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Pleistocene Extinctions and the Perceived Morphofunctional Structure of the Neotropical Felid Ensemble

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Abstract The felid Neotropical ensemble has experienced important changes from the Pleistocene to the present, the extinction of sabertooth cats being the most significant. Assuming that the morphofunctional structure of the Neotropical felid ensemble was maximally expressed when machairodontines were present, we added specimens of *Smilodon fatalis* and *S. populator* to a morphological dataset inclusive of all extant species of Neotropical felids to explore the hypothetical effect of extinction of machairodontines on the perceived morphofunctional structure of the ensemble. We studied 321 specimens of 12 extant species of Neotropical felids plus *S. populator* and *S. fatalis* by measuring 123 skull and postcranial morphofunctional variables. We used Principal Component Analysis to find morphofunctional

patterns of the skull, postcranium, and both combined (with and without correction for size) of both ensembles, past (with *Smilodon*) and present (with *Smilodon* lost to extinction). Canonical Phylogenetic Ordination was performed to assess the degree of phylogenetic influence on this morphospace. We also explored the effect of including homotherines in the Pleistocene guild by including specimens of North American *Homotherium serum*. Size was the principal factor structuring ensembles. Important morphological characters were associated to ecological performance of species. A pattern of bodily proportions was apparent: more stout species with larger skull, longer rostrum, stronger bite force, and longer pectoral crests, versus gracile, jumping species with opposing characters. The felid morphospace shrank after the extinction of *Smilodon* and *Homotherium*, but the configuration of the portion of space containing extant felids remained stable. This pattern is associated with deep phylogenetic roots.

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Introduction

At present 12 species of felids of three phylogenetic lineages coexist in the Neotropics, occupying every kind of biome available in the region, from highland deserts (e.g., *Leopardus jacobita*) to tropical rainforests (e.g., *Leopardus tigrinus*). Size range of these species spans two orders of magnitude and varies from very small (about 1.5 kg in *Leopardus guigna*) to large felids, represented by *Puma concolor* (25–80 kg) and *Panthera onca* (30–121 kg; Oliveira 1994; Sunquist and Sunquist 2002, 2009). These felids also differ among each other on the frequency with which they climb trees; the Neotropics are home to one of the best climbers in the world, the margay (*Leopardus wiedii*;

Oliveira 1994; Sunquist and Sunquist 2002, 2009). Although rich and diverse, the Neotropical ensemble of felids lacks some distinct morpho- or etho-types present in other continents, such as the running cheetah (*Acynonix jubatus*; Africa and Asia), the social lion (*Panthera leo*; Africa and Asia), or the small mammal specialist serval (*Leptailurus serval*; Africa; Sunquist and Sunquist 2002, 2009). During the Pleistocene, this ensemble was richer; an extinct subfamily of felids, machairodontines, had representatives in South America. Here, the extinct sabertoothed cat guild was dominated by *Smilodon*, including the best known *Smilodon populator* and *S. fatalis*, although recent fossil discoveries have firmly established the presence of *S. gracilis* and members of the homotherine sabertoothed clade in the continent (Mones and Rinderknecht 2004; Rincón et al. 2011). These sabertoothed cats were very large felids, able to hunt very large prey (e.g., Prevosti and Vizcaíno 2006; Lewis and Lague 2010), using a hunting technique that must have differed from that of extant felids due to the presence of long canines (Simpson 1941; Gonyea 1976b; Emerson and Radinsky 1980; Akersten 1985; Turner and Antón 1997; McCall et al. 2003; Schmieder, unpublished; Merriam and Stock 2001; Antón et al. 2004; Argot 2004a). These felids used their strong necks to close their gape by lowering the skull while the mandible was fixed to the prey, so their long canines sheared off the victim's neck, cutting through the important vessels of the neck and damaging digestive and respiratory pathways (e.g., Emerson and Radinsky 1980; Turner and Antón 1997; Schmieder, unpublished; Antón et al. 2004).

Felids as a group have been intensively studied from a morphofunctional perspective (e.g., Werdelin 1983; Kiltie 1984, 1988; Dayan et al. 1990; Schmieder, unpublished; Christiansen 2007, 2008; Lewis and Lague 2010; Morales and Giannini 2010, 2013; Prevosti et al. 2010; Sicuro and Oliveira 2010; Sicuro 2011). Most of these works focused on the skull, and only a few of them dealt with postcranial variation. These included morphological differences between felines and machairodontines (e.g., Merriam and Stock 2001; Lewis and Lague 2010; Meachen-Samuels 2012), but did not explore the morphological structure of ensembles. For instance, the South American felid ensemble has been previously studied only in regard to skull morphology (Kiltie 1984; Morales and Giannini 2010). However, postcranial variation has been considered a primary source of variation affecting ecological performance of different extant and fossil species (e.g., Spoor and Badoux 1988; Muizon and Argot 2003; Argot 2004a, b; Samuels et al. 2013). This variation proved to be essential in structuring felid ensembles in a way consistent with resource partitioning among antagonistic species of predators (see Morales and Giannini 2013).

The South American felid ensemble is the more recent one among continental ensembles. This is in part due to the late arrival of felids to the Neotropics after the land connection

between North and South America was definitely established at the Plio-Pleistocene boundary (c. 3 Ma.; Marshall 1988; Woodburne 2010). Since then, this ensemble has changed by local speciation of *Leopardus* and probably *Puma*, which led to the extant diversity, and extinction of a very different morphotype at the end of the Pleistocene, the sabertooth cats in the genera *Smilodon* and *Homotherium* (or may be middle Pleistocene for *Homotherium*; Werdelin et al. 2010; Rincón et al. 2011). In this paper we set out to explore the effect of these Pleistocene extinctions on the perceived structure of the morphofunctional space of the Neotropical felid ensemble by including the most common species of the sabertoothed cat guild in South America, *S. fatalis* and *S. populator*. For this task, we studied cranial and postcranial morphofunctional variation of all extant species, comparing the contribution of each data partition and their combined effects with and without the two best known species of Neotropical sabertooth cats. In addition, we explored the effect of including an homotherine form in the analysis. While *Homotherium venezuelensis* would have been the species of choice, material available from this taxon is not fully adequate for a metric analysis, and so we included a close North American relative, *H. serum*, for which complete and undeformed material has been published.

Materials and Methods

A total of 321 specimens (290 skull only, one postcranium only, 30 skull and postcranium combined) of the 12 species of extant Neotropical felids, plus two specimens of *S. populator* (one skull only, and one skull and postcranium) and one of *S. fatalis* (one skull) were examined in the following collections: American Museum of Natural History, New York, U.S.A. (AMNH); Centro Nacional Patagónico, Puerto Madryn, Argentina (CNP); Colección Boliviana de Fauna, La Paz, Bolivia (CBF); Centro de Ecología Aplicada, Junín de Los Andes, Argentina (CEA; Administración de Parques Nacionales); Colección de Mamíferos del Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza, Argentina (CMI); Colección del Grupo de Ecología Comportamental de Mamíferos, Bahía Blanca, Argentina (CGECM); Colección Mamíferos Lillo, Tucumán, Argentina (CML); Colección Privada Marcelo Carrera, Puerto Madryn, Argentina (MC); Field Museum of Natural History, Chicago, U.S.A. (FMNH); Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina (MACN and MACN-PV); Museo de Ciencias Naturales de la Universidad Nacional de Salta, Salta, Argentina (MCN-UNSa); Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú (MUSM); Museo de La Plata, La Plata, Argentina (MLP); Museo Municipal de Ciencias Naturales “Lorenzo Scaglia”, Mar del Plata, Argentina (MMP); Museo Nacional de Historia Natural, Montevideo,

Uruguay (MNHN); Museo Noel Kempf, Santa Cruz de la Sierra, Bolivia (MNK); and National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A. (USNM). Skeletons of *Leopardus jacobita* and of *L. colocolo* were not available in any of the visited museums. Two specimens of *H. serum* (one skull, and one skull and postcranium) from the Texas Memorial Museum (TMM) were studied through digital pictures kindly provided by Ascanio Rincón, plus figures from available literature (Meade 1961; Rawn-Schatzinger 1992; see below). We followed Wozencraft (2005) for systematic treatment of taxa and Johnson et al. (2006) for phylogenetic relationship among species. *Leopardus braccatus* and *L. pajeros* were not included as distinct species in Johnson et al. (2006); we added them to the phylogenetic subtree of Neotropical species as sister of *L. colocolo* following García-Perea (1994; see also Morales and Giannini 2010). *Smilodon* species were added as sister species of subfamily Felinae (Prevosti et al. 2010; Fig. 1). Only adult specimens were included in the analyses; they were recognized by full adult dentition and/or by the degree of epiphyseal fusion in long bones. For our analyses, specimens with almost complete postcranial elements were necessary, diminishing the actual set of specimens available in museums for this study (see also Morales and Giannini 2013). The list of specimens examined is provided in Appendix S1 (see Online Resource 1).

Smilodon is a widespread and well represented South American fossil genus; however, Homotherini species were also present during the Pleistocene. Based on the fossil record, it seems that *Smilodon* was the most abundant machairodont as compared with homotherines (e.g., Huáscar Azurdry 2000;

Mones and Rinderknecht 2004; Prevosti and Vizcaíno 2006; Prieto et al. 2010; Rincón et al. 2011). *Homotherium venezuelensis* was only recently described from northern South America (Mones and Rinderknecht 2004; Rincón et al. 2011). Unfortunately, the generally well-preserved skull is partially damaged and deformed, and a complete skeleton is lacking (see Rincón et al. 2011). Given that *Homotherium* constitutes a different morphotype among machairodonts (Lewis and Lague 2010), we also present an exploratory analyses including *Homotherium*, represented here by a closely related North American species, *H. serum*, for which complete skull and postcranium are available.

Following Morales and Giannini (2013) in their study of the African felid ensemble, we used a total of 123 morphometric variables selected to approximate form and function of skull (31) and postcranial (92) elements and specific muscles scars, which could be associated to performance during locomotion and hunting. These morphometric variables differ from those used for the African ensemble analyses in one measurement (length of the second metacarpal; McII), which we eliminated in order to maximize specimen number. For the analysis of the Neotropical ensemble with *S. populator* (hereafter Neotropical + *Smilodon*), we eliminated three measurements, given that they were lacking in the single nearly complete specimen of the fossil species available to us; these were width of the pelvis (WP), width of the pelvis at the ilia (WPI), and length of the transverse process of the first caudal vertebra (TCa1). In the analyses including *H. serum*, only 27 cranial variables were used, i.e., all but load arm of the upper carnassial (P4G), lower canine width (cW), mastoid processes width (MPW), and paracone of P4 (PP4). For postcranial and combined analyses, a reduced dataset was also used; skull dataset (12 variables): condylobasal length (CBL), intercanine width (ICW), upper canine width (CW), upper canine length (CL), occipital condyle width (OCW), alveolar lower tooththrow length (ATL), angular process depth (APD), lower canine width (cW), lower canine length (cL), load arm of the lower carnassial (Cm1), mental depth (MeD), and coronoid process depth (CPD); postcranial dataset (15 variables): length of the wing (= transverse process) of the atlas (WA), length of the spinous process of the axis (SA), length of the spine of the scapula (Sp), total length of the humerus (H), distal width of the humerus (HD), total length of the ulna (U), total length of the radius (R), length of the pelvis (P), length of the ilium (Li), length of the ischium (IQ), length of the femur (F), length of the tibia (T), length of the fibula (Fi), length of the calcaneus (N), and length of the talus (Ta).

Morphometric data were analyzed first using cranial and postcranial variables only and next using cranial and postcranial datasets combined (see Morales and Giannini 2013, for a cranial only analysis of Neotropical felids see Morales and Giannini 2010). Both datasets were also analyzed after correcting for size using Geometric Mean and Mossiman variables (Meachen-

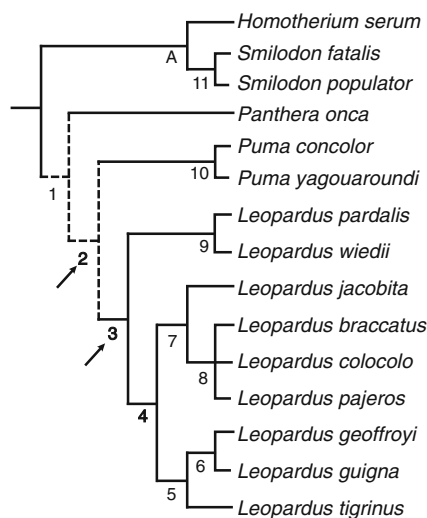


Fig. 1 Phylogenetic relationships among Neotropical felids. Numbers indicate partitions used for Canonical Phylogenetic Ordination method (CPO). Modified from Johnson et al. (2006; see text). Bold numbers and arrows indicate significant clades individually and after stepwise method, respectively, for CPO analysis of untransformed combined dataset of the Neotropical + *Smilodon* ensemble. Note partitions 1 and A are identical for coding, thus, partition A was eliminated as dummy variable

Samuels and Van Valkenburgh 2009a,b; Morales and Giannini 2010, 2013).

We used Principal Component Analyses (PCA) based on variance-covariance matrices with transformed (size-corrected) and untransformed data to recover morphological patterns of the ensemble (see Morales and Giannini 2010, 2013). We used Canonical Phylogenetic Ordination (CPO; Giannini 2003) to evaluate the influence of phylogeny on the patterns of morphological variation. In CPO, clades are independent variables that may explain some variation of a main matrix (Giannini 2003), here the various morphofunctional datasets. Clades used in this analysis are those of Fig. 1; their statistical significance was tested with 4999 unrestricted Monte Carlo permutations setting a conservative $\alpha=0.01$ (see Morales and Giannini 2010, 2013).

Results

Main results of PCAs of all three ensembles were summarized in Figs. 2, 3, and 4 (see also Table 1, and S1, S2, S3, S22, S23 of Online Resource 1). Variance percentages and principal variables correlated to positive and negative sides of each axes of each PCA are represented in these figures. Only outstanding results are reported here.

In all untransformed data analyses, PC1 explained >95 % of total variation (Figs. 2a, b, 3a, b, e, f, and 4a, c, e), and all variables were positively correlated with it, thus representing size variation. Three to five groups were recognized in Neotropical and Neotropical + machairodont ensembles, respectively (Figs. 2, 3 and 4). PC2 in these analyses explained between 0.4 and 2.3 % of total morphological variation.

Transformed data analyses in the three ensembles yielded a PC1 that explained over 35 % of morphological variation; spatial distribution of species in PCA plots of transformed postcranial only and combined datasets were different from those of the corresponding untransformed data analysis. Dispersion of specimens was wider, but not always among species (Figs. 2a, b, 3a, b, e, f and 4a, c, e versus Figs. 2c, d, 3c, d, g, h and 4b, d, f, respectively). PC2 in these analyses explained 12.6–28.7 % of morphofunctional variation. In these morphospaces, machairodont species fell closer to other Neotropical felines, to the extent of being “identical” in cranial morphology to other large felids (cf. Figs. 2d, 3 and 4).

After removing *Smilodon* and *Homotherium*, species of the Neotropical ensemble spread throughout the PC1-PC2 plane, reaching complete segregation in the combined transformed dataset (Fig. 3g). Possibly, increasing sample size in some species may reduce perceived segregation in these analyses.

When studying Neotropical and Neotropical + *Smilodon* ensembles, a general pattern was found in every analysis involving postcranial data: on PC2 an inverse relationship was recovered between the length of the pectoral ridge (PR)

versus the length of the hind limb (e.g., F, T, Fi, MtII, MtIII, MtV, see Fig. 3). Also, when correcting the postcranial and combined datasets for size, small felids seem to have proportionally longer limbs, except for *Puma yagouaroundi*, which segregates (on PC1) from species of *Leopardus* of comparable size (Figs. 3c, d, g, h and 4d). The importance of the postcranial data is reflected in the fact that ordination diagrams of combined untransformed or transformed data analyses of both ensembles showed similar distributional patterns to those in the postcranial data analyses (Figs. 3a, b, c and 4c versus Figs. 3e, f, g and 4e; see also Morales and Giannini 2010, 2013).

In transformed postcranial analyses of both ensembles (Fig. 3c, d), a general morphological pattern is recognized: most species occur on the positive side of the PC2 describing a more “typical” felid morphotype, and *L. wiedii* and *P. concolor* were the two more deviated species from this “common” morphology. The same occurs in the combined dataset size corrected of the Neotropical ensemble (Fig. 3g).

In addition, from the analysis of the combined dataset of the Neotropical ensemble (Fig. 3e), a particular pattern of bodily proportions emerges: large-headed felids with a long rostrum, pectoral and temporal musculature relatively well developed, and short legs, particularly the hind limb, versus the opposite. The inverse relationship between head size and length of the hind limb is also present in the combined analysis including *H. serum* (Fig. 4e).

The morphofunctional structure observed when including *Homotherium* was similar to the Neotropical + *Smilodon* ensemble, except that *Homotherium* segregated along the negative side of PC2 as opposed to *Smilodon* when postcranial data were included in the analysis, due to relatively longer fibula and tibia which composes a quite different sabertooth morphotype. In addition, for the postcranial and combined size corrected analyses, the close position between *P. concolor* and *P. yagouaroundi* in the morphospace is remarkable (Fig. 4d,f).

Phylogenetic Patterns

Phylogenetic pattern of the combined untransformed dataset of Neotropical + *Smilodon* analysis is summarized in Fig. 1 and Tables S14 and S15 (Online Resource 1). For results of other analyses, please see Tables S4 to S21 in Online Resource 1.

In general, morphological variation of the studied group correlates with phylogenetic relationships as expected for closely related species. But a general tendency is evident; cranial morphology seems more closely related to phylogeny along its history, while postcranial and general morphology (combined dataset) variation was strictly associated to deep nodes in the phylogenetic history.

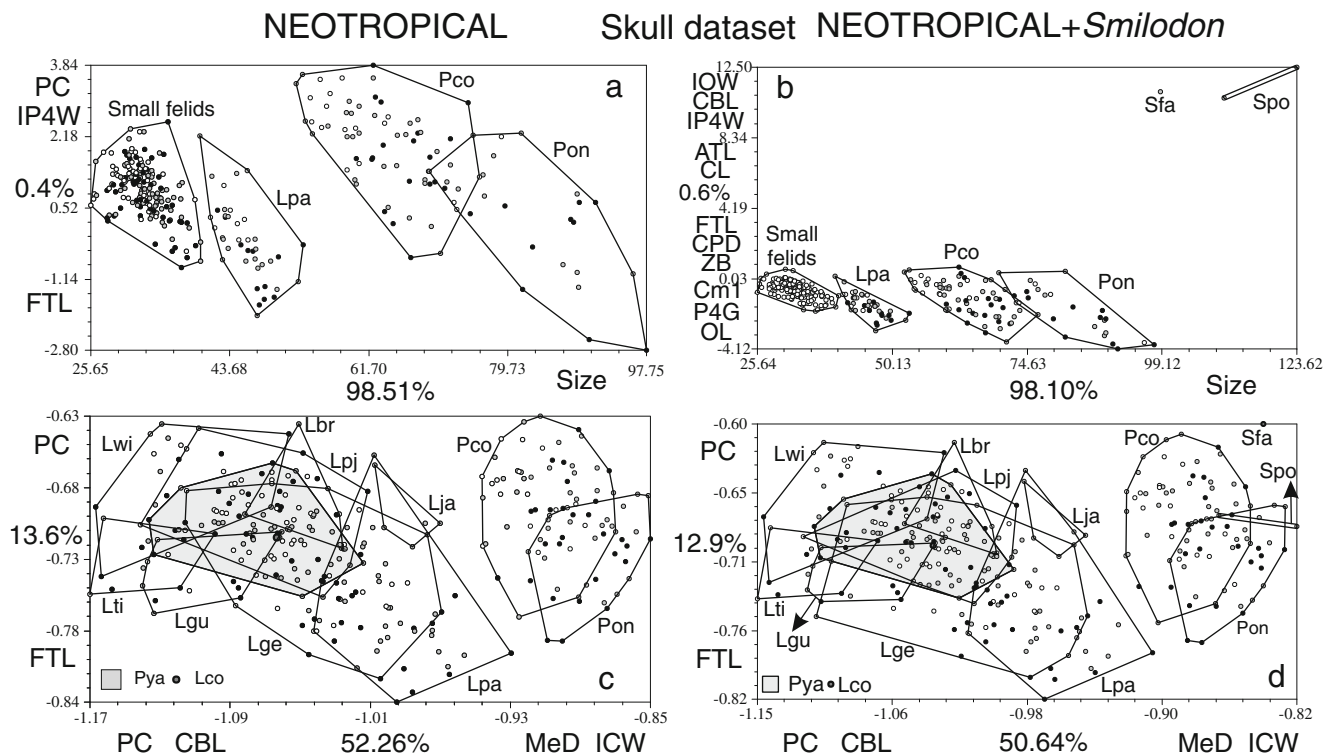


Fig. 2 Normalized ordination diagrams of principal component analysis (specimen cores scaled to unit eigenvector) performed for: **a, c** extant Neotropical ensemble of felids; **b, d** Neotropical + *Smilodon* ensemble of felids. **a, b** Skull-only dataset; **c, d** Skull-only dataset size corrected. Abbreviations: Lbr, *Leopardus braccatus*; Lco, *Leopardus colocolo*;

Lge, *Leopardus geoffroyi*; Lgu, *Leopardus guigna*; Lja, *Leopardus jacobita*; Lpa, *Leopardus pardalis*; Lpj, *Leopardus pajeros*; Lti, *Leopardus tigrinus*; Lwi, *Leopardus wiedii*; Pco, *Puma concolor*; Pon, *Panthera onca*; Pya, *Puma yagouaroundi*; Sfa, *Smilodon fatalis*; Spo, *Smilodon populator*

Discussion

In the present as in the recent past, the Neotropical felid ensemble was functionally structured on the basis of size variation. The morphospace expanded by cranial and postcranial variables was wider in our simulated Pleistocene ensemble, where the machairodonts *S. populator*, *S. fatalis*, and probably *Homotherium* (based on *H. serum*) occupied an extreme position, making up a size group that was lost to extinction. These species also segregated because of particular features that likely represent adaptations to a distinct mode of hunting.

Results considering only the extant Neotropical ensemble generally confirmed ecomorphological patterns reported in Morales and Giannini (2010) and will not be discussed in detail. The addition of machairodonts manifested some differences with felines that have been previously reported, especially regarding skull morphology. For instance, our results support the reported weaker bite force of machairodonts with respect to felines (see Simpson 1941; Emerson and Radinsky 1980; Akersten 1985; Biknevicius 1996; Turner and Antón 1997; Schmieder, unpublished; Merriam and Stock 2001; Antón et al. 2004; Christiansen 2007). Remarkably, when controlling for the effect of size, *Smilodon* species mixed with large felines in morphospace (Fig. 2d), resembling to some extent results in

Prevosti et al. (2010). Thus, part of the difference between skulls of extant felines and machairodonts may be a function of allometry.

It was postcranial variation that mostly reflected the morphofunctional distinction between Neotropical felid ensembles during the Pleistocene and in the present. This data partition recovered as key certain variables that estimate divergences in hunting modes between *Smilodon* and the felines, and locomotion modes among extant species (see below). With postcranial data, even after correcting for size, *Smilodon* species segregated as a distinct group on the basis of characters that revealed a particular ecomorphology. As in the skull, part of the postcranial differences between *Smilodon* and felines have also been suggested previously, e.g., short limbs (particularly zeugo- and autopods), the length of the wing of the atlas (WA) and the spinous process of the axis (SA), and the wide distal end of the humerus (HD) (Turner and Antón 1997; Schmieder, unpublished; Argot 2001; Antón et al. 2004, 2006; Flores and Díaz 2009; Ercoli, unpublished; Ercoli et al. 2012; Lewis and Lague 2010; Morales and Giannini 2013; Meachen-Samuels 2012, see also Appendix S2 in Online Resource 1). The inverse relationship between long pectoral ridge (suggesting strong adduction of arms) and short hind limbs (low center of gravity and strong anchoring of hind limbs among other functions) is key and suggests that

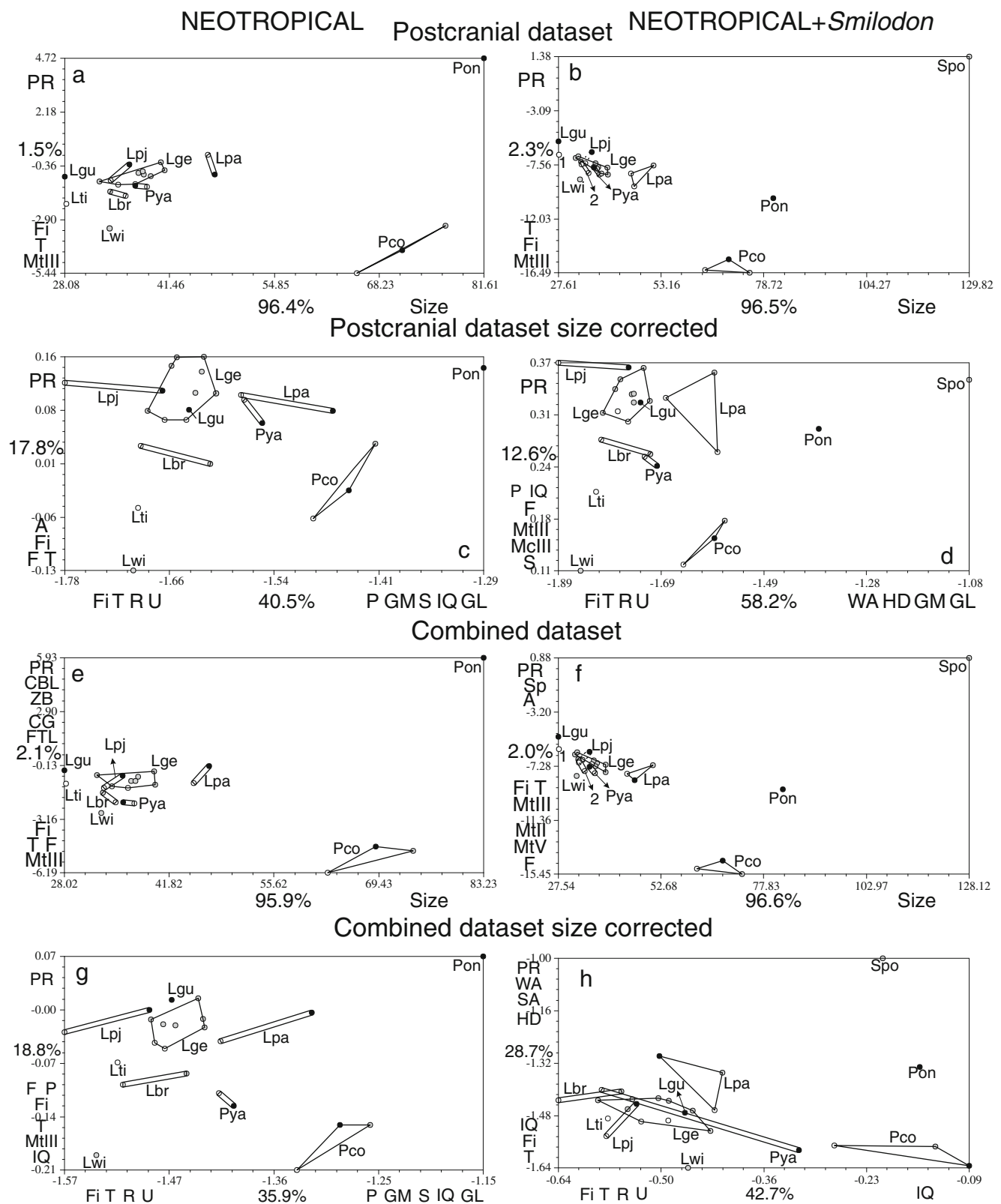


Fig. 3 Normalized ordination diagrams of principal component analysis (specimen cores scaled to unit eigenvector) performed for: **a, c, e, g** extant Neotropical ensemble of felids; **b, d, f, h** Neotropical + *Smilodon* ensemble of felids. **a, b** Postcranial-only dataset; **c, d** Postcranial-only dataset size corrected; **e, f** Combined dataset; **g, h** Combined dataset size

corrected. Abbreviations: 1, *Leopardus tigrinus*; 2, *Leopardus braccatus*; Lbr, *Leopardus braccatus*; Lge, *Leopardus geoffroyi*; Lgu, *Leopardus guigna*; Lpa, *Leopardus pardalis*; Lpj, *Leopardus pajeros*; Lti, *Leopardus tigrinus*; Lwi, *Leopardus wiedii*; Pco, *Puma concolor*; Pon, *Panthera onca*; Pya, *Puma yagouaroundi*; Spo, *Smilodon populator*

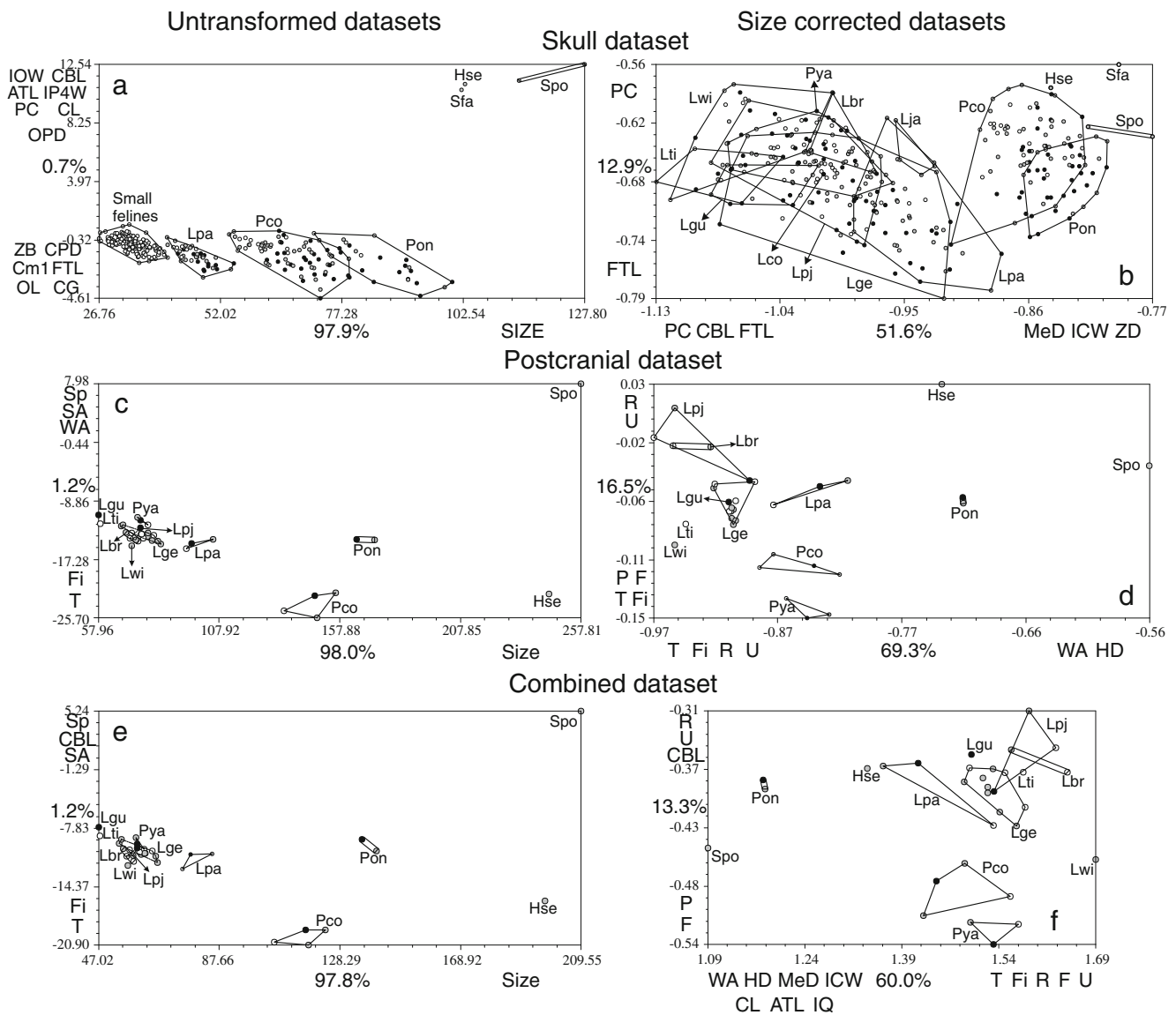


Fig. 4 Normalized ordination diagrams of principal component analysis (specimen cores scaled to unit eigenvector) performed for the Neotropical + *Smilodon* + *Homotherium* ensemble of felids. **a, b** Skull-only dataset; **c, d** Postcranial-only dataset; **e, f** Combined dataset. **a, c, e** uncorrected datasets; **b, d, f** size corrected datasets. Abbreviations: Hse, *Homotherium*

serum; Lbr, *Leopardus braccatus*; Lge, *Leopardus geoffroyi*; Lgu, *Leopardus guigna*; Lpa, *Leopardus pardalis*; Lpj, *Leopardus pajeros*; Lti, *Leopardus tigrinus*; Lwi, *Leopardus wiedii*; Pco, *Puma concolor*; Pon, *Panthera onca*; Pya, *Puma yagouaroundi*; Sfa, *Smilodon fatalis*; Spo, *Smilodon populator*

S. populator would have been capable of powerful but slow movements, able to bring down very large prey, giving away some of its cursorial abilities for the advantage of hunting by ambush (Argot 2004b; see also Appendix S2 in Online Resource 1). In turn, a shorter pectoral crest in other cats can be just a consequence of small size, which allows actions without real adaptations (Jenkins 1974; Morales and Giannini 2013). Results (especially of the extant Neotropical ensemble) also recovered particular limb proportions of *L. wiedii* and *P. concolor* (i.e., long hind limbs), which we associate with jumping (Howell 1944 in Gonyea 1976a) and probably acceleration ability (see also discussion below). The

long hind limbs of *L. wiedii* would allow it to move ricocheting between stems and trunks. Because *L. wiedii* consumes only small prey (Konecny 1989; Redford and Eisenberg 1992; Emmons and Feer 1997; Wang 2002), a well-developed pectoral musculature is not required for its hunting strategy. This would be in line with the suggestion that the length of the pectoral crest (not its antero-posterior development) also can be related to degree of circumduction of the forelimb around the shoulder joint (see also Morales and Giannini 2013 and Appendix S2 in Online Resource 1).

Some additional characters place *Smilodon* in a particular position in morphospace, including the origin area of the m.

Table 1 Summary of results of the Neotropical + *Smilodon* ensemble. Analyses using skull, postcranial, and combined datasets with and without size correction

	Cr	Cr-SC	Pcr	Pcr-SC	Cr-Pcr	Cr-Pcr-SC
% PC1	98.10	50.64	96.53	58.24	96.56	42.74
Positive variables on PC1	All	MeD ICW	All	WA HD GM GL	All	IQ
Negative variables on PC1	–	PC CBL	–	Fi T R U	–	Fi T R U
% PC2	0.64	12.91	2.32	12.56	2.02	28.74
Positive variables on PC2	IOW CBL IP4W ATL CL	PC	PR	PR	PR Sp A	PR WA SA HD
Negative variables on PC2	FTL CPD ZB Cm1 P4G OL	FTL	T Fi MtIII	P IQ F MtIII McIII S	Fi T MtIII MtII MtV F	IQ Fi T
N° of groups by size	4	–	5	–	5	–
Retained clades (CPO)	3 2 4 1	3 1 7 4 6 8 2	2 4	2 4 6	2 3	3 2
% Filog.	65.0	23.8	72.3	40.1	74.6	30.2

Cr skull dataset, Pcr postcranial dataset, Cr-Pcr combined dataset, -SC size corrected. %PC1 and %PC2 indicates percentage of variation explained by first and second axes of each of the Principal Component Analyses (PCA). Important variables in each analysis and each axes are listed for comparative purposes with the following abbreviations: A length of the origin of the m. anconeus, ATL alveolar lower tooththrow length, CBL condylobasal length, CL upper canine length, Cm1 load arm of the lower carnassial, CPD coronoid process depth, F length of the femur, Fi length of the fibula, FTL fossa temporalis length, GL origin of the gastrocnemius caput laterale, GM origin of the gastrocnemius caput mediale, HD distal width of the humerus, ICW intercanine width, IOW interorbital width, IP4W Inter-carnassial width, IQ length of the ischium, McIII length of the third metacarpal, MeD mental depth, MtII length of the second metatarsal, MtIII length of the third metatarsal, MtV, length of the fifth metatarsal, OL orbital length, P length of the pelvis, P4G load arm of upper carnassial, PC postorbital constriction, PR pectoral ridge, R length of the radio, S length of the symphysis pelvis, SA length of the spinous process of the axis, Sp length of the spine of the scapula, T length of the tibia, U length of the ulna, WA length of the wing of the atlas, ZB zygomatic breadth. Percentage of morphological variation explained by the group of retained clades in forward stepwise selection in CPO is indicated (% Filog). Retained clades after stepforward are listed in the order they were retained, and were (see Fig. 1): 1 Machairodontinae† vs Felinae, 2 felines vs. pantherines, 3 (*Leopardus*), 4 ((*L. jacobita* (*L. braccatus*, *L. colocolo*, *L. pajeros*))(*L. tigrinus* (*L. guigna*, *L. geoffroyi*))), 5 (*L. tigrinus* (*L. guigna*, *L. geoffroyi*)), 6 (*L. guigna*, *L. geoffroyi*), 7 (*L. jacobita* (*L. braccatus*, *L. colocolo*, *L. pajeros*)), 8 (*L. braccatus*, *L. colocolo*, *L. pajeros*)

gastrocnemius (for both caput laterale and mediale; GL and GM), and the length of the ischium (IQ). On this basis, *Smilodon* would have retained some sprinting abilities because femur extension may have been comparable to other large felids (Fig. 3d, h). However, variation in other characters (e.g., zeugopod length), perhaps of allometric nature, may antagonize with that potential mechanical advantage (see

Morales and Giannini 2013 and Appendix S2 in Online Resource 1).

The morphofunctional pattern emerging from the combined dataset of the Neotropical ensemble compares (although not exactly) to the one discovered for the African ensemble of extant cats (see Morales and Giannini 2013). Specifically, the opposition of robust species with large skull, long rostrum,

and strong bite force (larger m. temporalis), combined with long pectoral crest, versus species more specialized in jumping, here *P. concolor* and *L. wiedii* (as compared with similar-sized species), with overall small skulls and long hind limbs (Fig. 3e). This would support the suggestion that strenuous activities require mass reduction in body parts not directly intervening with them, such as the skull (Taylor et al. 1974; Hildebrand and Hurley 1985). In turn, the greatest differences between Neotropical and African ensembles may be due to the absence of highly cursorial felids in the former. The position of *H. serum* in Fig. 4c, reveals a smaller skull and longer hind limbs; this morphology supports previous suggestions of jumping capacity for this species (see Rawn-Schatzinger 1992).

Postcranial and combined analyses including *H. serum* differ from those of the Neotropical + *Smilodon* analyses. Unfortunately, we could not measure the length of the insertion of the pectoral muscles (pectoral ridge, PR) in *H. serum*, the most important variable on the PC2 for structuring the other ensembles, as sometimes the end of this insertion is not readily available from pictures (see Appendix 1 in Morales and Giannini 2013 for measurement definition). Three main results are notable. First, size is still the main (latent) variable structuring ensembles, and general considerations for *Smilodon* are also true for *Homotherium* (e.g., Meade 1961; Rawn-Schatzinger 1992; Lewis and Lague 2010). Second, *Homotherium* emerged as a distinct “morphotype” when contrasted to *Smilodon*, and when correcting for size, it was placed closer to felines than to *Smilodon*, reminiscent of results in Meachen-Samuels (2012). *Homotherium serum* was a more gracile species than *Smilodon* but likely still able to hunt large prey. Third, lacking a strong adaptive feature (the length of the pectoral ridge), *P. concolor* and *P. yagouaroundi* displayed a similar morphology after correcting for size. A similar result was previously reported by Herrington (1983 in Herrington 1985).

In a more comprehensive perspective, a salient result of our analyses is that the Neotropical ensemble seems to have maintained its chief structuring force (size and hunting-related variation) through time and across major extinction events. Without *Smilodon*, the perceived morphofunctional structure of the ensemble (i.e., as seen through the specific PCA axes projections) remained relatively unchanged, so describing variation probably due to allometry. As ordination in the morphospace among extant species is similar with and without *Smilodon*, principal components rotated only slightly, reflecting variation largely in the same directions. Although these results should be tested by including *H. venezuelensis* and more individuals, we expect little change given the close similarity with *H. serum*.

Much of this morphofunctional pattern had historical causes. Morphological variation of Neotropical felids correlated with phylogeny, as may be expected for closely related

species. Cranial morphology significantly varied all along the felid tree, while postcranial variation was associated strictly to backbone nodes. Given the influence of the postcranium, the latter is also the case in the combined set: a deep historical effect on the morphofunctional structure of the Neotropical felid ensemble. That this is true for both ensembles, past (with *Smilodon* and *Smilodon* + *Homotherium*) and present, is consistent with the fact that the influential backbone nodes are older than the Pleistocene extinction event that eliminated the sabertoothed cats and drastically changed the species composition of the ensemble.

Conclusions

The Neotropical felid ensemble is structured morphofunctionally on the basis of size variation, both the extant ensemble and the hypothetical Pleistocene ensemble simulated by inclusion of *Smilodon* and *Homotherium*. Still, additional morphological variation revealed major differences between machairodonts and felines, which could be associated with specific hunting techniques depending on prey size, as well as different modes of locomotion among extant neotropical felids. Important characters for species segregation were mostly postcranial. In the Neotropical + *Smilodon* ensemble, these characters depicted the ability of *Smilodon* to hunt (take down) very large prey. Also, results reflected the jumping ability in *L. wiedii* and *P. concolor*.

An emerging functional pattern in both ensembles, Neotropical and Neotropical + *Smilodon*, was the inverse relationship between the length of the posterior leg and the length of the pectoral ridge of the humerus. In the extant ensemble, stout species with larger skull, longer rostrum, stronger bite force, and longer pectoral crests opposed more gracile species with jumping abilities showing contrasting attributes. Segregation of species in morphospace was greater when including postcranial variables in the analysis, confirming that postcranial information commands the morphofunctional structuring of felid ensembles. Extinction of the distinct *Smilodon* morphotype, as modeled in our analyses by including two of the species, had the effect of shrinking the total occupied morphospace without altering much the configuration of extant species in that space. The likely cause of such a pattern lies on the pervasive effect of size and its allometric implications with deep phylogenetic roots.

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