SHORT COMMUNICATION

Evolutionary ecomorphology of the Falkland Islands wolf *Dusicyon australis*

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ABSTRACT

The Falkland Islands wolf *Dusicyon australis* is an extinct canid that was once the only endemic terrestrial mammal to inhabit the Falkland Islands. There is still a puzzling picture of the morphological adaptations of this wolf that quickly evolved from its mainland fossil ancestor: *Dusicyon avus*. We employ a geometric morphometric approach to identify patterns of skull shape variation in extant canids and *Dusicyon* spp. The Falkland Islands wolf and its fossil ancestor show a more carnivorous feeding morphology than other South American foxes, and they cluster morphologically with jackals. This supports convergence in skull shape between *Dusicyon* and Old World canids, although the convergence is not as strong as that exhibited by their sister hyper and hypocarnivorous taxa.

Key Words: canidae, convergence, *Dusicyon*, mandible, skull.

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INTRODUCTION

The Falkland Islands wolf *Dusicyon australis*, also known as the warrah, was the only land mammal recorded in the Falkland Islands. It went extinct in approximately 1876, due mainly to human persecution. Recent DNA analyses found that the closest extant relative of the warrah is the maned wolf *Chrysocyon brachyurus* that inhabits mainland South America (Slater et al. 2009a). The wolf's closest fossil relative was *Dusicyon avus* (recorded in Brazil, Argentina and Chile from the late Pleistocene until 3000 years ago), which bore a close similarity to the *Lycalopex* foxes but possibly had a more carnivorous feeding morphology (Prevosti et al. 2011).

Previous morphological comparisons provided a puzzling evolution for the Falkland Islands wolf: Hamilton Smith (1839) was the first to classify this taxon in the genus *Dusicyon* and identified similarities with the coyote *Canis latrans* that were later confirmed by Huxley (1880). Pocock (1913) and Kraglievich (1930) compared *Dusicyon australis* with extant foxes of the genus *Lycalopex.* Other morphological interpretations include the classification by Cabrera (1931) of the warrah as *Canis antarticus,* and the analyses of Clutton-Brock et al. (1976) and Van Gelder (1978) suggesting that *Dusicyon* skull morphology was similar to that of *Canis* spp. Such a mosaic of evolutionary characters led us to question whether the morphology of the Falkland Islands wolf and its ancestor could be better interpreted by simultaneously comparing their cranial and mandibular shape with that of extant canids. Figueirido et al. (2013) demonstrated that crania and mandibles provide stronger insights into feeding adaptations of carnivores if interpreted in conjunction. By looking at these structures using a geometric morphometric framework, we aimed to test first, whether the warrah and its fossil relative show morphological similarities to Old World canid species in the cranium and the mandible; and second, whether such similarities are strong enough to support morphological convergence between distantly related canid lineages.

METHODS

We took standard photographs of skulls in ventral view and mandibles in lateral view for 130 specimens belonging to 25 wild canid species (Appendix S1). The software tpsDig2.17 (Rohlf 2015) was used to landmark these images: 15 landmarks were placed on the cranium and 21 landmarks on the mandibles (Fig. 1c, Appendix S2) to describe functionally the areas relevant to feeding adaptations (Meloro 2011; Meloro et al. 2015a).

Generalised Procrustes Analysis was employed to translate, scale and rotate separately the raw landmark coordinates of crania and mandibles (Rohlf & Slice 1990). Coordinates of multiple specimens were averaged per species and the two subsets of shape coordinates were combined to generate rotation-free shape variables inclusive of both the cranium and the mandible shape (the skull shape dataset; Adams 1999). A phylogenetic consensus tree with branch lengths expressing time of divergence was generated following the topology of Lindblad-Toh et al. (2005) and adding the fossil *Dusicyon avus* after Austin et al. 2013 (Appendix S3).

Phylomorphospace was employed to visualise patterns of shape variation between species and identify areas of potential convergence. Unweighted Pair Group Method with Arithmetic Mean (UPGMA) cluster analysis was subsequently performed on procrustes distances to identify patterns of cophenetic similarities in canid skull shape. Taxa potentially convergent with *Dusicyon* spp. were selected after inspection of the UPGMA tree. Convergence in the skull shape morphospace was tested by applying distance-based metrics recently introduced by Stayton (2015): C_1 quantifies the magnitude of the phenotypic distance between two lineages that is lost by subsequent evolution; C_2, C_3 and C_4 measure the degree of convergence (higher values represent higher convergence); C_5 counts the number of lineages entering a region of a convergent morphospace. These metrics were also computed on a selection of other emerging convergent taxa for comparison. Phylogenetic evolutionary rates were finally produced on skull shape coordinates to compare the lineage inclusive of the Falkland Islands wolf and its ancestor with other canid lineages (Adams 2014). Meloro et al. (2015b) recently demonstrated that this approach can be used to explain convergent patterns in carnivores' morphology. All the analyses were repeated on the cranium and the mandible shape datasets separately to confirm patterns observed by merging the two into the skull shape dataset.

RESULTS

A phylomorphospace of skull shape (Fig. 1a) showed the morphology of the bat-eared fox *Otocyon megalotis* to be substantially divergent from that of other species due to its relatively short rostrum and wide mandibular ramus (positive scores for Principal Component 1). Both *Dusicyon* spp. clustered in the central region of the morphospace together with Old World jackals (*Canis* spp.). Hypercarnivorous dogs including *Lycaon*, *Cuon* and the New World *Speothos* all had negative scores for Principal Component 2. This pattern of morphospace occupation persisted when cranium and mandibles were analysed separately (Appendices S4 and S5).

UPGMA cluster analysis showed clustering of the *Dusicyon* spp. with Old World jackals (Fig. 1b). The cluster had a high cophenetic correlation value (r = 0.887) and the position of *Dusicyon* spp. remained relatively unchanged when UPGMA trees were repeated for cranial and mandibular shape datasets (Appendices S6 and S7). Other emerging clusters included the hypercarnivore group *Lycaon*, *Cuon*, and *Speothos* and the hypocarnivores *Chrysocyon, Vulpes bengalensis,* and *Vulpes pallida*. The distance-based metrics supported convergence between *Dusicyon* and jackals in all datasets except the cranium, however convergence was low compared to that obtained for hyper- and hypocarnivorous (Table 1).

Phylogenetic evolutionary rates of skull shape data differed significantly among canid clades (σ ratio=2.421, P=0.025); the group "*Chrysocyon*, *Speothos*, *Dusicyon*" showed the fastest rate (σ = 1.52E-05), followed by "*Cerdocyon*, *Lycalopex*" (σ = 9.68E-06), then Old World Canini (σ = 9.59E-06) and the Vulpini tribe (σ = 6.26E-06, Appendix S8). This pattern emerged also in the cranial dataset, while for the mandible the sigma ratio was not significantly different from random expectation (Appendices S8 and S9).

DISCUSSION

Skull shape is often the result of a compromise between functional adaptation and phylogenetic constraint in the Carnivora. Canids appear to be no exception. By combining cranial and mandibular shape data, we provided support for morphological convergence between the South American *Dusicyon* spp. and the Old World jackals. These species were traditionally interpreted as generalist predators that show no particular modification in the cranium or the mandible when compared to hypercarnivorous dogs (Slater et al. 2009b). Our phylomorphospace confirms this: there is close clustering of *Lycaon*, *Cuon* and the New World *Speothos* due to their ability to generate high bite forces relative to their body weight (Damasceno et al. 2013). We also identified convergence between the maned wolf *Chrysocyon brachyurus* and two species of foxes (*Vulpes bengalensis* and *Vulpes pallida*). The skull shape of *Chrysocyon* is characterised by a relatively small zygomatic arch, small upper carnassial (P4, 4th premolar) and a narrow muzzle, traits unusual for such a large wolf (Bubadue et al. 2016): this could explain similarities with hypocarnivorous *Vulpes* spp. The relatively small dentition and wide angular process of the aberrant bat-eared fox *Otocyon megalotis* relates to a termite eating specialisation that requires quicker chewing cycles but low bite forces (Ewer 1973). In contrast, the centre ground of skull morphospace is occupied by generalist *Canis* and *Dusicyon* spp., characterised by a wide elongated muzzle, short zygomatic arch, large lower carnassial (m1, 1st molar) and thick elongated corpus mandibulae (Appendices S4 and S5). In all cases, their morphology differs substantially from those of Old World (*Vulpes* spp.) and New World (*Lycalopex* spp.) foxes. What could have generated such a pattern? We identified higher rates of evolutionary shape transformations in South American canids than in Old World Canini and Vulpini, thus supporting the morphospace invasion of *Dusicyon* into *Canis*, *Speothos* into hypercarnivores *Lycaon* and *Cuon*, and *Chrysocyon* into hypocarnivore *Vulpes* spp. Anecdotal observations by Darwin suggested that, in the Falkland Islands wolf, a relatively carnivorous diet might have evolved rapidly due to its isolation on an island with abundant marine mammals and nesting birds, later supplemented by the introduction of domestic animals (Quillfeldt et al. 2008). Prevosti et al. (2015) recently also predicted a carnivorous diet for the mainland *Dusicyon avus* that was probably capable of scavenging Pleistocene megafauna herbivores. Such a scavenging adaptation might have generated the substantial differentiation between the *Dusicyon* skull morphology and that of other South American foxes, although this divergence is not as extreme as found in the hypercarnivore *Speothos* and the hypocarnivore *Chrysocyon*.

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Figure Legends

Fig. 1. (a) Skull phylomorphospace for a sample of 25 species of canids. Deformation grids at the bottom show coordinated shape changes between crania and mandible from negative (left) to positive (right) Principal Component (PC) 1 vector scores. The white circles represent reconstructed ancestral shape coordinates in the phylomorphospace. Abbreviations: SA = South American; Falkland clade = *Chrysocyon* + *Speothos* + *Dusicyon*; OW = Old World; var. - variance. (b) UPGMA cophenetic tree based on Procrustes distances generated by skull shape data. Cophenetic correlation is 0.887. Colour code follows clade subdivision as in (a). (c) Cranium and mandible of Falkland Islands wolf showing the outlined landmark configuration (for details see also Appendix S2).

Tables

Table 1. Similarity-based measures of convergence and their P values for the groups: *Dusicyon* spp. and Old World jackals, hypercarnivores (*Lycaon*, *Cuon* and *Speothos*), and hypocarnivores (*Chrysocyon*, *Vulpes bengalensis* and *Vulpes pallida*). The first two Principal Components axes were used, from the whole skull shape dataset, and from the cranium and the mandible separately. Significance is highlighted in bold.

			C_1	C_2	C_3	C_4	C_5
Dusicyon spp. and jackals	Skull	Parameter	0.282	0.007	0.008	0.016	3.000
		P value	**0.043**	0.239	0.446	0.398	0.106
	Cranium	Parameter	0.271	0.008	0.009	0.016	4.000
		P value	0.055	0.205	0.389	0.384	0.075
	Mandible	Parameter	0.285	0.008	0.009	0.017	4.000
		P value	**0.043**	0.185	0.390	0.322	**0.051**
Hypercarnivores	Skull	Parameter	0.494	0.024	0.027	0.051	3.000
		P value	**0.011**	**0.002**	**0.015**	**0.009**	**0.001**
	Cranium	Parameter	0.270	0.017	0.020	0.035	4.000
		P value	0.102	**0.028**	0.054	0.053	**0.025**
	Mandible	Parameter	0.443	0.023	0.024	0.049	4.000
		P value	**0.025**	**0.007**	**0.031**	**0.015**	**0.001**
Hypocarnivores	Skull	Parameter	0.531	0.028	0.032	0.032	3.000
		P value	**0.019**	**0.015**	0.060	0.076	0.126
	Cranium	Parameter	0.654	0.033	0.038	0.039	3.000
		P value	**0.007**	**0.008**	**0.029**	**0.036**	**0.005**
	Mandible	Parameter	0.419	0.024	0.026	0.026	5.000
		P value	0.052	0.051	0.127	0.151	**0.030**

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 List of taxa and number of specimens whose crania and mandibles were included for morphometric analyses.

Appendix S2 Landmark configuration employed to describe cranial (a) and mandibular (b) shape.

Appendix S3 Information on phylogeny and divergence time dating.

Appendix S4 Phylomorphospace obtained for the cranium shape dataset.

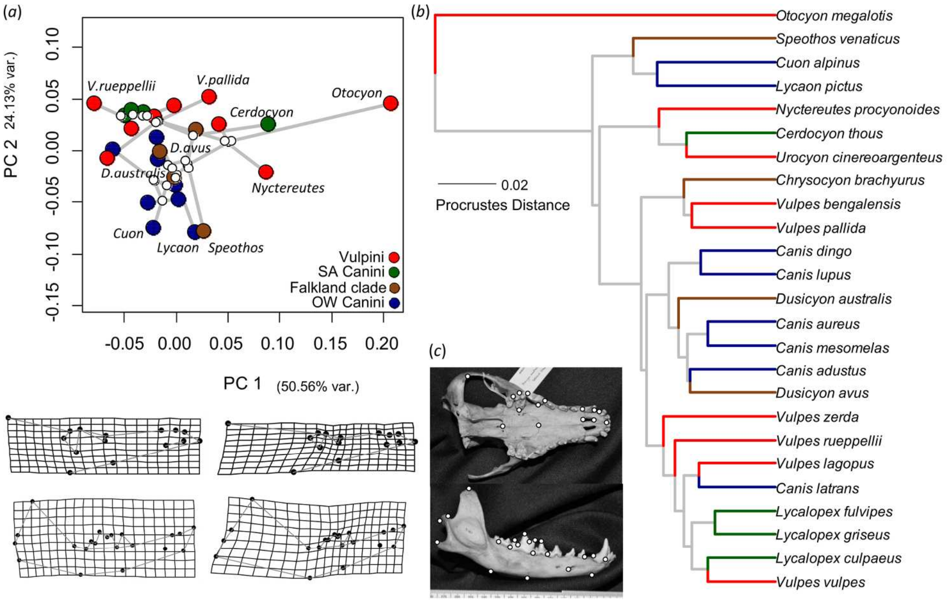
Appendix S5 Phylomorphospace obtained for the mandible shape dataset.

Appendix S6 UPGMA tree based on cranium shape data.

Appendix S7 UPGMA tree based on mandible shape data.

Appendix S8 Sigma evolutionary rates computed on skull, cranial and mandible shape data for different Canidae clades (a, b).

Appendix S9 Sigma evolutionary rates computed on skull, cranial and mandible shape data for different Canidae clades (a, b).



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