brownian motion, and K>1 signifies that they are more similar than expected.

Table 2: Discriminant Function Analysis Misclassification

Group	Tooth	Phylo. Signal	Percent Misclass.
Carnivora	Upper	1	55.1%
Carnivora	Upper	0.1	50.5%
Carnivora	Lower	1	37.5%
Carnivora	Lower	0.1	40.4%
Caniformia	Upper	1	50.7%
Caniformia	Upper	0.1	46.5%
Caniformia	Lower	1	32.4%
Caniformia	Lower	0.1	35.3%
Feliformia	Upper	1	41.7%
Feliformia	Upper	0.1	25.0%
Feliformia	Lower	1	38.9%
Feliformia	Lower	0.1	25.0%

3. **Predicting diet: we found high rates of misclassification across the Carnivora**, whether we accounted for strong phylogenetic signal or not. When suborders were analyzed separately, percent misclassification for feliforms decreased substantially when ignoring phylogeny, but did not for caniforms. This stresses the strong linkage between phylogeny, tooth shape, and diet in the feliforms (Table 2).

Percent misclassification of diet estimated using phylogenetic discriminant function analysis for Carnivora as well as the individual suborders. For each clade, the percent misclassification is shown when assuming high (1) and a low (0.1) phylogenetic signal.

Carnassials of *Ursus arctos* — Upper / Lower

Carnassials of *Panthera pardus* — Upper / Lower

Caniformia / Feliformia

Conclusion

- The lower carnassial provides better estimates of diet than the upper carnassial. The percentage misclassified is lower than, and in one case equal to, the rates for the corresponding upper carnassial.

- Across Carnivora, phylogeny is linked to tooth shape and diet. This greatly reduces the utility of landmark geometric morphometrics to infer the diet of distantly related, extinct species. If phylogeny too greatly informs diet, then we may not reliably predict the diet of species that are not closely related to the extant species we have analyzed. However, because the phylogenetic signal is so strong within feliforms, we may be able to use simply phylogeny to predict the diet of extinct, but closely related, feliform species.

- Our ongoing efforts to identify a method to reliably and quantitatively classify diet across Carnivora are now focused on the use of geometric morphometric outlines. For both carnassials, the Principal Component Analysis revealed two prominent ways landmarks could move in order to achieve similar elongations of shearing surfaces. These patterns are strongly associated with phylogeny. We suspect that outlines may be able to ignore these landmark variations, and therefore have a weaker association with phylogeny. Not only could this provide a method of predicting diet of distantly related species, but it could potentially do so without the separate analysis of feliforms and caniforms.

References

- Adams, Dean C. "A Generalized K Statistic for Estimating Phylogenetic Signal from Shape and other High-dimensional Multivariate Data." *Systematic biology* (2014): syu030.

- Adams, Dean C., and Erik Otárola-Castillo. "geomorph: an R package for the collection and analysis of geometric morphometric shape data." *Methods in Ecology and Evolution* 4.4 (2013): 393-399.

- Hopkins, S.B. & Price, S. A. (in prep). "Testing the strength of evolutionary correlations between dental morphology and diet in extant Carnivora."

- Meloro, Carlo. "Feeding Habits of Plio-Pleistocene Large Carnivores as Revealed by the Mandibular Geometry." *Journal of Vertebrate Paleontology* 31.2 (2011): 428-446.

- Motani, Ryosuke, and Lars Schmitz. "Phylogenetic versus functional signals in the evolution of form–function relationships in terrestrial vision." *Evolution* 65.8 (2011): 2245-2257.

- Rohlf, F.J. (2005). tpsDig2, digitize landmarks and outlines, version 2/11/05. Department of Ecology and Evolution, State University of New York, Stony Brook, New York.

- Van Valkenburgh, Blaire. "Déjà vu: the evolution of feeding morphologies in the Carnivora." *Integrative and Comparative Biology* 47.1 (2007): 147–163.

- All photos are public domain unless noted otherwise