

# Morphofunctional patterns in Neotropical felids: species co-existence and historical assembly

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Extant felids are morphologically homogeneous, probably as a result of recent radiation and constraints from their predatory specializations. The Neotropical assemblage comprises 12 of the 41 extant felid species, which occupy all habitats available, with many species coexisting locally. We studied this assemblage on the basis of 31 craniodental variables reflecting morphofunctional variation, measured from 229 specimens representing all 12 species. Multivariate patterns were summarized allowing for phylogenetic covariation. Additional factors (geographical distribution, use of habitat and stratum, and activity pattern) were coded for each species. As expected, body size accounted for most variation, covarying with membership to three deep clades and, to a lesser extent, with large-scale geographic variation. The species tend to segregate in morphospace plus one or more factors (e.g. habits) that make interspecific overlap in niche space minimal. Using dated phylogenies, biogeographic history, and the fossil record, we reconstructed the historical assembly of the Neotropical felid guild. We found a pattern of successive invasions and speciation in which new lineages occupied previously vacant areas of morphospace, or new species occupied overlapping areas but with contrasting habits. This may be general among antagonistic species of historically structured guilds, and we predict similar patterns in other continents. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2010, **100**, 711–724.

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## INTRODUCTION

Extant felids are the top predators in most habitats worldwide (Wozencraft, 2005). As members of a distinct and relatively recent (Late Miocene) clade (Johnson *et al.*, 2006), felid species are remarkably homogeneous in morphology, and presumably also in function (Christiansen, 2008). Felids share a number of anatomical characters associated with the predation of vertebrates, such as a short rostrum, wide and strong zygomatic arches, strong canines, and reduced postcanines except for hypercarnivorous carnassials (Ewer, 1973). Many previous morphological studies of felids focused on phylogeny (Salles, 1992), taxonomy

(Werdelin, 1983), ecology including prey size preference (e.g. Meachen-Samuels & Van Valkenburgh, 2009), arboreal habits and adaptations to different habitats (e.g. Gonyea, 1978; Jenkins & McClearn, 1984; Hoogesteijn & Mondolfi, 1996), ontogeny and growth (Fagen & Wiley, 1978; García-Perea, 1996; Gay & Best, 1996; Giannini *et al.*, 2009; Segura & Flores, 2009), and biogeography (Meijaard, 2004). Only a few workers have attempted to understand morphofunctional structuring within felid assemblages. Kiltie (1984, 1988) compared tropical assemblages of felids from the Neotropics, Africa, and Asia with the goal of understanding interspecific size ratios in a competition context. Dayan *et al.* (1990) traced character displacement in Asian desert felids. More recent studies revealed differences between the morphologically homogeneous species of extant felids

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versus the highly divergent machairodontids (Christiansen, 2008; Slater and Van Valkenburgh, 2008). This study focuses on the morphofunctional structure of the Neotropical felid assemblage, which comprises 12 of the 41 extant species of felids (García-Perea, 1994; Wozencraft, 2005; Buckley-Beason *et al.*, 2006). These species belong to three distinct felid clades: the ocelot [*Leopardus pardalis*; (Linnaeus, 1758)] lineage (nine species of *Leopardus*), the puma [*Puma concolor* (Linnaeus, 1771)] lineage (two species of *Puma*), and the *Panthera* lineage, represented by the jaguar [*Panthera onca* (Linnaeus 1758)]. Neotropical felids inhabit environments from sea level to 5000 m a.s.l., from cloud- and rainforests to xeric savannas, high Andean steppes, Pampas grasslands, and swamps. These species broadly overlap geographically, and many of them coexist on a local scale (Oliveira, 1994).

Johnson *et al.* (2006) provided a comprehensive phylogenetic hypothesis of relationships among felids, also estimating the age and possible geographic origin and dispersal route of each lineage around the world. This generates the unprecedented opportunity to reconstruct the assemblage history of a guild like the Neotropical felids from a morphofunctional perspective. Felids were major participants in the Great American Biotic Interchange (GABI), invading South America in successive waves (Turner and Antón, 1997), speciating *in situ* (Mattern & McLennan, 2000; Johnson *et al.*, 2006), re-invading the source continent, North America (e.g. Culver *et al.* 2000; Eizirik *et al.*, 2001), and losing lineages to the Pleistocene extinctions (McKenna & Bell, 1997). This rich history probably affected the assembly of the extant felid guild in the Neotropics as we perceive it.

Here, we report morphofunctional variation of the skull in Neotropical species, and evaluate the role of large-scale geographic variation and phylogeny in shaping the observed variation. Next, we set out to reconstruct the assembly of the extant Neotropical felid guild by integrating morphofunctional patterns with historical information (clade membership and sequence of arrival), and ecological and biogeographical data. As a result, a pattern of species segregation at several levels emerges, which may be explained by the remarkable morphofunctional homogeneity among felid species and their antagonistic interactions, and may have parallels in the history of other continents.

## MATERIAL AND METHODS

### SAMPLE AND VARIABLES

We examined 229 skulls with a complete measurement data set, from the 12 currently recognized species of Neotropical felids (García-Perea, 1994;

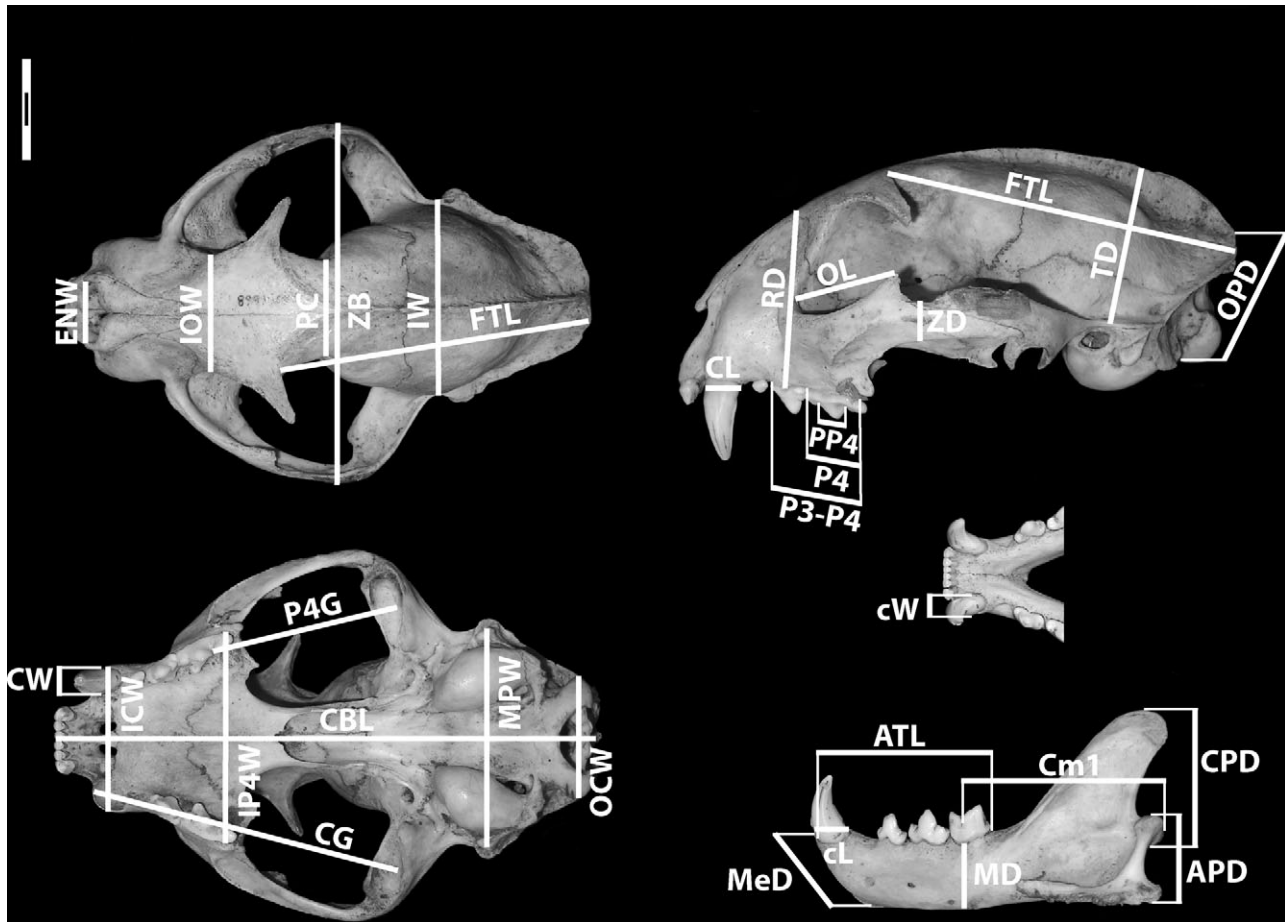
Wozencraft, 2005). Only wild adult specimens were used: these were recognized by a fully erupted permanent dentition. The list of specimens and their collection localities is provided in Appendix S1. The arrangement of genera follows that of Wozencraft (2005).

We defined 31 craniodental variables representing the size and shape of major structures of the felid skull, which were selected as descriptors of key skull dimensions and on the basis of presumed function (Fig. 1). Most of these variables were taken or modified from Biknevicius (1996), Gay & Best (1996), Giannini, Abdala & Flores (2004), and Werdelin (1983), and all are described in detail in the Appendix. In addition, we assigned each specimen to a Neotropical ecoregion, as defined by Brown *et al.* (2006; for Argentina), Ibisich & Mérida (2003; for Bolivia), the North American Mammals, Smithsonian Institution (2009; for Central and North America), and Archibold (1995; for the remainder of South American areas), adding a category for riparian environments that are important forest corridors in open areas. We included ecoregions representing the provenance of at least one of the specimens. These ecoregions were classified in three alternative schemes representing contrasting major habitat types or biomes (Fig. 2): (a) tropical wet forest scheme – all (including seasonal and montane) moist forests of the Neotropics, except the Patagonian temperate rainforests, versus all other habitats pooled; (b) wet forest scheme – all moist forest habitats, including the Patagonian temperate rainforests, versus all other habitats pooled; and (c) steppe and savanna scheme, with three categories – steppe, savanna (including dry forest), and wet forest (with the latter as defined in b).

### DATA ANALYSIS

In order to summarize morphometric variation, we performed a principal component analysis (PCA) based on a variance-covariance matrix of untransformed measurements for all 229 specimens. This analysis is expected to recover the variance structure of the data with minimal distortion (James & McCulloch, 1990). On the PCA ordination diagram we traced polygons joining conspecific individuals, and marking males, females, and specimens of unknown sex. A second PCA analysis was performed using variables corrected by the geometric mean (each species measurement divided by the  $n^{\text{th}}$  root of the product of values of a species vector of  $n$  variables) in order to correct for overall size effect, as used in Meachen-Samuels & Van Valkenburgh (2009).

A subset of the 191 specimens that were positively assigned to an ecoregion as defined above was subject to three additional multivariate analyses. First, we



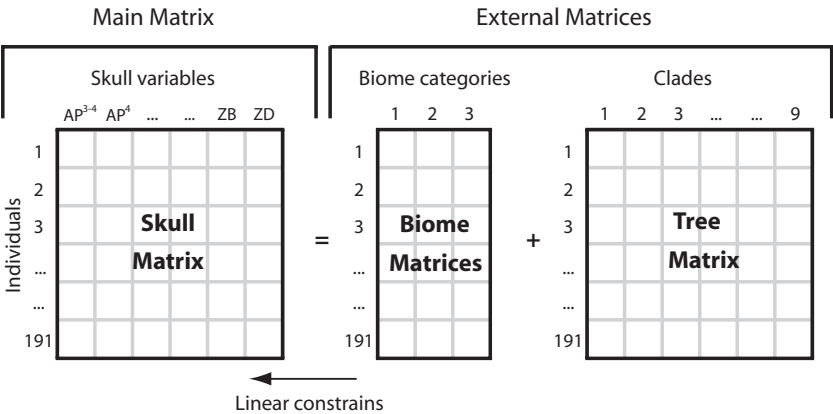
**Figure 1.** Morphological variables measured in specimens of Neotropical felids shown on a *Leopardus pardalis* skull (CBF 4668). For definitions and descriptions see Appendix. Scale 10 mm.

carried out a redundancy analysis (hereafter RDA; Rao, 1964; ter Braak, 1995) to test whether large-scale geographic variation (major biome types) was associated with a fraction of the morphometric variation. RDA is an ordination technique deriving from PCA, with a linear constraint represented by explanatory variables of an external matrix (see details in ter Braak, 1995; Fig. 3). In our study the main matrix is represented by 191 specimens from 12 felid species  $\times$  31 morphofunctional cranial variables, hereafter termed the 'skull matrix'. The external matrix is represented by the assignment of the 191 specimens to each of the categories from the biome classifications, hereafter termed the 'biome matrix'. Each scheme of biome classification (see above) was tested separately. Significance was evaluated using 4999 unrestricted Monte Carlo permutations for individual biome categories, using forward stepwise addition when appropriate (i.e. in the case of the steppe and savanna scheme, with more than two categories). In all cases the alpha level of significance was set to 0.01.

We used a phylogenetic comparative method, canonical phylogenetic ordination (CPO; Giannini, 2003), to determine the morphofunctional variation explained by historical factors (phylogeny), and its covariation with other factors (biomes). CPO is a form of canonical ordination that uses the nested set of clades to which the taxa of the main matrix belong as an external matrix. In this application, CPO was a variance-covariance RDA, again with the skull matrix as the main matrix (Fig. 3). The external matrix consisted of a set of binary variables coding the clade membership of each individual and species, hereafter termed the 'tree matrix'. We used the tree from Johnson *et al.* (2006) as a reference to construct our tree matrix, pruned to include only Neotropical taxa, to define clade variables 1–9, as shown in Figure 4. To this pruned tree we added two species not included in Johnson *et al.* (2006): Pantanal cat [*Leopardus braccatus* (Cope, 1889)] and Pampas cat [*Leopardus pajeros* (Desmarest, 1816)], which are taxonomic splits of colocolo [*Leopardus colocolo* (Molina, 1782)] (García-Perea, 1994). We placed these species in a

Ecoregions	a	b	c
Delta and islands of the Paraná River <sup>2</sup> Dry forests of Chiquitania <sup>3</sup> Paraná Rainforest <sup>2</sup> Petén-Veracruz Moist Forests <sup>4</sup> Riparian Environments Sierra Madre de Oxaca Pine-oak Forests <sup>4</sup> Southwestern Amazonian Forests <sup>3</sup> Talamancan Montane Forests <sup>4</sup> Tropical Forests <sup>1</sup> Yungas Rainforests <sup>2</sup>	Tropical Wet Forest	Wet Forest	Wet Forest
Patagonian Temperate Rainforests <sup>2</sup>			
Cerrado <sup>3</sup> Chaco Dry Forest <sup>2,3</sup> Espinal <sup>2</sup> Flooding savannas <sup>3</sup> Jalisco Dry Forests <sup>4</sup> Monte Desert <sup>4</sup> Sinalcan Dry Forests <sup>4</sup> Tamaulipan Mezquital <sup>4</sup> Tropical Savannas <sup>1</sup>	Not Tropical Wet Forest	Not Wet Forest	Savanna
Arid Regions <sup>1</sup> High Andes <sup>2</sup> Pampas <sup>2</sup> Patagonian steppe <sup>2</sup> Puna <sup>2</sup> Southern Puna Highlands <sup>3</sup> Temperate Grasslands <sup>1</sup> Western Gulf Coastal Grasslands <sup>4</sup>			

**Figure 2.** Classification of ecoregions in three distinct schemes grouping different biomes (see text). 1, Archibold (1995); 2, Brown *et al.* (2006); 3, Ibisich & Mérida (2003); 4, the North American Mammals, Smithsonian Institution (2009).



**Figure 3.** Scheme of the ordination methodology followed in this study (see text). For simplicity, only the biome matrix (from the steppe and savanna scheme, see text) is represented.





the literature (e.g. Mattern & McLennan, 2000; Sunquist & Sunquist, 2002, 2009). The relative importance of each factor in the segregation of species within the assemblage was estimated by the simple ratio of the number of times a factor appeared in a cell of Table 1, and the number of total possible interactions among the 12 species of felids (66 pairwise comparisons). As an example, the species pair formed by *L. colocolo* and *L. braccatus* can be differentiated by geographic distribution (D in Table 1), so this pair contributed to our estimation of the importance of distribution in discriminating cat species overall: the relative importance of D was 25%. Note that factors are not exclusive, so for instance distribution and size can both differentiate members of a species pair, thus contributing to the score of each factor.

## RESULTS

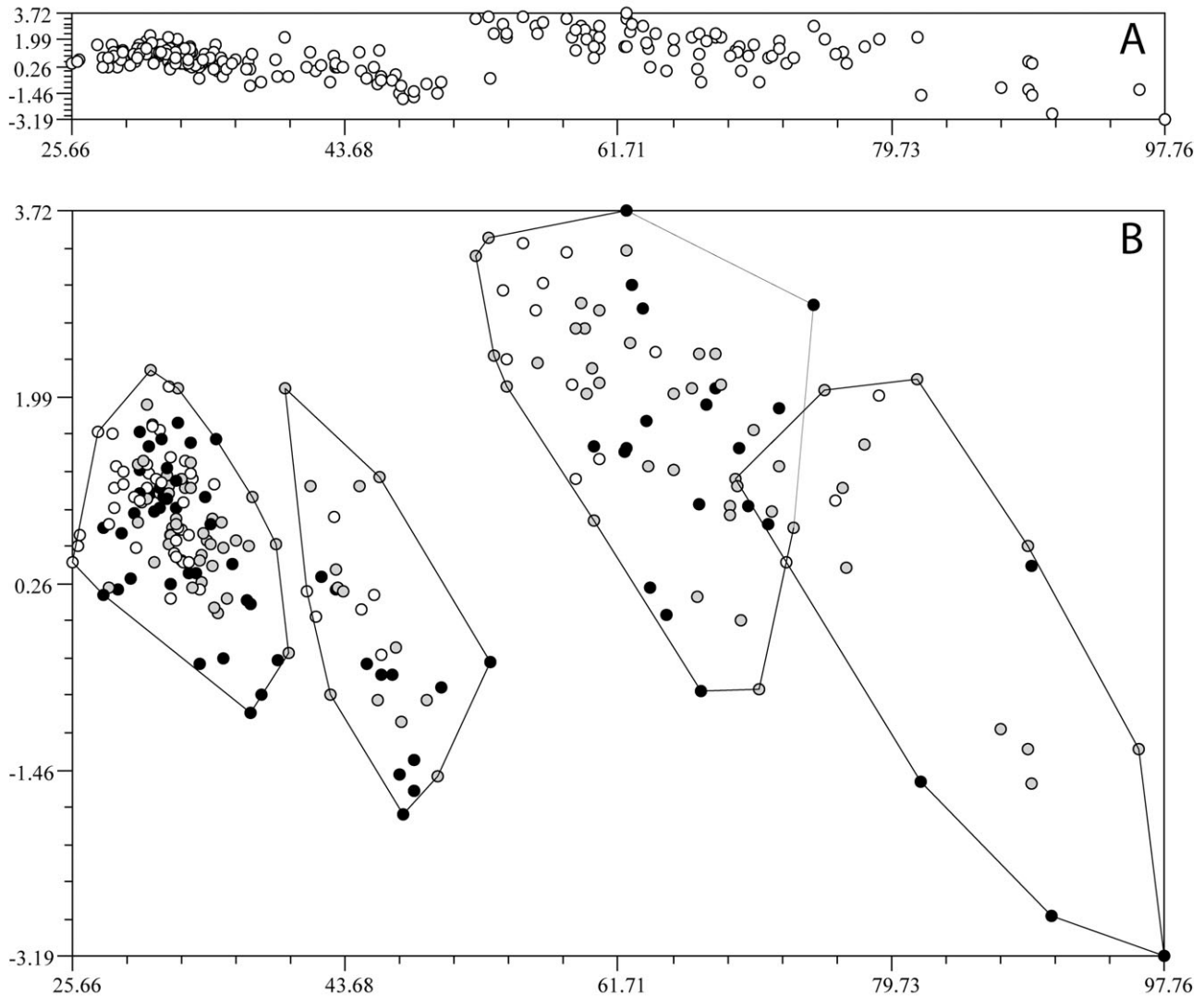
### MORPHOFUNCTIONAL PATTERNS

The first PCA axis (PC1) explains almost all of the morphofunctional variation in the data (> 98%; Table 2). All variables are positively correlated with PC1 and depict a nearly continuous interspecific gradient of body size (Fig. 5A; Table 2). The width of the postorbital constriction (PC) and the length of the fossa temporalis (FTL) showed the highest loadings in the positive and negative ends of PC2, respectively. These variables reflect variation in the space available for the origin of the temporalis muscle, and therefore PC2 represents a residual index of relative bite force among individuals of similar size. That is, individuals with similar PC1 scores should have stronger bite forces if they lie towards the negative end of PC2 (with a smaller postorbital constriction and a longer fossa temporalis), and vice versa. A third variable, the intercanassial width, also showed a high positive score in PC2: i.e. individuals at the positive end of PC2 exhibit a wide posterior palate. The normalized (scaled to unit eigenvector) plane of axes 1 and 2 reveals a diagonal pattern of variation. The strong negative slope of the long axis of species' polygons probably reflects allometric components of the size variation, affecting each species in a similar fashion (Meachen-Samuels & Van Valkenburgh, 2009). Three clear groups of specimens were evident: the small Neotropical cats, the mid-sized *Leopardus pardalis* and the two largest Neotropical species (*Puma concolor* and *Panthera onca*). There was no overlap in morphospace among these groups. Males of the majority of species (closed circles in Fig. 5B) tended to appear in the bottom-right corner of the corresponding species polygon (large individuals with a stronger bite force), whereas females (open circles in Fig. 5B) tended to locate in the top-left corner (the

**Table 2.** Results of principal component analyses: loading of each variable on the first three axes extracted and the corresponding eigenvalues, percentage of total variation per axis, and cumulative percentage of successive axes (% ac.). For a list of definitions of the variables, see the Appendix

Variables	Axes		
	I	II	III
APD	8.09	0.01	0.81
ATL	19.48	0.97	-1.32
CBL	44.99	-0.87	-1.35
CG	32.09	-0.53	-0.54
CL	4.66	0.04	-0.42
cL	4.35	0.14	-0.40
Cm1	17.88	-1.37	0.31
CPD	13.41	-0.58	0.26
CW	3.86	0.16	-0.21
cW	3.17	0.05	-0.28
ENW	8.68	0.72	0.20
FTL	27.38	-2.82	0.74
ICW	15.76	0.90	-0.18
IOW	10.43	0.62	0.78
IP4W	20.08	2.26	0.42
IW	19.67	1.43	-0.37
MD	6.93	-0.22	-0.19
MeD	12.70	-0.11	-1.00
MPW	19.59	0.37	-0.22
OCW	8.42	0.48	0.00
OL	7.88	1.15	1.37
OPD	15.33	-0.51	-1.48
P3-P4	9.59	1.41	-0.20
P4	5.33	0.80	-0.20
P4G	18.38	-1.41	0.31
PC	6.61	2.80	-0.61
PP4	2.17	0.36	-0.03
RD	19.82	1.18	1.02
TD	16.18	-1.03	0.43
ZB	36.10	0.37	1.83
ZD	5.45	0.73	0.62
Eigenvalues			
$\lambda$	9491.68	38.74	17.33
%	98.57	0.40	0.18
% ac.	98.57	98.97	99.15

statistical significance of these dimorphic trends was not assessed because of the low sample size for most species). *Leopardus guigna* Molina, 1782, *L. pajeros*, and *Puma yagouaroundi* (É. Geoffroy Saint-Hilaire, 1803) seem not to respond to this general dimorphic trend, with *Leopardus wiedii* (Schinz, 1821) showing the greatest gender overlap. The size-corrected PCA (Figure S1; Table S1) showed a similar pattern of variation (i.e. the same basic ordering of species) with two differences: a greater interspecific overlap and an



**Figure 5.** Ordination diagram of the principal components analysis. A, specimen scores scaled proportionally to the variation of each axis ( $\lambda_i^{0.5}$  for the  $i$ th PC axis, with  $\lambda$  representing the  $i$ th eigenvalue). B, normalized ordination diagram (specimen scores scaled to unit eigenvector). Females (open circles), males (black solid circles) and specimens of unknown sex (gray solid circles) are indicated. From right to left, polygons enclose specimens of jaguar, puma, ocelot, and small felids.

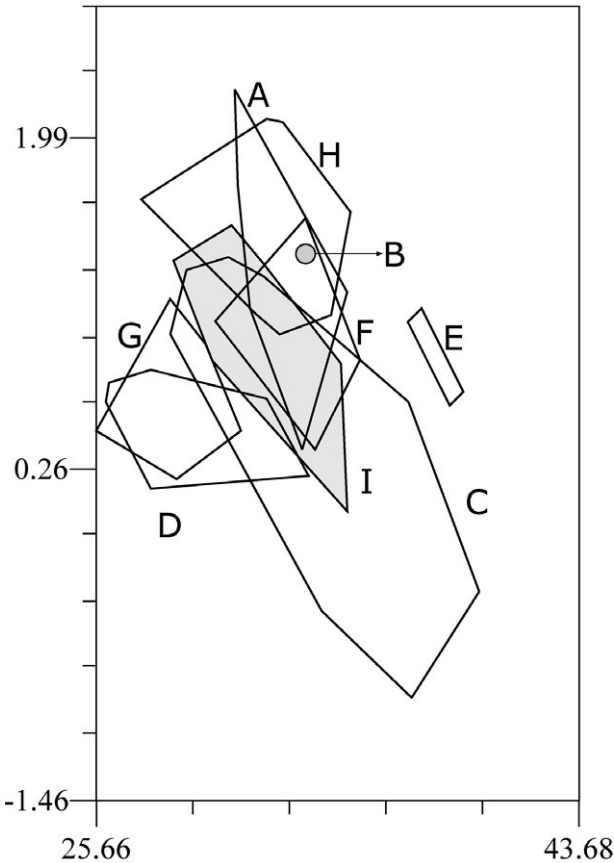
expanded space occupied by *Leopardus geoffroyi* (d'Orbigny and Gervais, 1844), which reflects the high phenotypic plasticity of this species.

#### INTERSPECIFIC OVERLAP AND SEGREGATION

Small cats exhibited a large degree of interspecific overlap in the PCA plot (Fig. 6). However, most pairs or triads of closely related species were clearly segregated in morphospace (Fig. 7A–C). Specifically, *Puma concolor* and *Puma yagouaroundi* (Fig. 7A), *L. pardalis* and *L. wiedii* (Fig. 7B), and the narrowly overlapping *L. geoffroyi*, *Leopardus tigrinus* (Schreber, 1775), and *Leopardus guigna* (Molina, 1782; Fig. 7C), which

partially segregate geographically. By contrast, members of the colocolo group overlap extensively in morphospace (Fig. 7D), but are clearly separated geographically.

The primary source of segregation among all possible species pairs was morphology (either size or bite force; *c.* 83% of pairs). Habitat preference explained *c.* 35% of segregation within species pairs. Meanwhile, activity pattern and habits, as well as geographical distribution, were primarily important in segregating the highly overlapping jaguarundi (*Puma yagouaroundi*), margay (*L. wiedii*), and kodkod (*L. guigna*) from the remaining species of the assemblage.



**Figure 6.** Normalized ordination diagram of principal components analysis zooming in on the area of small Neotropical felids to show patterns of overlap and segregation. Individuals from each species are enclosed in a polygon. Notice the morphofunctional overlap among small Neotropical felids. Abbreviations: A, *Leopardus braccatus*; B, *Leopardus colocolo*; C, *Leopardus geoffroyi*; D, *Leopardus guigna*; E, *Leopardus jacobita*; F, *Leopardus pajeros*; G, *Leopardus tigrinus*; H, *Leopardus wiedii*; I, *Puma yagouaroundi*.

**REGIONAL AND HISTORICAL PATTERNS**

The RDAs using biome matrices resulted in only one classification, the steppe and savanna scheme, significantly explaining some fraction of the morphometric variation, albeit modestly (6.5% of total inertia). This scheme was subsequently used in partial CPO analysis. We first tested phylogenetic groups individually: almost all clades were significant at the  $\alpha = 0.01$  level (Table 3). After selection the reduced tree matrix successively incorporated the *Leopardus* clade (marked 2 in Fig. 4), followed by the basal split that separates specimens of *Panthera onca* from the remainder of the sample (clade 1), and finally the tree partition that separates margay + ocelot within *Leopardus* (clade 3; Table 3). In the partial CPO, the biome matrix was tested using clades 1, 2, and 3 as covariables. We

**Table 3.** Results of canonical phylogenetic ordination for the Neotropical felid assemblage. Total variation explained by the final model (after forward stepwise selection of variables) is 66.3%. Clades are numbered as in Figure 3.

Test	Clade	Variance %	F value	P
Individual	1	34.1	98.3	0.0002
	2	49.4	184.6	0.0002
	3	2.2	4.3	0.0376
	4	32.9	92.6	0.0002
	5	4.7	9.1	0.0024
	6	21.9	53.1	0.0002
	7	4.6	9.2	0.0028
	8	15.5	34.8	0.0002
	9	18.5	42.8	0.0002
Forward stepwise	2	50.0	184.6	0.0002
	1	14.1	72.7	0.0002
	3	2.2	11.7	0.0010
	5*	n/a	0.4	0.5426

\*Not included in the forward stepwise selection process ( $P > 0.01$ ).

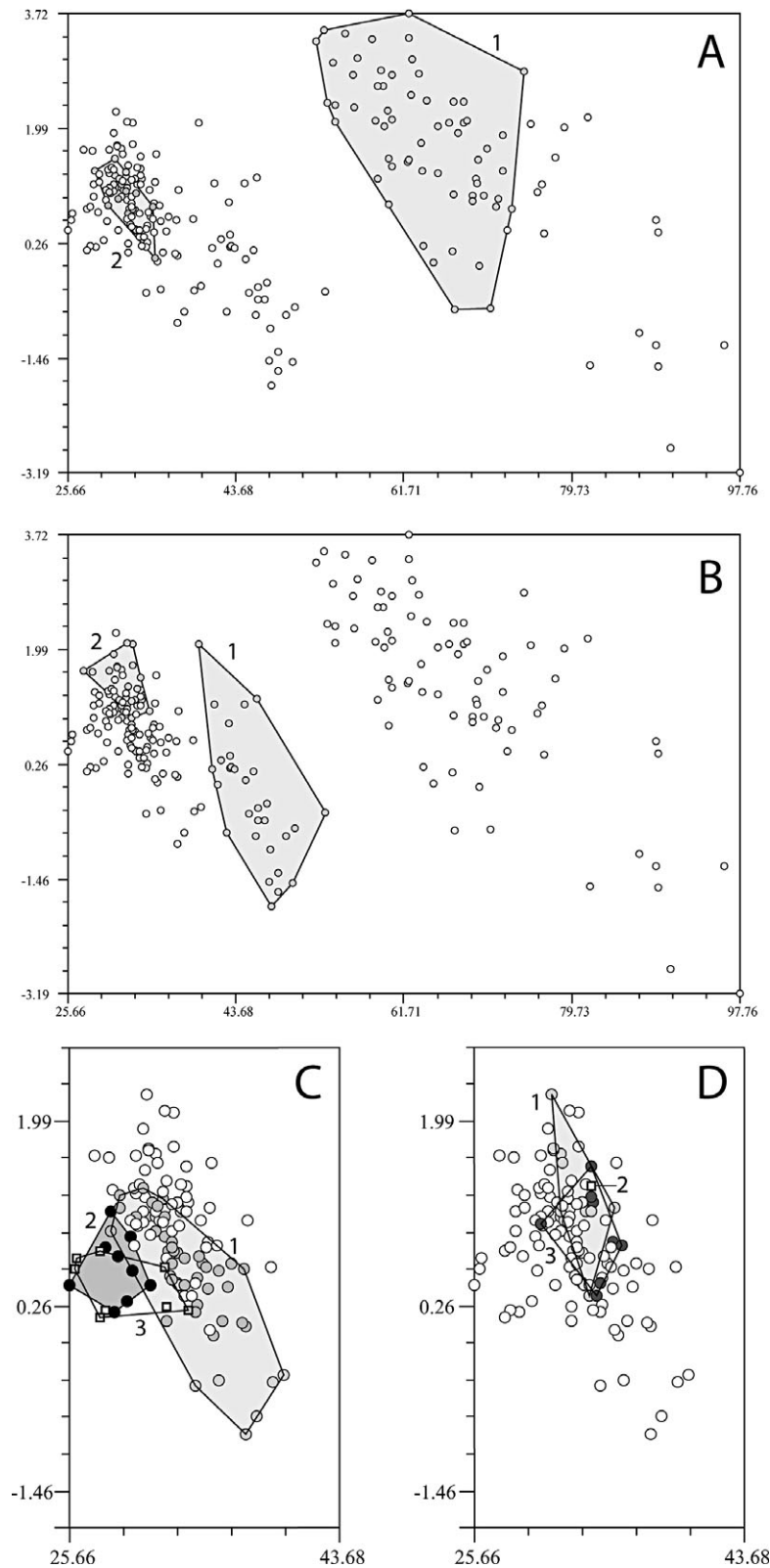
detected a small but still significant fraction of morphofunctional variation associated with biomes that was independent of phylogeny ( $F = 5.12$ ,  $P = 0.005$ ).

DISCUSSION

**MORPHOMETRIC VARIATION IN REGIONAL AND HISTORICAL CONTEXTS**

As seen in other interspecific morphological analyses of the felid skull (Christiansen, 2008; Kiltie, 1984, 1988; Werdelin, 1983), the Neotropical assemblage is essentially size-structured. This is an expected result given that the felid skull exhibits a remarkable interspecific homogeneity, functionally associated with a uniform bite (Christiansen, 2008). However, the specific impact of this size-dominated pattern on assemblage structure is not well understood. If apart from allometric scaling all felids look alike, widespread species coexistence at the regional and local scales requires specific explanatory mechanisms (see below). Our analysis also reveals more subtle variation related to bite force. At the intraspecific level, males have a narrower postorbital constriction and a longer temporal fossa, as compared with females (Fig. 5B), and consequently have a stronger bite force through the action of the *musculus temporalis* (Moore, 1981). These results concur with the intraspecific findings of Gay & Best (1995) for the puma, Hoogesteijn & Mondolfi (1996) for jaguar, and agrees with the sexual dimorphism noted for Geoffroy's cat (*L. geoffroyi*; Ximenez, 1975), ocelot (Murray & Gardner, 1997), and oncilla (*L. tigrinus*; Sunquist & Sunquist, 2009).





**Figure 7.** Phylogenetic segregation in morphospace between sister species or among triads of closely related species (see text). A, (1) *Puma concolor* and (2) *Puma yagouaroundi*. B, (1) *Leopardus pardalis* and (2) *Leopardus wiedii*. C, (1) *Leopardus geoffroyi*, (2) *Leopardus guigna*, and (3) *Leopardus tigrinus*. D, (1) *Leopardus braccatus*, (2) *Leopardus colocolo*, and (3) *Leopardus pajeros*.

It also agrees with the less marked sexual dimorphism noted in margay (Oliveira, 1998a), the species with greater gender overlap in morphospace in our study, and with a varying geographic pattern of sexual dimorphism in jaguarundi (Oliveira, 1998b). As suggested by Dayan *et al.* (1990), sexual dimorphism is likely to be important in resource partitioning among felids. In the Neotropical assemblage, sexual dimorphism appears to structure a modest fraction of the morphofunctional variation (contributing to PC2 in Fig. 5B).

Our results suggest that relatively old events of cladogenesis had a lasting effect on the shaping of the extant Neotropical felid guild. Results from CPO indicate that basal splits in the pantherine and *Leopardus* tree partitions, plus the speciation event that originated the ocelot and margay, significantly explained up to two-thirds of the morphological variation observed in the skull of Neotropical felids. This deep time imprint on the present-day relationships in morphospace represents inherited phylogenetic structure co-varying with morphofunctional traits that have direct impact on the observed guild structure of Neotropical felids. By contrast, large-scale spatial variation (morphological differences associated with individuals from different biomes) played a relatively minor role in structuring the felid morphospace.

#### PATTERNS OF OVERLAP AND SEGREGATION

Overlap in the skull morphospace is interpreted as morphofunctional similarity. Here we dissect patterns of segregation in morphospace, first among closely related species, and next within phylogenetically heterogeneous groups of species that overlap in morphospace.

Closely related species show a clear pattern of almost complete segregation in morphospace (Fig. 7A–C). The morphofunctional overlap among *L. geoffroyi* versus *L. guigna* and *L. tigrinus* is limited, as is the overlap of their geographical distribution in the wild. The morphological overlap between kodkod and oncilla is large, but these species are completely separated geographically. Species in the colocolo group overlap extensively in morphospace, but, notably, all three species are allopatric.

Morphofunctional variation, chiefly size and bite force, arises in > 80% of the possible pairwise differences among species (Table 1). The remainder of species pairs segregated in habitat preference, geographical distribution, habits, or activity pattern, in that order (Table 1). Habitat preference was the second most frequent differential factor among Neotropical species, occurring in *c.* 35% of the possible pairwise comparisons between species. There are four species of primarily forest cats (*L. guigna*, *L. pardalis*,

*L. tigrinus*, and *L. wiedii*), and six species distributed primarily in open areas [*L. braccatus*, *L. colocolo*, *L. geoffroyi*, *Leopardus jacobita* (Cornalia, 1865), and *L. pajeros*], with *Puma concolor*, *Puma yagouaroundi*, and *Panthera onca* occurring in both types of habitats (at least historically). Forest cats do not overlap morphologically, excepting oncilla and kodkod, which are allopatric, whereas felids from open areas overlap extensively in morphospace, but again show geographic and habitat segregation.

Habits and activity pattern were important factors for only two species: margay and jaguarundi, respectively. Arboreality in margay is notable within the family, and most of the prey items listed in its diet are arboreal prey (Sunquist and Sunquist, 2002, 2009; Oliveira, 1998a, contra Wang, 2002). Kiltie (1984) found that jaguarundi and margay were cranially almost identical, and suggested that these species segregated by means of a differential use of stratum reflected in the postcranium and their locomotor habits. In addition, the jaguarundi is predominantly diurnal (Konecny, 1989; Oliveira, 1998b), which is in strong contrast with all other Neotropical felids. This seems to be a key ecological character given that the jaguarundi extensively overlaps morphofunctionally with many small Neotropical cats (see the next section for further discussion).

Geographical distribution appeared as a segregating factor in *c.* 25% of the possible pairwise interactions among Neotropical cats (Table 1). Of these, 50% corresponded to *L. guigna* versus other cats, so distribution per se seemed to play only a limited role at the assembly level, although it may be key among species from open areas (e.g. in the colocolo group).

#### ASSEMBLING THE NEOTROPICAL FELID GUILD

We detected both phylogenetic and ecoregional structuring in correlation with morphofunctional variation in the Neotropical felid guild. Here we develop a series of hypotheses that may explain coexistence in the Neotropical regional assemblage as a function of clade membership and sequence of arrival from North America, as well as ecological and biogeographical factors.

The first felids to invade the Neotropics gave rise to the ocelot lineage, currently composed of nine species, the ancestor of which is dated to around 5 Mya (Early Pliocene; Johnson *et al.*, 2006). The fossil record does not directly contradict the molecular dating; however, the first undisputed appearances of felids, '*Felis*' *vorohuensis* and *Leopardus pajeros* (= *L. colocolo*), are more recent, dating from the Middle Pleistocene (latest Ensenadan 0.78–*c.* 0.5 Mya, both from the Pampean region of Argentina; Prevosti, 2006). '*Felis*' *vorohuensis* has been considered close to the ancestral

stock of the ocelot lineage (Seymour, 1999; Prevosti, 2006). The ocelot lineage radiated within the Neotropical region (Johnson *et al.*, 2006), occupying all habitats available while demonstrating relatively modest morphofunctional variation (small-to-mid-sized cats). The closest relatives among these species showed extensive geographic segregation, or subtle but still important morphofunctional segregation when sympatric. Examples of the former include the kodkod–oncilla pair; examples of the latter include the *L. jacobita*–*L. colocolo* and *L. pajeros* group in the highlands.

Next, *Puma concolor* and *Panthera onca* established populations in South America during the Late Pliocene (Johnson *et al.*, 2006) or later (first fossil records date from the Early Middle Pleistocene; McKenna & Bell, 1997; Pomi & Prevosti, 2005; Turner and Antón, 1997). These large felids occupied a vacant region of the South American felid morphospace. Machairodontine cats such as *Smilodon populator* Lund, 1842 and *Smilodon fatalis* Leidy, 1868 were already present in South America (McKenna & Bell, 1997; Turner and Antón, 1997). Derived machairodontines diverged in skull morphology from extant felids in most significant ways (Christiansen, 2008; Slater and Van Valkenburgh, 2008), so their niche interactions were probably limited.

Finally, at some point between the Late Pliocene (Johnson *et al.*, 2006) and Late Pleistocene [either during the Bonarian (0.5–0.13 Mya) or Lujanian (0.13 Mya–8.5 Kya), based on the fossil record; Prevosti, 2006], *Puma yagouaroundi* appeared in South America (probably originating there). This species overlaps extensively in skull size and morphology with most of the small *Leopardus* (e.g. Kiltie, 1984), and is sympatric or syntopic with many of them (Oliveira, 1994; Sunquist & Sunquist, 2002, 2009). However, the jaguarundi is predominantly diurnal (Oliveira, 1994, 1998b). Diurnal versus nocturnal predators in the same area encounter different prey or the same prey in different activity phase (e.g. resting versus foraging); they also have distinct rates of encounter with other predators (more frequent in nocturnal species), and therefore do not face the same risks from antagonistic situations. In this way, we hypothesize that the jaguarundi, a late-comer in the Neotropical felid assemblage, segregated along another niche dimension (daily activity pattern), and thus was able to tolerate extensive morphofunctional overlap with a number of previously established species of small felids of the older *Leopardus* stock.

In summary, the Neotropical felid guild seemingly assembled in two phases. First, a pool of early colonizers, ancestors of the ocelot lineage, established and diversified geographically within morphofunctionally conservative boundaries. Second, subsequent coloniz-

ers were added by the occupation of vacant areas in the morphospace in the case of non-overlapping large felids, or by the insertion of extensively overlapping species with contrasting habits, as in the case of a small felid, the predominantly diurnal jaguarundi. Thus, the emerging pattern of guild organization among Neotropical felids seems to be one of a historically structured group of similar antagonistic species that tend to segregate primarily in morphospace, and next in regional occupation and other niche dimensions, including habits and activity patterns. We hypothesize that this pattern may be general for relatively homogeneous groups like Neotropical felids, and thus we expect parallel patterns of niche structuring in other continents.

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## APPENDIX

Definition of morphometric variables used in this study, listed alphabetically. Anatomical terms follow Evans (1993). Most of the measurements were taken or modified from Biknevicius (1996), Gay & Best (1996), Giannini *et al.* (2004), and Werdelin (1983). Abbreviations of dental elements: C, upper canine; c, lower canine; I, upper incisor; i, lower incisor; M, upper molar; m, lower molar; P, upper premolar; p, lower premolar. Element position is indicated by a numeral (e.g. P3 is the third upper premolar).

**APD, angular process depth:** Vertical dimension from the dorsal edge of the mandibular condyle to the ventral edge of the angular process of the mandible. Horizontal reference is a line joining the base of C and the mandibular condyle.

**ATL, alveolar lower toothrow length:** Distance from the rostral edge of c to the caudal edge of m1.

**CBL, condylobasal length:** Horizontal dimension from prosthion (rostralmost edge of premaxilla at the midline) to the caudal border of occipital condyles.

**CG, load arm of C:** Distance between the rostral edge of the alveolus of C and the mediolateral mid-point of the posterior edge of the glenoid fossa.

**cL, lower canine length:** Distance from rostral to caudal aspect of the base of c.

**CL, upper canine length:** Distance from rostral to caudal aspect of the base of C.

**Cm1, load arm of the lower carnassial:** Distance from the caudal edge of the mandibular condyle to the notch of m1. The horizontal reference is a line joining the base of C and the mandibular condyle.



*CPD, coronoid process depth:* Distance from the ventral edge of the mandibular condyle to the dorsal edge of the coronoid process. The horizontal reference is a line joining the base of C and the mandibular condyle.

*cW, lower canine width:* Distance from lateral to medial aspect of the base of c.

*CW, upper canine width:* Distance from lateral to medial aspect of the base of C.

*ENW, external nostril width:* Distance between medial edges of left and right premaxilla at the external nasal aperture.

*FTL, fossa temporalis length:* Maximal length of the temporal muscle impression, from the postorbital process to the nuchal crest.

*ICW, intercanine width:* Distance between lateral edges of the alveoli of left and right C.

*IP4W, intercanassial width:* Length between lateralmost edges of the alveoli of left and right P4.

*IW, intermeatal width:* Braincase width at the suprameatal ridge of the squamosal (just dorsal to the left and right external acoustic meati).

*IOW, interorbital width:* Distance between medial edges of the left and right orbits.

*MD, mandible depth:* Distance between the alveolus of m1 and ventral edge of mandibular body under the notch of m1.

*MeD, mental depth:* Distance from the dorsalmost edge of the mandibular symphysis between the alveoli of left and right i1 to the ventro-caudalmost point of the mandibular symphysis.

*MPW, mastoid processes width:* Distance between the lateroventral edge of the left and right mastoid processes.

*OCW, occipital condyle width:* Distance between the lateral edges of the left and right occipital condyles.

*OL, orbital length:* Distance between the anterior-most point of the orbital rim to the apex of the *processus frontalis* of the jugal.

*OPD, occipital plate depth:* Distance between basion (middle of the ventral margin of foramen magnum) and inion (central surface point at the junction of the sagittal and nuchal crests).

*P3–P4, alveolar length of P3 + P4:* Distance between anterior edge of the alveolus of P3 and the posterior edge of the alveolus of P4.

*P4, alveolar length of P4:* Distance between anterior and posterior edges of the alveolus of the P4.

*P4G, load arm of upper carnassial:* Distance from the caudal notch of P4 to the mediolateral midpoint of the caudal surface of the glenoid fossa.

*PC, postorbital constriction:* In *Panthera* specimens, PC is measured in the lesser constriction of the two constrictions that can be present.

*PP4, paracone of P4:* Distance between the anterior and posterior notches of P4.

*RD, rostral depth:* Distance from the lateral border of the alveolus of P3 to the nasion (junction on the medial plane of the left and right nasofrontal sutures).

*TD, temporal depth:* Distance from the suprimeatal ridge of the squamosal to the highest point of the temporal line or sagittal crest. The horizontal reference is a line joining the base of C and the mandibular condyle.

*ZB, zygomatic breadth:* Distance between lateral borders of left and right zygomatic arches.

*ZD, zygomatic depth:* Distance between ventral and dorsal borders of the zygomatic arch measured just behind the *processus frontalis* of the jugal at the anteriormost point of the suture temporozygomatica.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Normalized ordination diagram of the principal components analysis (specimen scores scaled to unit eigenvector), corrected for overall size effect following Meachen-Samuels & Van Valkenburgh (2009). Females (open circles), males (black solid circles), and specimens of unknown sex (gray solid circles) are indicated. 1. *Leopardus tigrinus*, 2. *Leopardus wiedii*, 3. *Leopardus guigna*, 4. *Leopardus pajeros*, 5. *Puma yagouaroundi*, 6. *Leopardus geoffroyi*, 7. *Leopardus colocolo*, 8. *Leopardus braccatus*, 9. *Leopardus pardalis*, 10. *Leopardus jacobita* (white outlined circle), 11. *Puma concolor*, 12. *Panthera onca*.

**Table S1.** Results of principal component analyses, corrected for overall size effect following Meachen-Samuels & Van Valkenburgh (2009): loadings of each variable on the first three axes extracted and the corresponding eigenvalues, percent of total variation per axis, and cumulative percentage of successive axes (%ac.). For acronyms of variables see Appendix.

**Appendix S1.** Specimens examined.

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