

Evolution of the sabertooth mandible: A deadly ecomorphological specialization



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ABSTRACT

Saber-toothed cats were armed with formidable weapons. They evolved a number of highly derived morphological features, most notably a pair of extremely long upper canines, which makes them unique within the felid family. Although the sabertooth character evolved several times among carnivorous mammals, sabertooth clades mostly had disjunctive occurrences both in space and time, and no sabertooth is alive today. We studied the rates of phenotypic and taxonomic diversification in the mandible of sabertooths, as compared to the rates calculated for both extinct and extant conical toothed cats. We found that the mandible's shape and physical properties in sabertooth clades evolved at distinctly higher rates than the rest of the felid tree. In addition, sabertooths had similar speciation rate to conical toothed cats, but statistically higher extinction rate. The wealth of morphological specializations required to be a sabertooth, and their tendency to focus on large-sized species as prey, was likely responsible for such high extinction rate, and for the peculiar, disjunctive patterns of sabertooth clade occurrence in the fossil record.

1. Introduction

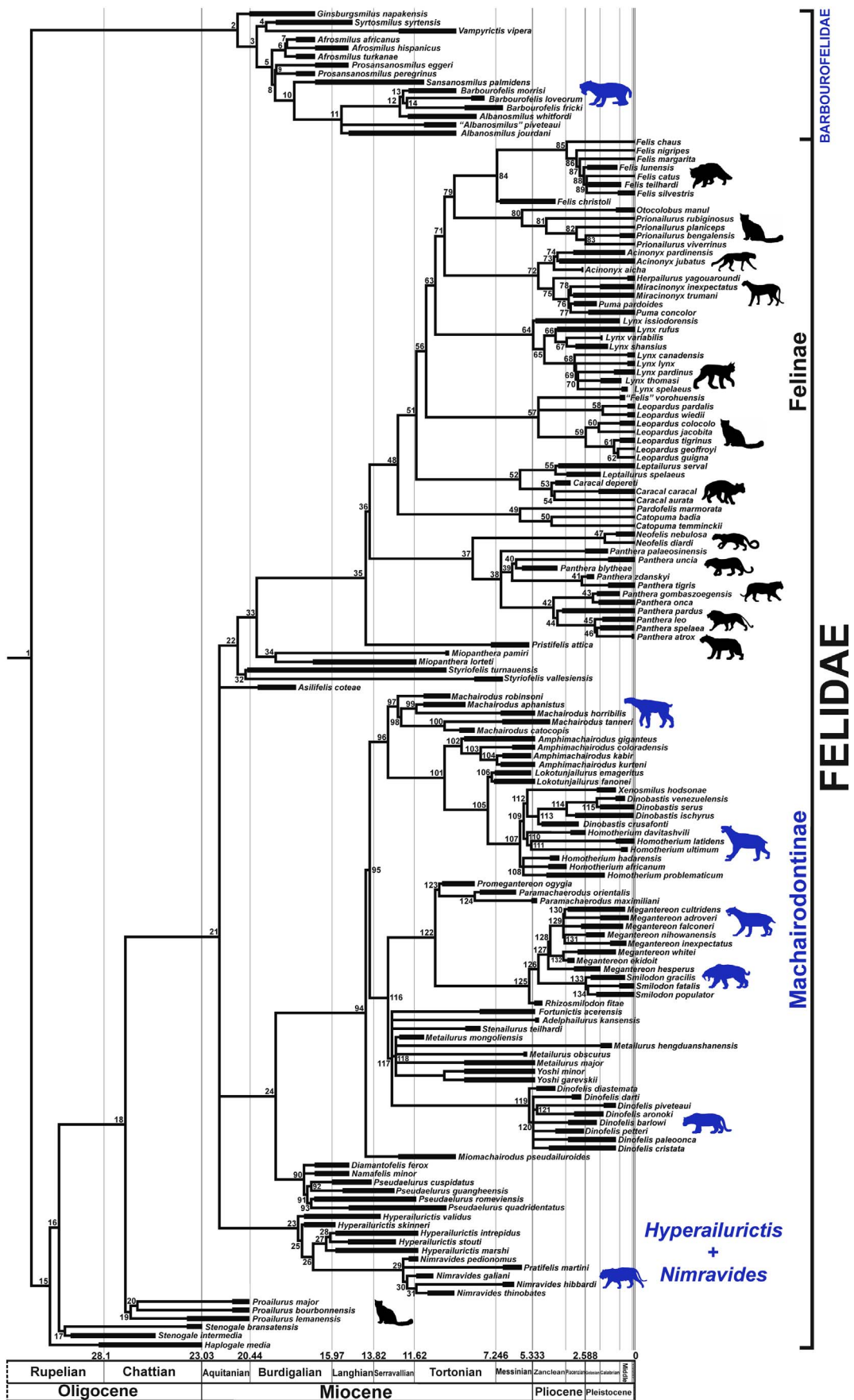
Felids (Mammalia, Carnivora) form a morphologically homogenous, monophyletic clade, including strictly carnivorous species. In contrast to other meat-eating mammals, felids only retain the anterior, slicing portion in their lower molars, while the crushing part (the talonid) is lost (Meloro et al., 2007; Van Valkenburgh, 2007). Felids (Felidae plus Barbourufelidae families) can be ecomorphologically subdivided into two categories: conical-toothed cats and sabertooths (Van Valkenburgh, 2007). The former borrow their name from the shape of their canines in cross section (Martin et al., 2000). They include the modern cat genera such as *Felis*, *Panthera*, and *Acinonyx*. Sabertooth cats were characterized by laterally-compressed, extremely long upper canines, procumbent incisors, reduced coronoid process, and low glenoid fossa

(Christiansen, 2008a, 2008b, 2006; Slater and Van Valkenburgh, 2008). All of these features conferred on sabertooths a unique killing behavior. The success of the sabertooth morphology is testified by its iterative evolution among meat eating mammals (Van Valkenburgh, 2007). Sabertooths are known among Thylacosmilidae, an extinct clade of South American marsupials of the Miocene and Pliocene (Antón, 2013), and Creodonta, which lived in North America in the Paleocene and Eocene (Antón, 2013). Within Carnivora, the sabertooth morphology appeared in the Nimravidae family, which emerged in late Eocene (Bryant, 1991), the Barbourufelidae family (known from the early Miocene, Morlo et al., 2004), and in the true cat subfamily Machairodontinae, which radiated between Miocene and Late Pleistocene (Hunt Jr., 1996; Werdelin et al., 2010).

Sabertooths' highly derived cranial morphology (Christiansen,

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Fig. 1. Phylogenetic tree of all Felidae plus Barbourfelidae taxa included in this study. Black bars indicate stratigraphic durations. Solid lines represent the phylogenetic relationships. Node numbers in the tree identify individual, monophyletic clades. Sabertooth taxa are highlighted with blue silhouettes. *Barbourofelis fricki*, *Miracinonyx trumani*, *Homotherium venezuelensis*, *Megantereon* and *Panthera atrox* images by Zimices. *Felis silvestris*, *Proailurus*, *Prionailurus*, *Smilodon fatalis*, *Nimravides* and *Leopardus* images by Steven Traver (public domain); *Acinonyx* by Nicubunu (public domain); *Lynx* by GrandeChartreuse; *Caraacal aurata* by Roderic Page and Lois Page. *Neofelis diardi* (public domain). *Panthera uncia* and *Dinofelis* images by Lukasiniho. *Panthera tigris* by Sarah Werning. *Panthera leo* (public domain). *Machairodus* image by Dantheman9758. All images except *Felis silvestris*, *Proailurus*, *Prionailurus*, *Smilodon fatalis*, *Nimravides*, *Acinonyx*, *Leopardus* (in public domain), *Panthera uncia* and *Dinofelis* (Creative Commons Attribution-NonCommercial-ShareAlike 3.0) are licensed under Creative Commons Attribution 3.0 license. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2008a; McHenry et al., 2007; Wroe et al., 2008), and the extremely long yet fragile upper canines, did not allow the exploitation of a wide prey spectrum (Mondanaro et al., 2017). The peculiar morphology and narrow feeding niche make sabertooths the most specialized among mammalian carnivores (Binder and Van Valkenburgh, 2010; Emerson and Radinsky, 1980; Goswami et al., 2011; Randau et al., 2013). In ecological terms, specialization usually translates in competitive advantages (or reduced competition) over other guild members. Yet, it may also be associated with increased extinction risk (Cardillo et al., 2005; Colles et al., 2009; Kingsolver and Pfennig, 2004; Raia et al., 2016; Slatyer et al., 2013).

Herein, we collected and analyzed the largest felid plus barbourfelid mandible collection to date in order to better understand the evolutionary processes leading to the sabertooth specialization. We used Geometric Morphometrics to retrieve information on mandible shape and mechanical performance. Then, we inferred a felid plus barbourfelid phylogenetic hypothesis (Fig. 1) to compute rates of morphological evolution, and tested for phenotypic rate shifts in the tree, under the hypothesis that the sabertooth character represents a morphological discontinuity in felid evolution. We further presumed that the acquisition of the sabertooth morphology increased extinction rates (Liow, 2004; Van Valkenburgh, 2007; Raia et al., 2011). To test for this hypothesis, for each of the two felid ecotypes (conical-, and saber-toothed) we calculated diversification rates and its components (i.e. rates of speciation and extinction) directly from the fossil record, and contrasted sabertooth's versus conical-toothed's rates.

2. Materials and methods

2.1. Data and tree

We assembled an informal, time-calibrated phylogenetic supertree containing 157 species representing all extant and extinct valid taxa, as based on the extensive review of the primary literature on felid systematics and phylogeny (see Table S3 and supplementary material for details about the tree preparation). The tree was later pruned to the 88 species (felids plus barbourfelids taxa) for which we had phenotypic data (Table S1), and including all of the species for which at least one complete mandible is known.

Three sets of phenotypes were tested. Shape, as represented by PC axes derived from shape decomposition through geometric morphometrics (see below), loading data calculated by finite element analyses of the mandibles in Piras et al. (2013), and body size (represented by the logarithm of the centroid size, the square root of the sum of squared distances of the landmarks from centroids, derived from geometric morphometrics).

2.2. Geometric morphometrics

We assembled a dataset of 721 felid mandible pictures in lateral view, taken from the scientific literature and from original photographs, representative of 88 species. The choice of mandibles over skulls helps maximizing sample size (because the mandible is a flat bone more likely to be preserved unaltered as a fossil remain), allows 2D analysis, and avoids including functional information in the data unrelated to feeding habitus (because the mandible solely functions as a feeding device, whereas the skull houses the brain and sense organs).

Morphological analyses were performed using Geometric

Morphometrics (Adams et al., 2004). This method retrieves shape data from anatomical objects after removing non-shape information related to size, position and orientation, by means of Generalized Procrustes superimposition (GPA; Rohlf and Slice, 1990). GPA works on a set of homologous landmarks configurations digitized directly on each picture. Procrustes coordinates of each landmark configuration, as produced by GPA, were then subjected to Principal Component Analysis (PCA; Rohlf and Slice, 1990) to decompose shape variation into orthogonal axes of maximum variation. PC scores and the stress variables were eventually used for comparative analyses, and to test for shape and stress differences between ecotypes (sabertooths vs conical teeth) and families, either considering or ignoring phylogenetic effects.

2.3. Stress data

The way physical loadings at biting diffuse across the mandible depends on its shape. Assuming the bone physical properties are constant across mammals, bone geometry could thus be used to infer the degree of loading (stress) across the mandible regions. Finite Element Analysis (FEA) serves this goal, and has been extensively used to infer bone performance for fossil and living mammals (Rayfield, 2007; Piras et al., 2013). Herein, we used the FEA data produced in Piras et al. (2013), focusing on two stress metrics, the Von Mises stress, and surface traction force calculated on the dorso-caudal outline of the coronoid process, which provides the attachment area for the temporalis muscle. Surface traction is the reaction force (the physical loading) exerted at biting (Piras et al., 2013). Von Mises stress is a good predictor of resistance to failure for brittle materials such as bone. It is proportional to the strain energy of distortion mathematically related to the maximum shear stress.

2.4. Rates of phenotypic evolution

There are a number of methods described in literature to compute rates of shape evolution through time, and between clades (Adams and Collyer, 2017; Alfaro et al., 2009; O'Meara, 2012; Price et al., 2016; Revell et al., 2008; Serb et al., 2017). Most of them rely upon a given evolutionary model, typically the Brownian motion, and departures thereof, to identify rate shifts and trend through time. Recently, increased emphasis is given to methods that assume no a priori evolutionary model (Elliot and Mooers, 2014; Thomas and Freckleton, 2012), especially because model-based approaches to the study of trait-linked phenotypic and taxic diversification may be severely flawed (Cooper et al., 2016; Freckleton, 2009). RRphylo (Castiglione et al., 2018) is a recently implemented approach based on the RidgeRace (Ridge Regression for Ancestral Character Estimation) by Kratsch and McHardy (2014) which allows computing a vector of evolutionary rates (β) for a continuous trait over all branches of the phylogeny. This method works without any a priori assumption about the tempo and mode of phenotypic evolution. Under RRphylo, phenotypic evolutionary rates are computed as regression coefficients for each branch of the tree. Furthermore, unlike other PCMs (Phylogenetic Comparative Methods), RRphylo can deal with both extinct and extant phylogenies (Castiglione et al., 2018).

We searched for shifts in the Brownian rate across the tree by means of restricted maximum likelihood fitted with the function brownieREML in phytools (Revell, 2012), in the univariate case, or mvBM in mvMORPH (Clavel et al., 2015) in the multivariate case.

The distribution of evolutionary rates depends on the distribution of branch lengths and on the tree topology (Bapst, 2014). Every phylogenetic tree represents at best a phylogenetic hypothesis, which should be evaluated against alternative topologies, and branch lengths. To account for phylogenetic uncertainty, we wrote an R function that changes the tree topology and branch lengths. For every given species, the function swaps the phylogenetic position up to two nodes distance. For instance, the topology ((A,(B,C)),D) could be swapped to the forms ((C,D),(A,B)); (((B,D),A),C) and so on, but preserving all tip to root distances. In addition, each node age except the root is randomly set at any age between the age of its parental node, and the age of its oldest daughter node.

Once the shifts were located by the multiple rate BM approach, we identified the branches presumed to evolve under the shifted rates. Then, we ran RRphylo 100 times with the ‘swapped’ phylogenies, and retrieved the β rates. At each repetition, we contrasted the β rates of the branches presumed to evolve under the shifted Brownian rate to the β rates of the rest of the tree. This allows testing whether RRphylo rates distribution is consistent with the identification of shifts in the Brownian rate, while accounting for phylogenetic uncertainty.

2.5. Rates of taxonomic diversification

We estimated speciation and extinction rates directly from the fossil record (i.e. without using the phylogeny) using a database consisting of 1914 fossil occurrences (Table S2) representing 227 felid and barbooufelid named species (which were then synonymized, see supplementary material for detail), using the software PyRate (Silvestro et al., 2014a). The record spans from the Late Eocene to the Holocene. We treated the temporal range assigned to each fossil occurrence (based on stratigraphic boundaries) as uncertainties in the dating and generated 10 replicated data sets by randomly resampling the occurrence ages from these ranges (Silvestro et al., 2014b). All PyRate analyses outlined below were therefore repeated on 10 replicated data sets. In a first set of analyses we jointly estimated 1) preservation rates (i.e. expected number of occurrences per sampled lineage/Myr), 2) speciation and extinction times for all lineages in the data set, and 3) speciation and extinction rates (i.e. expected number of speciation/extinction events per lineage/Myr) and their variation through time. PyRate estimates these parameters in a Bayesian framework and we ran 20,000,000 Markov Chain Monte Carlo (MCMC) iterations to sample their posterior distribution. We used a preservation model named Time-variable Poisson Process (TPP), which relaxes PyRate’s default Poisson process (Silvestro et al., 2015, 2011) by estimating independent preservation rates within predefined time frames. We modeled independent preservation rates for each geological epoch between the Eocene and the Holocene. For comparison we also ran the analyses using the default non-homogeneous Poisson process (NHPP) of preservation with rate heterogeneity among lineages (NHPP+Gamma; (Silvestro et al., 2014b). We then combined the results from the 10 replicates and plotted the marginal speciation and extinction rates through time and calculated the estimated times of speciation and extinction of all lineages in the data set. We repeated the analyses on the two felid sabertooth clades by subsetting the initial data set: Machairodontinae (61 species, 629 occurrences) and Barbooufelidae (15 species, 68 occurrences). The times of speciation and extinction of felid lineages as estimated by PyRate provided the input data to the subsequent analyses.

To assess whether average extinction rates are higher in sabertoothed cats than in conical-toothed lineages we implemented a birth-death model where independent extinction parameters are assigned to individual lineages based on their a priori assignment to either category. Lineages for which the ecotype could not be determined were assigned a third independent rate. Under this model (implemented in the latest PyRate release; <https://github.com/dsilvestro/PyRate>), posterior extinction rates for each ecomorphotype (μ_{conical} and μ_{saber} , respectively) are jointly sampled. We ran the analyses for 500,000 MCMC

iterations sampling every 500 iterations. We considered the extinction rates to be significantly different between ecomorphotypes, if δ_{μ} falls outside the 95% credibility interval of the difference between their posterior samples ($\delta_{\mu} = \mu_{\text{saber}} - \mu_{\text{conical}}$). Since conical toothed cats are still living today whereas sabertooths are not, we ran additional tests to assess whether recent extinctions might be affecting the estimated extinction rates associated with each ecomorphotype. To that end, we truncated the analyses at different time thresholds set to at 1, 2.58 (Pliocene/Pleistocene), and 5.33 (Miocene/Pliocene) Ma, respectively. We excluded all taxa that had no fossil occurrence prior to the threshold and considered as extant all taxa with occurrences more recent than the threshold (sabertooth species included). We summarized the estimated extinction rates as described above.

Because extinction rates were suggested to correlate positively with body size (Cardillo, 2005), we further implemented a new model in PyRate, where extinction rates are modeled in a species-specific fashion as a function of both a continuous trait (body size) and a discrete trait (ecotype). The implementation builds upon the Covar model (Silvestro et al., 2014a) and allows to estimate the effect of a discrete trait on extinction rates while accounting for the effect of a continuous trait. Thus, the extinction rate of a species i with body mass b_i and tooth morphology (ecotype) j is expressed as in Eq. (1):

$$\mu_i = \exp(\log(\mu_j) + \alpha_{\mu} \log(b_i)) \quad (1)$$

where α_{μ} is the correlation parameter describing the variation of extinction associated with body mass and μ_j is the mean extinction rate associated with ecotype j . The parameter α_{μ} can take negative or positive values indicating negative or positive correlation with body size, whereas the μ_j values are informative of the mean extinction rate associated to the discrete trait after accounting for differences in body mass.

3. Results

3.1. Geometric morphometrics

The first four PCs explain cumulatively 77.7% of total variance. In particular, PC1 captures 44.7% of shape variance. This axis is a good descriptor of the morphological difference between.

sabertoothed and conical-toothed cats. Positive values of this axis are associated with long and slender jaws typically of modern felids and characterized by the absence of the mandibular flange medially to the upper canines, which is typical of a number of sabertooths. Towards negative values the coronoid process is much lower and the mental process appears, which are two traits typical of sabertooths (Fig. 2).

Mandible shapes differ among monophyletic clades (Table 1) and, more importantly, among ecotypes (i.e. comparing sabertooths to conical-toothed felids). The same differences persist when phylogenetic effects are accounted for (Table 1).

3.2. Rates of phenotypic evolution

A significant rate shift in the felid tree was found to apply to the homotheriini clade within machairodonts for shape. In terms of the variance of the Brownian process calculated for individual clades for the shape data, the largest rates invariably accrue to clades nested within machairodonts (Table 2A, Fig. 3).

In terms of the variance of the Brownian process calculated for individual clades for the stress data, a significant rate shift pertains to the Smilodontini, within machairodonts. Besides Smilodontini, other large rates accrue to the *Hyperailurictis* + *Nirmravides* clade, and machairodonts as a whole (Table 2B, Fig. 4).

Eventually, we found no significant shift in the rate of centroid size evolution.

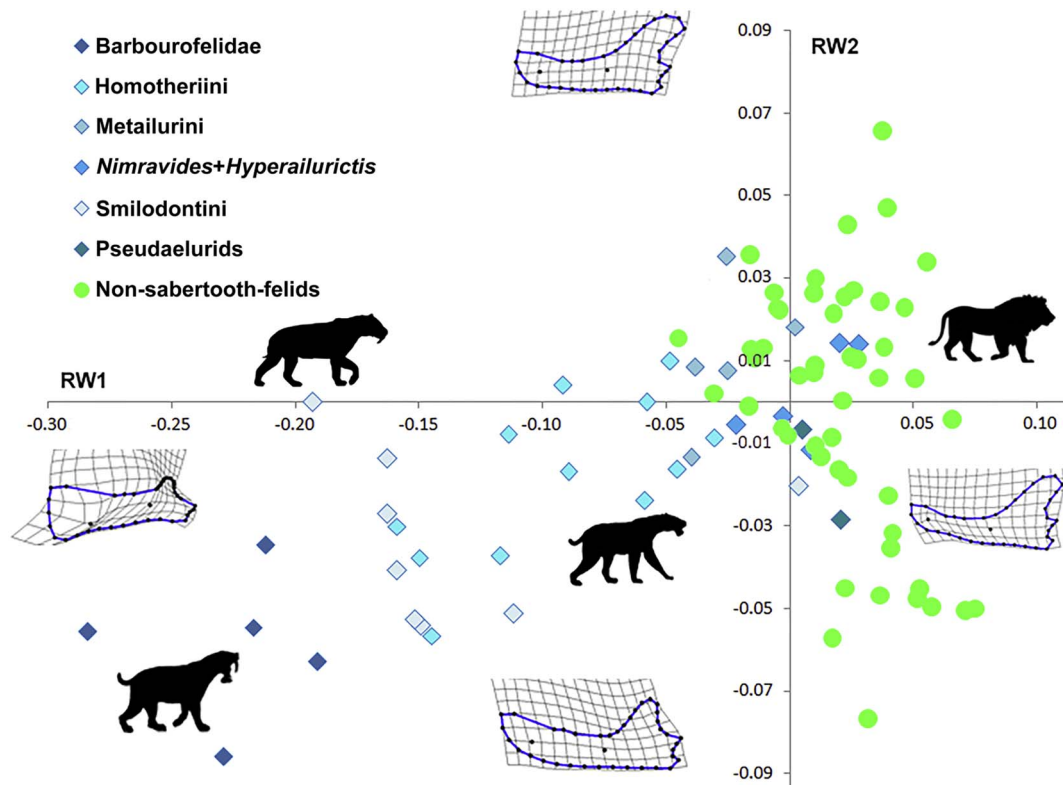


Fig. 2. Plot of PC1/PC2 scores. Clades are reported in the legend. The thin plate spline deformations corresponding to the axes extreme values are reported.

3.3. Rates of taxonomic evolution

Our diversification rate analyses indicate that both felids and barbourfelids diversified under essentially constant speciation rates (Figs. S1–S3) throughout the past > 30 Myr. Overall extinction rates were also fairly stable until the Pliocene and smaller than speciation rates, thus yielding positive net diversification. Towards the recent, and in particular since the late Pleistocene, the extinction rates have increased dramatically from 0.35 (95% CI: 0.26–0.43) in the early Pliocene to 0.99 (95% CI: 0.58–1.34) in the late Pleistocene and Holocene.

In keeping with our prediction, we found that extinction rate was significantly higher in sabertoothed cats. Indeed, the extinction rate in sabertooths was 50% higher than extinction rate in conical toothed lineages: $\mu_{saber} = 0.485$ (95% CI: 0.365–0.603), $\mu_{conical} = 0.322$ (95% CI: 0.253–0.392). The difference in extinction rates is significant with a

posterior probability $P(\mu_{saber} > \mu_{conical}) = 0.991$ (Fig. 5). Truncating the data to ignore recent extinctions from the analysis did not alter significantly the results, indicating that the sabertooth ecomorphotype has been prone to higher extinction rate throughout the Neogene and Quaternary (Fig. S4). These results remained essentially unchanged after accounting in the model for the possible effect of body mass on extinction rates. We found no evidence for a correlation between body size and extinction rates $\alpha_{\mu} = 0.031$ (95% CI: -1.837–1.997) and the extinction rates in sabertooths and conical-toothed lineages remained unchanged.

Per-family analyses reveal machairoidonts diversification rate intensely declined since the beginning of the Pleistocene, by virtue of a threefold increase in extinction rate by that time (Fig. S1). In barbourfelids we found slowly declining net diversification rates, leading to their final demise (Fig. S2), but we did not detect significant rate

Table 1

A. Multivariate analysis of variance in shape and stress data differences among clades (machairoidontinae, barbourfelidae, felinae, hyperailurictinae) and ecotypes (sabertooths versus conical toothed cats). B. Analysis of variance in centroid size differences among clades and ecotypes (sabertooths versus conical toothed cats). Both MANOVA and ANOVA models were repeated taking phylogenetic effects into account ($P_{phylogenetic}$). Shape data: first four principal components of shape decomposition. Stress data: surface traction at the mandible coronoid and Von Mises stress. CS: centroid size.

A							
MANOVA models	Df	Wilks	Approx-F	Numerator Df	Denominator Df	P	$P_{phylogenetic}$
Shape~Clade	4	0.197	10.75	16	245.04	< 0.001	0.001
Shape~Ecotypes	1	0.323	43.47	4	83	< 0.001	0.001
Stress~Clade	4	0.338	9.05	12	215	< 0.001	0.001
Stress~Ecotypes	1	0.489	29.25	3	84	< 0.001	0.001
B							
ANOVA models	Df	Sum-Sq	Mean squares	F-value	P	$P_{phylogenetic}$	
CS~Clade	4	4.57	1.14	8.42	< 0.001	0.002	
CS~Ecotypes	1	4.28	4.28	31.84	< 0.001	0.001	

Table 2
Shifts in phenotypic evolution calculated with the multiple Brownian Rate approach.

A. Shape data			
Rate shift	logL best model	AIC best model	p value
Node (<i>Homotheriini</i>)	822.16	−1568.82	< 0.001
B. Stress data			
Rate shift	logL best model	AIC best model	p value against BM
Node (<i>Smilodontini</i>)	−4001.10	8034.13	< 0.001

shifts (possibly because of lack of statistical power associated with the small size of these datasets). As regards speciation rate, for all felids mean rate is 0.455 species per lineage per million years. Variation within the clades are minimal, being 0.440 for machairodontines, and 0.376 for barbourofelids.

4. Discussion

The mandible is the primary feeding device in carnivores (Meloro and O’Higgins, 2011; Meloro et al., 2008). Hence, understanding its evolution is instrumental to comprehend the evolution of carnivore ecomorphology. Geometric morphometrics indicates a clear separation

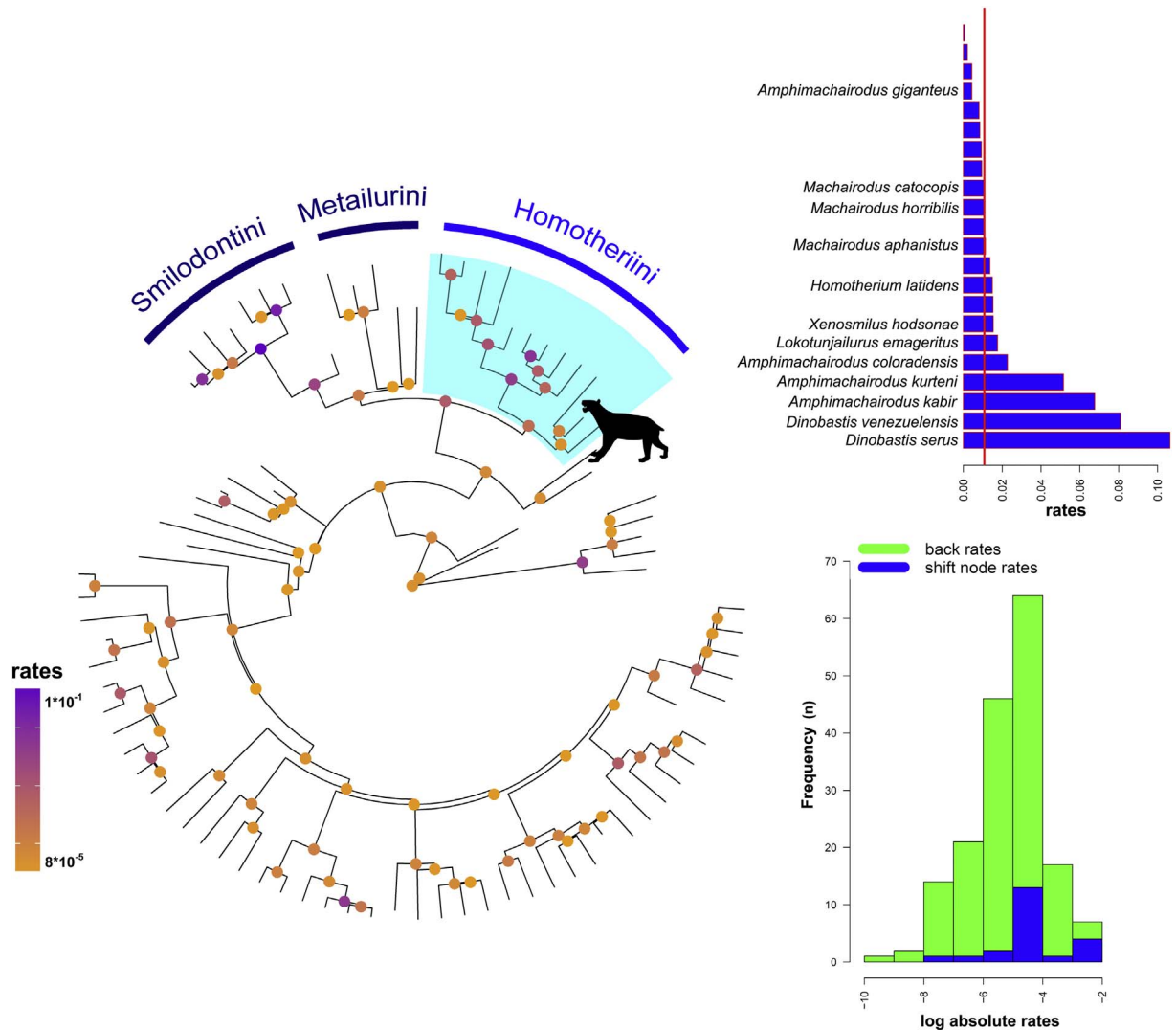


Fig. 3. The evolutionary rates of mandible shape on the Felidae tree. The tree on the left reports RRphylo rates (coloured dots, scaled according to the normalized distribution of absolute rate values, from low (orange) to high (purple) rates). Homotheriini, highlighted with a cyan semitransparent box, represent the only rate shift as indicated by the variable Brownian rate approach. On bottom right, the RRphylo rates (in absolute values) computed for the Homotheriini (blue) are plotted against the rates of the rest of the tree (green). On top right, the absolute rates of individual branches of the Homotheriini clade are collated in increasing rate value (blue bars), and contrasted to the average rate computed over the rest of the tree branches (the vertical red line). Bars without names correspond to internal nodes within Homotheriini. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

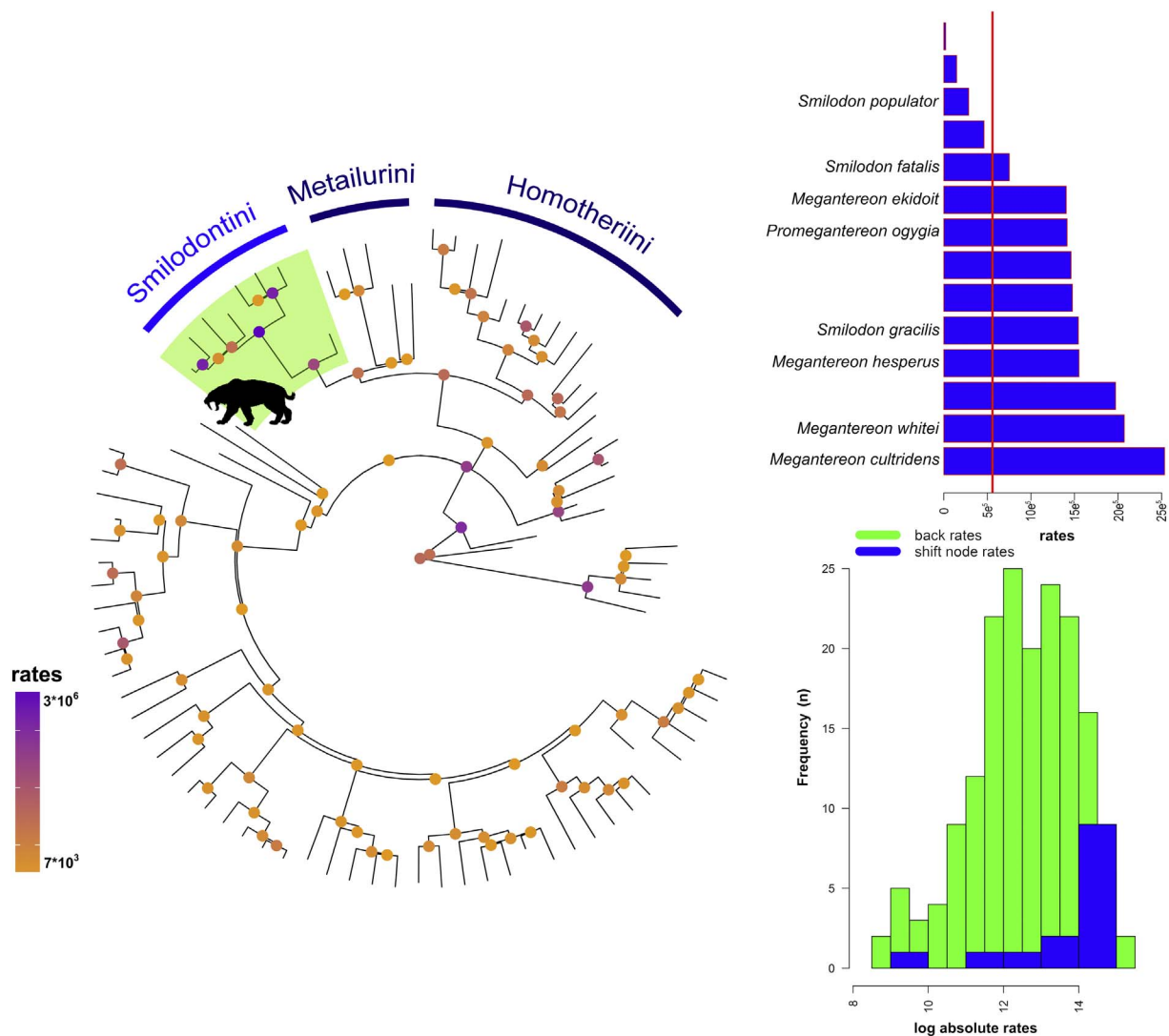


Fig. 4. The evolutionary rates of stress data on the Felidae tree. The tree on the left reports rates computed according to RRphylo (coloured dots, scaled according to the normalized distribution of absolute rate values, from low (orange) to high (purple) rates. Smilodontini, highlighted with a green semitransparent box, represent the only rate shift as indicated by the variable Brownian rate approach. On bottom right, the RRphylo rates (in absolute values) computed for the Smilodontini (blue) are plotted against the rates of the rest of the tree (green). On top right, rates of individual branches of Smilodontini (in absolute value) are collated in increasing rate value (blue bars), and contrasted to the average rate computed over the rest of the tree (the vertical red line). Bars without names correspond to internal nodes within Smilodontini. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

between sabertoothed and conical toothed cats in mandible shape (Fig. 2), which bears a profound adaptive significance. Sabertooths show a considerable reduction of the coronoid process as compared to other felids (Emerson and Radinsky, 1980). Linked to the smaller coronoid there is, in a number of sabertooths, the presence of the mental process, a bony protrusion protecting the extremely long yet fragile upper canines. This structure has been viewed as a compensation for the reduced coronoid (Meloro et al., 2011; Piras et al., 2013). Furthermore, the small coronoid lowers the mechanical advantage of the temporalis muscle (McHenry et al., 2007) and the degree of stretch of the muscle fibers when the jaws open (Van Valkenburgh, 2007). This is deemed to have helped sabertooths to increase jaw gape, which is necessary to effectively use their long upper canines to kill large sized prey (Emerson and Radinsky, 1980; Slater and Van Valkenburgh, 2008).

A significant shift in the rate of mandible shape evolution applies to scimitar-toothed cats (homotheriini) within machairodonts. Yet, in terms of physical loadings on the mandible (stress variables), a rate shift applies in coincidence with the clade including the most extreme, dirk-toothed sabertooths such as *Smilodon*. Interestingly, the third

machairodont clade, metailurini, does not show a significant rate shift in either shape or stress data. Most scholars agree that metailurini converged on modern pantherine cats in morphology and behaviour (e.g. *Dinofelis cristata* is usually perceived as the most pantherine-like of all machairodonts, Barycka, 2007). In addition, Metailurini had relatively shorter canines as compared to other sabertooths (van den Hoek Ostende et al., 2006).

The sabertooth character possibly evolved (or was recruited) for preying upon megaherbivores (Randau et al., 2013; Van Valkenburgh et al., 2015). Such narrow feeding niche (as well as the derived morphology) suggests sabertooths were highly specialized taxa. The virtue of specialization is that it confers immediate ecological advantages over competitors (Cantalapiedra et al., 2011; Holliday and Stepan, 2004), usually by means of large body size (Raia et al., 2012). The effects of specialization on diversification rates are not as easy to predict. On the one hand, it might reduce speciation rates (Rabosky and Hurlbert, 2015; Vrba, 1987). On the other, specialization by evolutionary novelty might promote diversification by expanding clades in novel regions of the morphospace where there is little competition (Ciampaglio et al., 2001; Jönsson et al., 2012). However, it is much more probable that

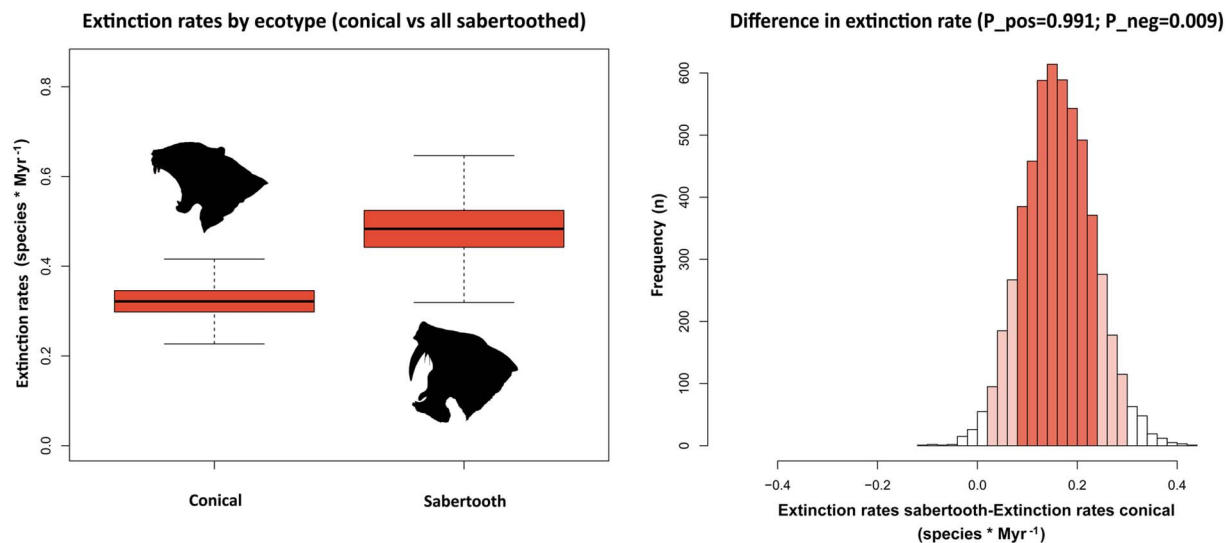


Fig. 5. Boxplot of the extinction rate per ecotype (left) and comparison of the difference in extinction rate per ecotype against null (right).

specialization increases extinction risk (Colles et al., 2009; Raia et al., 2016; Slatyer et al., 2013). Our data point to the latter. Regardless of which clade they actually belong to, our analysis of the fossil record indicates that the average extinction rate in sabertooths is 50% higher than in conical teeth. Since there is no statistically significant difference in speciation rate between the two ecotypes, diversification rate should necessarily be depressed by the sabertooth character. This might help explaining why there never were sabertooths of different clades living in the same ecogeographical region for long, and why sabertooth species are rare in the fossil record overall.

A positive relationship between large body size and extinction risk has been demonstrated to apply in mammals (Cardillo, 2005). Most sabertooth were in fact large by felid standards, which suggests the difference in extinction rate between the two felid ecomorphotypes could be subsidized by body size differences. However, we found no relationship between size and extinction rate in our data, and the pattern itself seems not to be linear (Ripple et al., 2017), and driven by ecological role and commonness, rather than body size per se (Safi and Petteorelli, 2010). Liow (2004, 2007) and Colles et al. (2009) found that morphologically deviant, ecologically specialized taxa tend to endure for shorter in the fossil record, an observation that concurs with the strongly held idea that specialists incur greater extinction risk in living biota (Cardillo et al., 2005; Colles et al., 2009; Kingsolver and Pfennig, 2004; Raia et al., 2016; Slatyer et al., 2013). Sabertooths perfectly fit this category. The significant rate shifts applying to either smilodontini and homoteriini (Figs. 3,4), the development of the peculiar upper canines, and the profound rearrangement of muscle attachments on the mandible, are all strongly suggestive of the fact that sabertooths are 'deviant' by felid standards. This study suggests that such highly derived morphology, coupled with the ecologically narrow niche was responsible for the comparatively short duration of sabertooths in the fossil record.

5. Conclusions

The sabertooth character evolved at least seven times among carnivorous mammals and mammal-like reptiles. Sabertooths shows an exceptionally specialized, highly derived morphology different clades converged upon. While the iterative evolution of the sabertooth character in mammals proves it is an evolutionary success, the extreme craniodental specialization the acquisition of the sabertooth morphology brings about implies increased extinction risk, which probably helps explaining why sabertooths were never very abundant in terms of species, and no sabertooth is alive today.

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