



Pleistocene extinction and geographic singularity explain differences in global felid ensemble structure

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Abstract

Extant felids are hyper-carnivorous predators that originated in Asia c. 11 Mya and diversified in 8 distinct lineages, with 41 species surviving to the Recent. These species occupy almost every terrestrial habitat available in the four continental land masses they occupy and exhibit morphological and behavioral specializations to various locomotor styles and hunting modes. Today, distinct felid ensembles inhabit each continent and major biogeographic region. How the differential structuring of these ensembles was generated, and which evolutionary processes shaped these differences across ensembles, are key emerging questions. Using multivariate statistics, we analyzed a large dataset of 31 cranial and 92 postcranial linear variables describing shape and functional proxies of the entire skeleton of extant felids. We statistically demonstrate the existence of nine felid morphotypes at the global scale, whose occurrence is characteristic of different continental or biogeographic ensembles. Phylogenetically explicit analyses show that morphotypes from different felid lineages converged in different continents, but still ensembles remain distinct due to the fact that various morphotypes are missing in several of those ensembles. However, fossil evidence suggests that most of these missing morphotypes were represented by species from those territories that went extinct during the Quaternary. Furthermore, reconstructing the hypothetical felid ensembles before Pleistocene extinctions rendered the continental felid faunas remarkably more similar to each other than they presently are, leaving their remaining, relatively minor differences to outstanding geographic singularities of each continental land mass.

Keywords Complete skeleton · Felidae · Ecomorphology · Macroevolution

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Introduction

An ensemble is a phylogenetically bound group of species that use a similar set of resources within a community (Fauth et al 1996). How ensembles of different organisms have formed along macro-evolutionary time expanses and across geography remains elusive (Stokstad 2009). Felids represent a recently radiated, widely distributed group of predators that may be used as example to explore the drivers structuring ensembles and how they change over time and space. Living cat species belong to subfamily Felinae that originated in Asia c. 11 Mya, during the late Miocene (Johnson et al 2006). Felinae diversified into 8 distinct lineages (Johnson et al 2006) and ancestral species of this successful carnivoran clade soon spread to all major landmasses they inhabit today—Eurasia, Africa and the Americas. With 41 species surviving to the Recent (Kitchener et al 2017), the group is arranged into characteristically distinct ensembles in each major landmass and biogeographic region (Johnson et al 2006; Table 1). At present, these various felid ensembles vary widely across continents, both in composition and ecomorphology. For example, the Neotropical region is richest in felid species (11 species); the Nearctic region virtually has no *Panthera* species (jaguars, *Panthera onca* Linnaeus 1758, are only marginally present in New Mexico) and no felids smaller than lynxes; only in Africa and the Middle East the fast-running cheetah (*Acynonix jubatus* Schreber 1775) is present. Continental ensembles differ also in more subtle morpho-functional structuring for reasons yet unknown. Remarkably, Pleistocene ensembles were richer, and they appear considerably different from those of today (e.g. Turner and Antón 1997), but how they differ and why, are still open questions.

Morphologically, extant felids are considered to be quite homogeneous, although some general differences have been recognized in skull shape and postcrania (e.g., Christiansen 2007, 2008; Lewis and Lague 2010; Sicuro and Oliveira 2010). Analysis of complete-skeleton datasets for Neotropical and African ensembles of felids identified general form differences among felid species which could be associated to locomotor modes (Morales and Giannini 2013a, b). This kind of integral analysis based on individuals with complete skeleton has not been performed for the whole subfamily, or indeed for any group of mammals, as it is extremely difficult to find museum specimens with both complete skull and most of their skeletal elements even for charismatic species like felids. This is an even larger problem for most fossil felid species that are known to have inhabited different continents; their phylogenetic relationship have been studied based on fragmentary material, and these studies provide descriptions of their general (known and estimated) anatomy but also reveal many instances of distributions that are at odds with present-day ensembles (e.g., lion-like forms in North America and cheetah-like species in North America, Europe and Asia; e.g., Barnett et al 2005 and 2006; Christiansen and Mazák 2008; Montellano-Ballesteros and Carbot-Chanona 2009).

In this work, we analyzed ensembles of felids across the Globe from an ecomorphological and macro-evolutionary perspective. Based on previous work (Morales and Giannini 2010, 2013a, b), we hypothesized that phylogeny and body size played a major role in the evolution of those ensembles. Using a comprehensive morphological approach based on carefully selected specimens with complete skull and postcrania, we propose that perceived differences between present-day morpho-functional ensembles are explained to some extent by singularities of continents and largely, by selective Pleistocene extinction.

Table 1 Conformation of studied ensembles

Sp	AMERICA		AFRICA				ASIA		
	N	NE	AF	AF-T	AF+SOAS	NAF+SOAS	EUAS	PAL	OR
Aju			X	X	X	X	X		
Cau			X	X	X				
Cca			X	X	X	X	X		
Cba							X		X
Ctk							X		X
Fbt							X	X	
Fca									
Fch					X	X	X		X
Oma							X	X	
Fmt			X		X	X	X		
Fng			X	X	X				
Fly			X	X	X	X	X	X	X
Fsi							X	X	
Hya	X								
Lco	X								
Lge	X								
Lgt	X								
Lgu	X								
Lja	X								
Lpa	X								
Lti	X								
Lwi	X								
Lse			X	X	X				
Lca		X							
Lly							X	X	
Liu							X	X	
Lru		X							
Pmm							X		X
Pbg							X		X
Pjv							X		X
Ppl							X		X
Pru							X		X
Pvi							X		X
Pco	X	X							
Ple			X	X	X		X		X
Pon	X								
Ppd			X	X	X	X	X		X
Pti							X		X
Pun							X	X	
Nne							X		X
Ndi							X		X

In the first line is the region in which each ensemble is included

AF Africa, *T-AF* Tropical Africa, *EUAS* Eurasia, *N* Neotropical (proxi for South America), *NAF* North Africa, *NE* Neartic (proxi for North America), *OR* Oriental, *PAL* Palearctic, *SWAS* South West Asia (=Middle East)

Materials and methods

Material studied

We measured linear morphometric data (see below) from 461 specimens representing all 41 currently recognized extant felid species (as in Kitchener et al. 2017) stored in the following collections: **Argentina**: Centro Nacional Patagónico, Puerto Madryn (CNP), Colección de mamíferos del Centro de Ecología Aplicada, Junín de los Andes (Dirección de Parques Nacionales; APN- provisional acronym), Colección de Mamíferos del Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza (CMI); Colección del Grupo de Ecología Comportamental de Mamíferos, Bahía Blanca (CGECM); Colección Mamíferos Lillo, Tucumán (CML), Private Collection Marcelo Carrera, Puerto Madryn (MC); Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires (MACN), Museo de Ciencias Naturales de la Universidad Nacional de Salta, Salta, Argentina (MCN-UNSa), Museo de La Plata, La Plata (MLP); Museo Municipal de Ciencias Naturales “Lorenzo Scaglia”, Mar del Plata, Argentina (MMPMa); **Bolivia**: Colección Boliviana de Fauna, La Paz (CBF), Museo Noel Kempf, Santa Cruz de la Sierra (MNK); **Peru**: Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima (MUSM); **United States**: Academy of Natural Science of Drexel University, Philadelphia (ANSP), American Museum of Natural History, New York (AMNH), Field Museum of Natural History, Chicago (FMNH), National Museum of Natural History, Washington D.C. (USNM); **Uruguay**: Colección Zoológica de Vertebrados, Facultad de Ciencias, Universidad de la República, Montevideo (ZVC-M), Museo Nacional de Historia Natural, Montevideo (MNHN). The greatest difficulty to sample felid specimens across these different institutions was the limited availability of complete skeletons of adult specimens. A complete adult dentition primarily defined the adult stage of the specimens, but whenever possible, we selected specimens with fully fused epiphysis of the long bones. Wild, sexed specimens were selected with priority. Specimens used are listed in Supplementary Appendix I.

Morphometric variables

We defined a set of 31 cranial and 92 postcranial variables with a descriptive and functional significance (Figs. S1–S4), e.g. the length of the olecranon is equivalent to the load-bearing arm of the m. triceps brachii for arm extension (O in Supplementary Fig. S3) and the condyle-basal length is often used as a proxy for body size of specimens (CBL in Supplementary Fig. S1). These sets were developed in previous studies (Morales and Giannini 2010, 2013a, b) and included key dimensions of the skull, selected vertebrae, girdles, limb long bones, autopods, and the tail (Morales 2012; Morales and Giannini 2010, 2013a, b). All variables are illustrated in Supplementary Figures S1–S4; a detailed description of variables is extracted from Morales and Giannini (2013b) and given in Supplementary Appendix II. Postcranial morphofunctional variables differ from Morales and Giannini (2013a, b) only in lacking one measurement related to the brachialis muscle and having in addition the length of tail. The latter is defined as the percentage of tail length (PT) with respect to the head plus body length, when this information was available for the specimen, or as the median from published data (chiefly Sunquist and Sunquist 2002, but adding other specific literature). To our knowledge this represents the most comprehensive dataset compiled to

date for extant felids. All measurements were taken using digital calipers to the nearest 0.1 mm.

Data analysis

We applied the multivariate ordination method, principal component analysis (PCA), for three different data sets, called “skull” with $N=451$ and including all 41 species; “postcranium” with $N=67$ and including 35 species from all genera; and “combined” dataset with $N=61$, including 34 species, also from all genera (see Morales and Giannini 2010, 2013a, b). These analyses (all based on variance–covariance matrices) were used to determine the ecomorphological structuring of skull and skeletal variation, separately and altogether; in this context, ordination plots resulting from each PCA are taken as representations of the ecomorphological space of all species of Felinae. In order to increase the number of specimens and species under analysis, we performed an additional PCA called “combined and reduced” dataset ($N=84$; 35 species) with a reduced number of variables, following Morales and Giannini (2013b; variables used for this analysis are marked with an asterisk in Supplementary Figs. S1–S4 and Appendix II) and adding tail length as described above.

All PCA were done also correcting for the influence of raw body size by using Mosimann variables and the geometric mean (see Morales 2012; Morales and Giannini 2010, 2013a). The geometric mean (GM) is a size variable derived from the N th root of the product of N measurements (here, all the variables measured in a specimen, transformed to base-10 logarithm). Using this value, each measurement is replaced by a Mosimann shape variable, i.e., the ratio of a particular measurement to the overall GM (Meachen-Samuels and Van Valkenburgh 2009a, b).

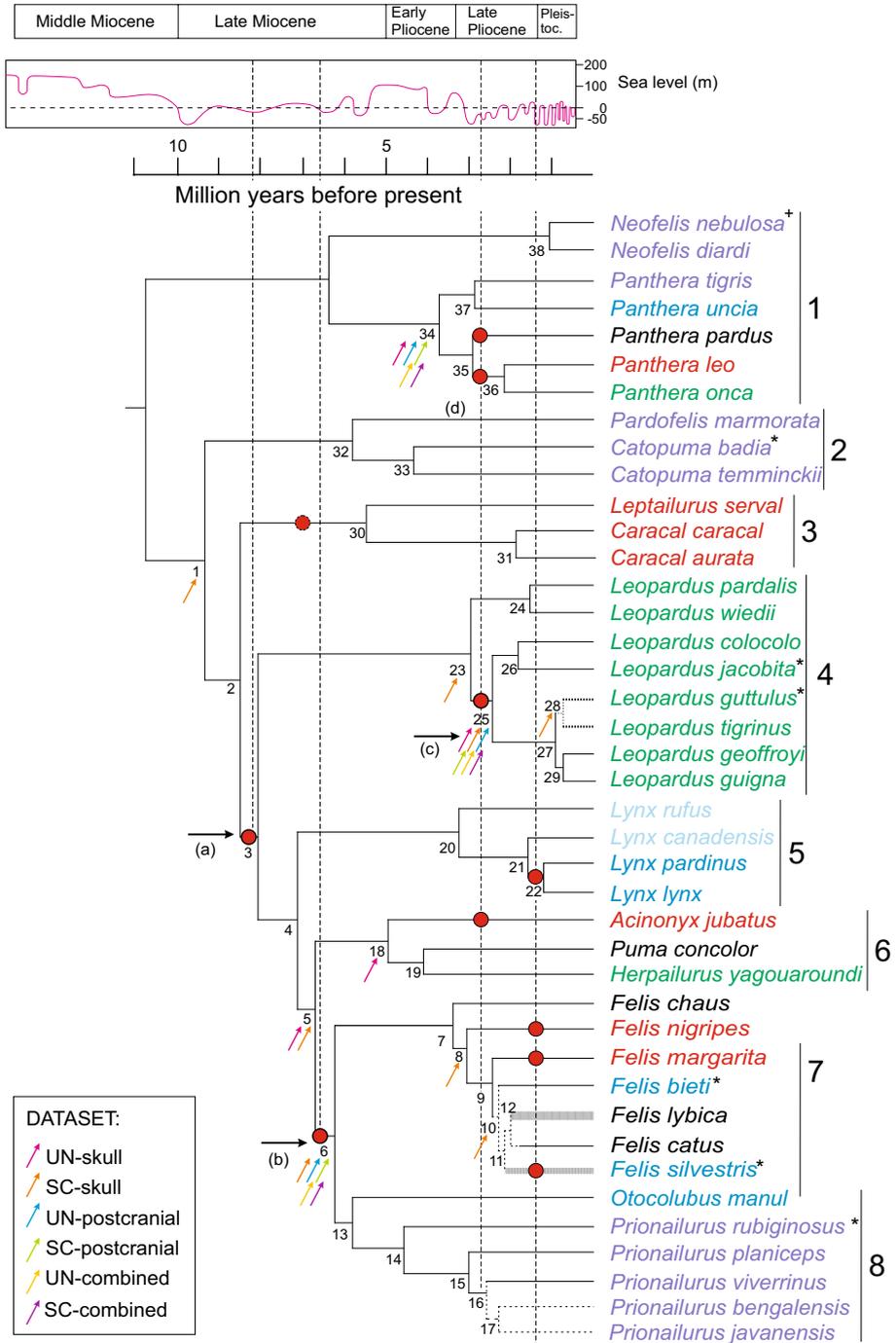
We quantified phylogenetic influence on the ecomorphological structuring using canonical phylogenetic ordination (CPO; Giannini 2003). This phylogenetic comparative method estimates historical effects on comparative data using the monophyletic groups of a cladogram (specifically, partitions of an unrooted network, which equivalent to clades of rooted trees; partition=node numbers in Fig. 1). CPO was originally defined as a multivariate PGLS, with the phylogeny incorporated as an explanatory variable set in a general linear model; this is in contrast with most PGLS, in which the phylogeny is coded in the error term (see Giannini 2003). CPO provides both, the statistical demonstration of phylogenetic signal and the specific-clade composition of that signal, because the explanatory variable set is composed of binary variables each representing one tree partition or clade. Thus, CPO via simulations is able to indicate which clades are significant (sequentially testing inclusion of clades in a final multivariate linear model) and the total variation explained by the selected tree partitions. Therefore, we choose CPO because it provides a complete rendering of the phylogenetic effect on the morphological data: both the size effect (total variance explained by the phylogeny) and the specific clades of that effect, all tested within a Monte Carlo simulation framework. We used the tree from Johnson et al. (2006) modified as shown in Fig. 1 following chiefly Kitchener et al. (2017) to include all species of extant felids. The tree modification consisted in pruning those species no longer recognized by the last taxonomic revision of the Family (Kitchener et al. 2017) and placing the new species considered valid in nodes according to their expected relationship (as in Kitchener et al. 2017). That is, these species were located as sisters of those species of which they were separated; for example, the terminal *Neofelis nebulosa* in Johnson et al. (2006) was split in the two sister species, *Neofelis nebulosa* and *Neofelis diardi* (following Buckley-Beason et al. 2006); or changing a relationship if suggested by new evidence, e.g. *Felis catus* was

Fig. 1 Phylogenetic relationships among 41 extant species of felids reporting significant partitions (arrows; ► Canonical Phylogenetic Ordination) for each analysis of skull, postcranium and combined datasets (see Supplementary Tables S3–S14 for more details). Phylogenetic relationships modified from Johnson et al. (2006) by adding newly recognized species following Kitchener et al. (2017). Dashed lines in the cladogram represent changes from the tree of Johnson et al. (2006). Species colors: blue, Palearctic; red, AF+SWAS; green, Neotropics; violet, Oriental; light blue, Neartic; black, more than one region. Vertical dashed lines, estimated dates for trans-continental migrations; Red dots, trans-continental migrations suggested by Johnson et al. (2006). UN-, untransformed data; SC, size corrected data. *Species with no postcranial data available; +, species with no combined data available. Numbers in clades represent partitions used for CPO analyses. Arrows represent retained partitions after stepwise selection (P value < 0.01). **a** 8.5–8.0 my migration from Eurasia to North America; **b** 6.7–6.2 my migration from North America to Asia; **c** 2.7 my, migration from North America to South America; **d** 2.7 my migration from Asia to Africa and Americas (data from Johnson et al. 2006)

changed as sister of *Felis lybica* instead of *Felis silvestris* after Driscoll et al. (2007) and Geigl and Grange (2018). Tree partitions were tested individually using 4999 Monte Carlo unrestricted permutations run with the program Canoco 4.02 (ter Braak 1995); significant tree partitions (alpha set to 0.01) were included in a forward stepwise model.

We used biogeographic regions suggested by Kreft and Jetz (2010) to construct ensembles by the simple presence of species in each region. We considered 6 regions as biogeographic ensembles: Neartic, Neotropical, Oriental, Palearctic, Tropical Africa and North Africa+South West Asia, but we also analyzed whole continents (see Table 1). Based on published data (e.g. Sunquist and Sunquist 2002, 2009; see Supplementary Table S1), we mapped known ecological features onto the PCA ordination diagram (combined and complete dataset). For prey size preference we followed Meachen-Samuels and Van Valkenburgh (2009b) and recognized three categories: (1) small prey consumers, felines that eat predominantly prey smaller than their own body size; (2) large prey consumers, felines that eat predominantly prey larger than their own body size; and (3) mixed-prey consumers, felines that consume both small and large prey indistinctly or according to availability. For habitat preference we classified three general groups: steppe, savanna, and forest. Lastly, for locomotion type we also followed Meachen-Samuels and Van Valkenburgh (2009b) considering the frequency of climbing: (1) terrestrial, including those species that rarely climb trees; (2) scansorial, species that climb frequently but rarely hunt on trees; and (3) arboreal, species that spend most of their time, and frequently hunt, on trees.

We defined morphotypes by grouping species that were close in morphospace in resulting ordination diagrams of combined dataset analyses, both reduced and complete (Fig. 2B and Supplementary Fig. S10). Using the untransformed “combined-and-reduced” dataset ($N=84$; 35 species), we applied a one-way analysis of similarity (ANOSIM) as implemented in PAST v. 3.12 (Hammer et al. 2001). This multivariate, non-parametric analysis is based on a ranked dissimilarity matrix and lacks normal and similarity-of-variance assumptions (Clarke 1993); ANOSIM was used to test whether the identified morphotypes were significantly distinct from each other in morphospace. This test was applied globally, and in pairwise morphotype comparisons using 9999 permutations. Additionally, we performed D-PGLS, which is a phylogenetic analysis of variance based on a generalization of phylogenetic general least squares (PGLS; Adams 2014). This analysis is appropriate for evaluating trends in high-dimensional biological multivariate data with a phylogenetic component. We applied D-PGLS using the mean axis coordinate (across specimens) for each species in all 28 PCA axes obtained from the PCA based on the same dataset. With D-PGLS we evaluated whether ecomorphs were significantly different among each other while accounting for phylogenetic relatedness. We used the tree modified from Johnson et al (2006; as in Fig. 1) and Grafen’s (1989) method to estimate branch lengths on the



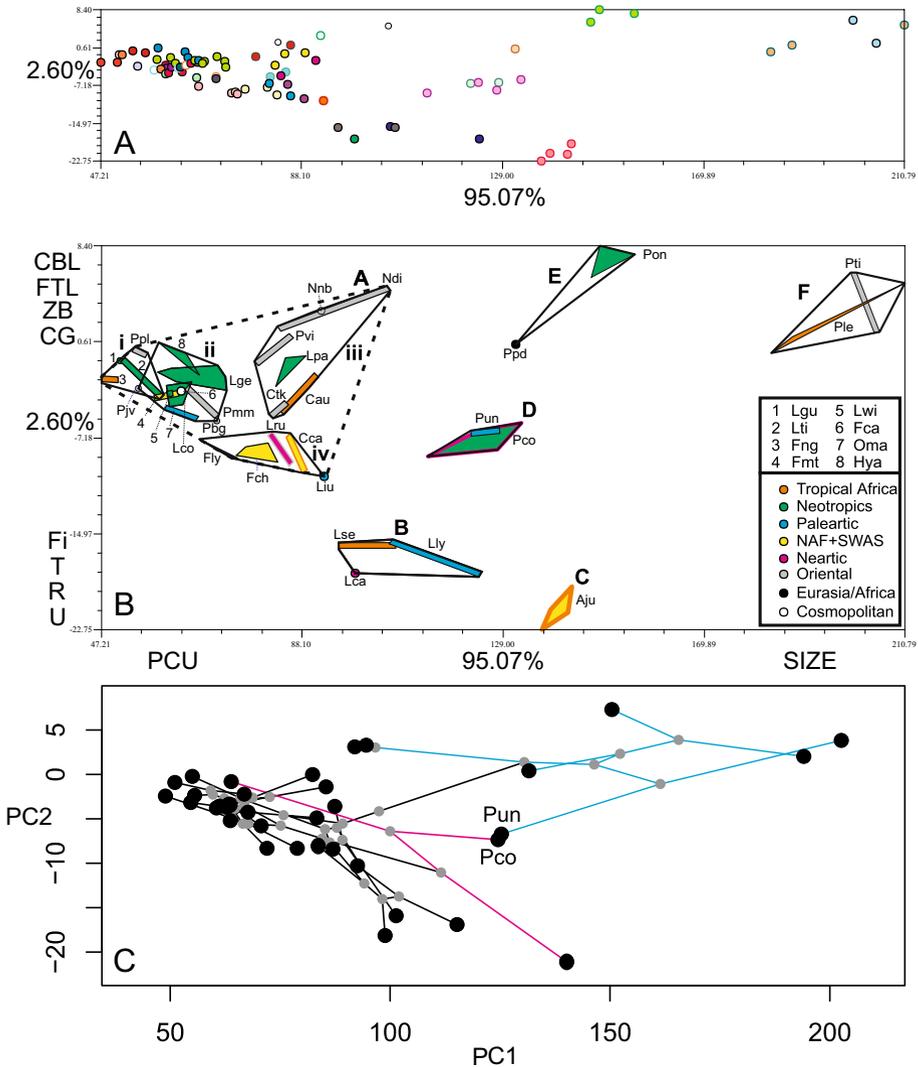


Fig. 2 a, b PCA plot of subfamily Felinae. Combined and reduced dataset (8 cranial + 19 postcranial variables; $N=84$; 35 species). **a** Specimen scores scaled proportionally to the variation of each axis ($\lambda^{0.5}$ for the i th PC axis, with λ representing the i th eigenvalue). Colors represent each species as seen in **b**. **b** Normalized ordination diagram (specimen scores scaled to unit eigenvector). Colors indicate the biogeographic region where the species are present. Polygons represent morphotypes: (A) generalized felids: (1) very small species; (2) small species; (3) mid-sized forest-dwelling species; (iv) jumping species; (B) second group of jumping species; (C) sprinting species; (D) rupicolous, or rock-dwelling species; (E) mid-to-large scansorial species; (F) large, predominantly terrestrial species. Aju, *Acinonyx jubatus**, Cau, *Caracal aurata*, Cca, *Caracal caracal*, Ctk, *Catopuma temminckii*, Fca, *Felis catus*, Fch, *Felis chaus*, Fmt, *Felis margarita*, Fng, *Felis nigripes*, Fly, *Felis lybica*, Hya, *Herpailurus yagouaroundi*, Lca, *Lynx canadensis*, Lco, *Leopardus colocolo*, Lge, *Leopardus geoffroyi*, Lgu, *Leopardus guigna**, Liu, *Lynx pardinus**, Lly, *Lynx lynx**, Lpa, *Leopardus pardalis*, Lru, *Lynx rufus*, Lse, *Leptailurus serval*, Lti, *Leopardus tigrinus*, Lwi, *Leopardus wiedii**, Ndi, *Neofelis diardi*, Nnb, *Neofelis nebulosa**, Oma, *Otocolubus manul*, Pbg, *Prionailurus bengalensis*, Pco, *Puma concolor**, Ple, *Panthera leo*, Pmm, *Pardofelis marmorata*, Pon, *Panthera onca*, Ppd, *Panthera pardus**, Ppl, *Prionailurus planiceps*, Pti, *Panthera tigris**, Pun, *Panthera uncia*, Pvi, *Prionailurus viverrinus*. **c** Phylomorphospace of extant felids obtained using PC1 and PC2 coordinates of combined reduced dataset using *convevol* package in R (Stayton 2015). Colors highlight the lion lineage (blue) and the puma lineage (pink). Grey dots represent internal nodes

phylogeny. We run the analysis with R package geomorph v. 3.3.1 (Adams et al 2020), conducting 999 permutations to assess statistical significance.

We searched for evidence of ecomorphological convergence (considered as a pattern-based concept) among species clustered in the same morphotype using the approach proposed by Stayton (2015). This distance-based technique calculates phenotypic similarity among putatively convergent species (statistic C1 in Stayton 2015) tested with respect to their ancestor; we applied this technique both to distance calculated over the original-variable data matrix, and to the matrix of PCA coordinates (all PCA axes, or rotated matrix), and used the tree modified from Johnson et al (2006) as in Fig. 1. For each species, we calculated the mean of measurements (or axis coordinate) across specimens and this value was introduced in the analysis. The observed C1 statistic was compared to a null expectation generated by 999 simulations of evolution under a Brownian Motion model (Stayton 2015). For convergence analysis we used *convevol* package in R (Stayton 2018; R Core Team 2020).

Finally, we reconstructed extant ensemble configuration by color coding the statistically significant morphotypes present in each ensemble (Fig. 3). On this layout, we reconstructed hypothetical Pleistocene Felinae ensembles by assigning fossil species to the morphotypes they putatively belong in, based on approximate size category, anatomical traits, and phylogenetic relationships (see references in Table 2) and adding them to the extant ensembles' configurations. We added Pleistocene fossil species separately in each major biogeographic

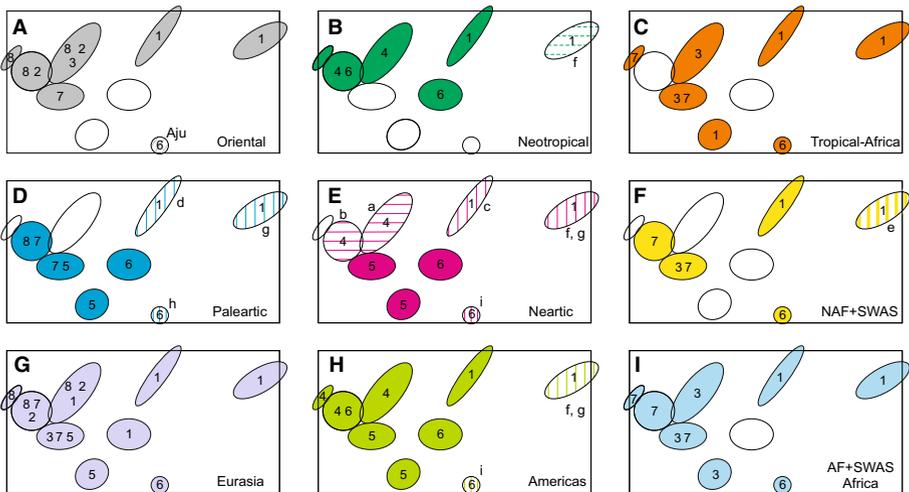


Fig. 3 Comparative morphotype composition of biogeographically defined felid ensembles, current (solid color) and hypothetical (dashed color) after adding Pleistocene species lost to extinction in different ensembles. Oblique dashing indicates that species representing the lost morphotype went extinct in historical times (the cheetah in the oriental region). Vertical dashing indicates morphotypes documented in the fossil record before Pleistocene extinctions in any given ensemble. Horizontal dashing indicates that species representing the morphotype were present in a restricted area of the geographical region before Pleistocene extinctions. Dotted-stripped morphotypes indicate that the presence of the morphotype is negligible in the ensemble (see Table 2). Numbers represent felid lineages present in each ensemble: (1) Lion; (2) Bay Cat; (3) Caracal; (4) Ocelot; (5) Lynx; (6) Puma; (7) Domestic Cat; (8) Bengal Cat. Low case letters represent fossil species as represented in Table 2

Table 2 Pleistocene species mapped to construct Pleistocene Ensembles

Species	Code Figure 3	Phylogenetic relationship/ morpho- type	Pleistocene ensemble	References
Ocelot	a	Ocelot	Neartic	Kurtén, (1965)
Margay	b	Margay	Neartic	Ray (1964) ^a , Kurtén (1965) ^a
Jaguar	c	Jaguar	Neartic	Kurtén (1965), Simpson (1941)
	d	Jaguar	Palaartic	Hemmer et al. (2010), Werdelin et al. (2010)
Lion	e	Lion	NAF+SWAS	Barnett et al. (2006, 2016)
North American lion	f	Lion	Neartic	Morgan and Seymour (1997), Barnett et al. (2006, 2009), Kurtén (1965, 1985), Kurtén and Anderson (1980), Yamaguchi et al. (2004)
			Neotropical ^b	Freudenberg, (1910), Haas et al. (2005), Montellano-Ballesteros and Carbot-Chanona (2009), Barnett et al. (2016),
European lion	g	Lion	Neartic	Barnett et al. (2016)
			Palaartic	Barnett et al. (2006, 2009), Baryshnikov and Boeskorov (2001), Burger et al. (2004), Kurtén (1965, 1985), Kurtén and Anderson (1980), Yamaguchi et al. (2004)
	h	Cheetah	Palaartic	Kurtén, (1968), Christiansen and Mazák, (2008)
North American cheetah	i		Neartic	Morgan and Seymour (1997), Barnett et al. (2005)
Puma-like	-	Puma	Palaartic	Madurell-Malapeira et al. (2010), Cherin et al. (2013)
Lynx	-	Lynx	Africa ^c	Geraads (1980)

In this table are only included those species which represent a morphotype that is currently absent in the ensemble but was present during at least part of the Pleistocene

No extensive enumeration of cites are given, just some selected ones

^aDescribed as jaguarundi, reassigned to *L. wiedtii* by Werdelin (1985)

^bPeruvian record for this species (Lemon and Churcher 1961) has been recently changed to *Panthera onca* (Seymour 2015), the Southernmost records of this species are from Tequisquiatic, Mexico (Freudenberg, W. 1910) and Chiapas, Mexico (Montellano-Ballesteros and Carbot-Chanona 2009)

^cThere is only one record of the lynx lineage in the Pleistocene of Africa, *L. thomasi* (Geraads 1980), in Morocco. This species is considered closely related to *L. pardinus* (Geraads 1980), occurring at the Iberian Peninsula, which during the Pleistocene would have been communicated with the North of Africa (e.g., Carbonell and Rodríguez 2000; Yavedra Sainz de los Terreros 2000). *Puma pardoides* and *Lynx thomasi* not shown in Fig. 3 as the morphotype is represented by extant species

region and continental mass, thereby completing the putative morphotype set per region otherwise lost to extinction (Fig. 3; Table 2).

Results

Each PCA, based on skull, postcranial, and combined datasets (reduced and complete), revealed particular aspects of ecomorphology of the global felid ensembles (see below and Fig. 2a, b, Table 3 and Supplementary Figs. S5-S15 and Table S2). However, postcranial data generally dominated the perceived morphofunctional patterns when combined with skull data (see Supplementary Figs. S5 versus S8 and S10), so the morphospace of the combined analyses were similar to those of the postcranial set. The analysis of the subset of 27 complete skeleton variables presented very similar results to those of the complete dataset of all skeleton (123 variables; see Fig. 2b versus Supplementary Fig. S10). Given this, we centered the discussion on the first set with more specimens and less (thereby redundant) variables (see detailed results in Supplementary Figs. S5-S15 and Table S2).

Complete-skeleton analyses (with the reduced number of morphometric variables) first revealed five contiguous groups defined along the PC1 (Fig. 2a, b and Supplementary Fig. S10). As predicted, these groups represented size, but more precisely concomitant size-related (likely static allometric) variation. An inverse relationship between leg length and skull size was apparent along the PC2: felids in the negative side of PC2 were long-legged, small-headed jumping or sprinting species (PC2 in Fig. 2b and Supplementary Fig. S10; see also Table 3 and Supplementary Table S2).

Patterns observed after mapping known ecological characteristics (locomotion, prey size and habitat) onto this morphospace are shown in Supplementary Figs. S11-S13. Overall, the felid morphospace (PC1+PC2) showed a pattern of species clustered by their common morphology and overall size, which translated into functional similarities. We statistically confirmed the presence of group structuring both using ANOSIM (Mean rank within=455.4; Mean rank between=2015; $R=0.8945$; $P\leq 0.001$) and D-PGLS ($F=47.365$ and $P=0.001$). We identified six major morphotypes in the felid morphospace, and some subtypes, thus totaling nine morphotypes (Fig. 2b and Supplementary Fig. S10). Our pairwise comparisons confirmed the significance of all nine groupings (9999 permutations each, all $P\leq 0.001$; sequential Bonferroni; Table 4). These significant groups included: (A) generalized felids, composed by all small and most median species (see below); within this main group, four subgroups could also be distinguished: (1) very small species, all terrestrial and small-prey hunters; (2) small species, small-prey hunters with various locomotor modes but no specific adaptations for climbing; (3) mid-sized forest-dwelling species, including felids with various locomotor modes and capable to hunt both small and large prey; and (4) small-to-mid-sized jumping species, mostly short-tailed species (all but *F. lybica* Foster, 1780) with extraordinary jumping capabilities. (B) specialized jumping species, with short tail and extraordinary jumping capabilities, but morphologically more derived than other jumping species (5); (C) sprinting species, including the single true sprinter, the cheetah; (D) rupicolous species, placing together *Panthera uncia* Schreber 1775 and *Puma concolor* Linnaeus 1771, thereby supporting Gonyea's (1976) proposal of pumas being primarily adapted to montane environments, in spite of the wide range of habitats occupied by this species; (E) mid-to-large scansorial species, which also hunt large prey; and finally, (F) large species, terrestrial large-prey hunters.

Table 3 Results of principal component analyses for reduced combined dataset with (*R-Comb-ZC*) and without size correction (*R-Comb*; $N=84$; 35 species): loadings of each variable on the first two axes extracted and the corresponding eigenvalues, percent of total variation per axis, and cumulative percentage of successive axes (%ac.)

Variables	<i>R-Comb</i>		<i>R-Com-ZC</i>	
	I	II	I	II
<i>Cranial variables</i>				
ATL	22.4867	5.8916	0.0079	0.0072
CBL	53.5791	14.1670	- 0.0184	0.0014
CG	38.2471	9.1970	- 0.0024	0.0038
FTL	28.9117	9.2767	- 0.0137	0.0061
IOW	13.5939	1.6882	0.0260	0.0080
MeD	14.1058	5.0140	0.0357	0.0262
PC	9.1216	- 1.5442	- 0.0230	- 0.0211
ZB	42.8260	9.2579	- 0.0096	- 0.0025
<i>Postcranial variables</i>				
A	23.1522	2.6559	0.0020	- 0.0084
F	69.2477	- 4.0465	- 0.0166	- 0.0168
Fi	53.0286	- 12.1355	- 0.0239	- 0.0250
GL	17.3612	- 1.8452	0.0402	0.0071
GM	16.3426	- 0.7766	0.0431	0.0048
H	59.9442	- 2.0544	- 0.0170	- 0.0166
HD	16.7434	3.4619	0.0314	0.0132
IQ	22.0292	0.6621	0.0236	0.0037
LDT	30.4505	1.3954	- 0.0004	- 0.0060
LI	30.3134	2.5081	0.0023	- 0.0016
MC	26.0971	3.6836	0.0108	0.0044
P	60.1684	4.4641	- 0.0038	- 0.0023
PQR	31.8648	3.3486	0.0097	- 0.0089
PR	41.2584	- 1.0842	- 0.0010	- 0.0048
PT	- 0.4540	4.7697	- 0.1106	0.0456
R	51.3015	- 10.3512	- 0.0137	- 0.0278
T	54.7688	- 11.6908	- 0.0246	- 0.0250
U	66.2882	- 8.3203	- 0.0154	- 0.0239
WP	12.6876	1.5069	- 0.0065	0.0099
WPI	31.8455	4.1040	0.0085	0.0053
Eigen values				
Λ	41,112.8271	1122.5276	0.0229	0.0072
%	95.0666	2.5957	51.4100	16.0516
% ac	95.0666	97.6623	51.4100	67.4616

For acronyms of variables see Supplementary Figs. S1-S4 and Appendix I

Canonical Phylogenetic Ordination indicated that common ancestry, as predicted, significantly explained from 30.9% and up to 71.4% of the morphological variation in skull, postcranium, and the two sets combined, with and without size-correction (Fig. 1; Supplementary Tables S3-S14). The tree partition that segregated the largest

Table 4 Results of Pairwise comparisons of ANOSIM analysis performed on untransformed combined reduced dataset ($N=84$; 35 species)

	Aii	D	Aiii	C	Aiv	B	Ai	F	E
Aii		0.0001*	0.0001*	0.0002*	0.0001*	0.0001*	0.0001*	0.0002*	0.0001*
D	1		0.0002*	0.0039*	0.0002*	0.0055*	0.0004*	0.0021*	0.0043*
Aiii	0.9468	0.9873		0.0006*	0.0001*	0.0004*	0.0001*	0.0002*	0.0003*
C	1	0.9603	1		0.0006*	0.0155*	0.0031*	0.0078*	0.0314*
Aiv	0.7957	0.999	0.3324	1		0.0003*	0.0001*	0.0001*	0.0004*
B	0.9998	0.7547	0.8583	0.95	0.8588		0.0015*	0.0076*	0.0086*
Ai	0.633	1	0.9847	1	0.9568	1		0.0013*	0.0029*
F	1	1	1	1	1	1	1		0.0089*
E	1	0.7738	0.9983	0.9479	1	0.9688	1	1	

Above, p values after sequential Bonferroni; below, R values for pairwise ANOSIM

*Statistically significant

pantherines [tiger, *P. tigris* Linnaeus 1758; lion, *P. leo* (Linnaeus1758); leopard, *P. pardus* (Linnaeus1758); jaguar, and snow leopard, *P. uncia* (Schreber 1775), partition 34 in Fig. 1] from all other felids was the most important one in all comparative analyses, but the one performed with skull dataset controlled by size (Supplementary Tables S4, S6, S8, S10, S12, S14). Postcranial and combined datasets, both untransformed and corrected by size, selected for the model the same partitions (see Fig. 1), i.e., partition 34 mentioned above, partition 25 (the group inclusive of most small *Leopardus* of the Americas, but *L. wiedii* Schinz 1821 and *L. pardalis* Linnaeus 1758) and partition 6 (the split of the domestic cat and the Bengal's cat lineages from the resto of the felids). Skull datasets incorporated more partitions to the model (especially the size corrected dataset). In the case of the skull dataset corrected by size, the most important group retained was 25 (a subgroup within *Leopardus*) and did not retain 34 in any step of the model (Table S6).

Our analyses allowed recognition of some morphotypes as the evolutionary product of lineage convergence, with evidence for more phenotypic similarity among species from different lineages than expected by chance. Those morphotypes were very small felids (Ai), small felids (Aii), mid-sized forest dwelling species (Aiii), small-to-mid-sized jumping species (Aiv), rupicolous species (D) and large species (F), in both the original-variables matrix and rotated (PCA-axes) matrix analyses (Table 5). This was also evident in the trajectory of descendant species in phylomorphospace (Fig. 2c). The most striking example of phylogenetic trajectory convergence is that of rupicolous *Puma concolor* from the Americas, and the snow leopard, *Panthera uncia*, from the Himalayas and up North to the Gobi and the Southern Siberian mountains (highlighted in Fig. 2c).

Reconstructed Pleistocene ensembles are shown in Fig. 3. Eurasia, Africa and the Americas, all exhibited the nearly complete set of nine morphotypes when Pleistocene fossils were relocated to the morphotype they putatively belong in (but see Africa below). Likewise, major biogeographic regions also recover a wider morphotype set after adding to the corresponding morphotypes those forms lost to Pleistocene extinctions, particularly the Neartic (5 morphotypes added) and the Palearctic (3 morphotypes added).

Table 5 Convergence test quantification as suggested by Stayton (2015) applied with complete and reduced dataset

Morphotype	C1-measurments	P value	C1-coordinates	P value
Ai	0.67698982	0.000	0.67698577	0.000
Aii	0.61377711	0.000	0.61377754	0.000
Aiii	0.68423091	0.000	0.68423207	0.000
Aiv	0.53384161	0.002	0.53384387	0.005
B	0.35332774	0.142	0.35332833	0.134
C	NA	NA	NA	NA
D	0.86351723	0.000	0.86351576	0.001
E	0.3519928	0.121	0.3519930	0.111
F	0.7788214	0.008	0.7788212	0.010

Morphotypes are those observed in Fig. 2. C1 calculates phenotypic similarity among putatively convergent species. C1 measurements include the results obtained using the morphometric matrix directly, with average values of measurements for species with more than one individual. C1 coordinates include results obtained using the coordinates of species of a principal component analysis, with average values of axis coordinate for species with more than one individual. Values in bold indicate statistically significant results

Discussion

Extant ensembles

The observed morphospace of extant felids obtained using skull and postcranial information altogether shows how size-related (likely mostly allometric) variation is a key factor. Size variation can be linked to different ecological aspects of felid species: groups specifically related to PC1 associated with a pattern of substrate use, such as arboreal and scansorial forms successively nested within the wider space of terrestrial forms, thereby restricting arboreality to small-to-mid-size felids (Supplementary Fig. S11). Size was also important when mapping preferred prey size, with PC1 showing a clear contrast between felids that mostly hunt and consume large prey, versus the remaining species, which specialize in hunting small or mix-sized prey (Supplementary Fig. S12). Size would not have such a strong effect on preferred habitats (Supplementary Fig. S13).

The evolutionary drivers for the existence of these groupings are unclear, but it seems likely that interspecific allometric change across species from different felid lineages gave rise to the main morphotypes recognized in this work. Felids are known for their considerable phenotypic plasticity when species co-exist in sympatry (Dayan et al 1990; Dayan and Simberloff 2005; Tellaache et al 2018). At a local scale, character displacement has been proposed among species and even between sexes of co-existing species (Kiltie 1984; Dayan et al 1990). This may apply at a wider geographic scale, for instance within continental ensembles (as could be interpreted when analyzing speciation in the caracal lineage; see Johnson et al 2006). However, at a global scale, observed groupings are not expected as a result of direct competition or sympatric niche partitioning, given that only subsets of species co-occur in one given continent or biogeographic region. Thus, forces driving or affecting the structuring of ensembles at that scale must be different. Remarkably, our results revealed that each global felid morphotype has representatives in several biogeographic regions, with no morphotype being exclusive of any region—not even the sprinting

morphotype, represented solely by the cheetah (Figs. 1, 3). It has been shown that reconstructed dispersal of ancestral species along the evolution of felid lineages has led to the settlement of different ensembles across biogeographic regions (Johnson et al 2006). The pattern we recovered thus reflects either lineage-level convergence of morphotypes across biogeographic regions (statistically demonstrated in six out of nine of the morphotypes recognized in this work), or common origin followed by active dispersal across major biogeographic barriers such as intercontinental ocean expanses. This strongly suggests that part of the involved species are evolutionarily heterogeneous (diverse origin) but ecomorphological equivalents (convergent) across biogeographic regions (Ricklefs 1998; Biggins et al 2011).

The unfolding of the present-day ensemble structure, and the macroevolutionary processes that shaped their differences, are therefore questions emerging from these patterns. Our comparative analyses revealed that phylogeny was one key factor: in our sample, results showed how phylogeny explains significant (and sometimes large) amounts of observed ecomorphological space structuring (see above). Remarkably, two of those significant partitions (see Fig. 1), retained in five or all of the six phylogenetic comparative analyses, coincide with previously proposed intercontinental migrations through Beringia (partition 6 at 6.7–6.2 my) and the Isthmus of Panama (partition 25 at 2.7 my). Also, the segregation of big felids (i.e. lion, tiger, jaguar, snow leopard and leopard) from the rest of the felids was recovered as an important partition with all datasets but transformed skull morphology only (Fig. 1). Other of these partitions defined lineages; partition 18, the puma lineage and partition 23, the ocelot lineage. That is, our analyses identified the key nodes that significantly explained the observed morphological structure, some of which were in turn associated with previously identified major biogeographic processes of intercontinental dispersal (see Johnson et al. 2006).

Pleistocene ensembles

The fossil record suggests that extinctions affected felids along their dispersal process, and after they settled in different continents (e.g., Turner and Antón 1997; Werdelin et al. 2010). Prevalent extinction of the large-terrestrial felid morphotype (Fig. 3) could suggest a connection with megafaunal extinctions (Koch and Barnosky 2006). We argue that Pleistocene extinctions of varying severity, worst in the Neartic due to extensive glaciation along most of the territory, blurred the ample felid ensemble similarity across all major global regions due to a combination of (1) pre-Pleistocene evolutionary convergence, and (2) biogeographic dispersal (e.g. Johnson et al. 2006). It is remarkable that the extinct sabretoothed subfamily Machairodontinae (not covered in this study) was also represented in all the same landmasses as extant Felinae, as well as in most current biogeographic regions (e.g., Turner and Antón 1997; Werdelin et al 2010), thus potentially evolving in parallel the same fate of extant groups.

Interestingly, not all biogeographic regions attained the full set of nine discovered morphotypes after accounting for documented Pleistocene extinctions. Most remarkable pattern was that of the ruficolour morphotype, absent in only one major land mass, Africa, where extensive mountain ranges are lacking, and isolated mountains are smaller and disconnected as compared with other continents (UNEP 2002; Price et al 2013). Also notable is the absence of the jumping, sprinting, and large felids morphotypes in South America, unexpected given the expanses of tropical savannah and other environments used by species of these morphotypes in other continents. In this case, the Panamanian land bridge

must have worked as a strong biogeographic filter (Behling et al 2010; Carrillo et al 2015; Bacon et al 2016), preventing these felid morphotypes (as well as many other different mammals, such as bovids) from colonizing South America. Altogether these patterns suggest two general, underlying factors for a given morphotype to be absent in a given biogeographic region: (1) failure of the species (or its ancestors) to overcome a biogeographic barrier or filter; and (2) lack of suitable habitat in the colonization target area.

Conclusion

Ecomorphological evolution of felids led to the appearance of nine, statistically recognizable morphotypes which originated repeatedly from the eight major phylogenetic lineages of Felinae. Three morphotypes, sprinting, mid-large scansorial, and large terrestrial (Fig. 2b and Supplementary Fig. 10) evolved from the same two lineages (puma lineage and lion lineage; 1 and 6 in Fig. 3) and were present in all land masses, thus requiring intercontinental dispersal for the given morphotype to be established in one given landmass. Morphotypes involving very small, small, mid-sized forest dwelling species, small-to-mid-sized jumping species, rupicolous species (puma and snow leopard) and very large pantherines (tiger and lion) evolved convergently in each land mass from various local lineages. These lineage-dependent processes of dispersal and/or convergence combined, inferred from phylogenetic comparative results, and interpreted in the light of biogeographic processes, led, in our reconstructions of Pleistocene ensembles, to the occurrence of all morphotypes in each major landmass, except when geographic singularities (e.g., lack of extensive mountain ranges, or suitable landbridge for dispersal) prevented arrival, establishment, or evolution of a given morphotype. Pleistocene extinctions further shaped the disparity of continental ensembles we see today by selective extinctions of varying severity. Hypothetical re-composition of extinct lineages in the four major landmasses inhabited by felids (the Americas, Africa, and Eurasia; Fig. 3), and in most large-scale biogeographic regions, rendered a remarkably homogeneous pattern of Pleistocene ensembles across the Globe. This led us to propose that Pleistocene extinctions and geographic singularities, imposed differences in otherwise remarkably uniform global felid ensembles originally shaped by processes of dispersal and convergence.

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Author contributions MMM and NPG conceived the ideas and designed methodology and contributed to the shaping and production of the manuscript. MMM measured all specimens, carried out the statistical analysis and prepared figures, tables and Supplementary Information. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability and material Data deposited in the Mendeley repository: <https://doi.org/10.17632/fntx8pt8fv.1>. Specimens used are stored in the Institutions declared in Material and Methods section.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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