Cranial disparity versus diversity in sabertoothed felids: a case of late morphospace saturation

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ABSTRACT - In this contribution I present the first diversity (number of taxa) versus disparity (explored morphospace) comparison of sabertoothed felids performed on craniomandibular and dental characters. The graphs obtained demonstrate how the morphospace exploration gradually increases in the group through time, reaching a maximum in the late Pliocene and during the Pleistocene. The latter time bins coincide with the appearance of all Eumachairodontia (with the exception of *Amphimachairodus*), i.e. true "saberteeth". This is linked to major cranial modifications connected to the evolution of the characteristic hypertrophied and flattened upper canines. The continuous increase in occupied morphospace indicates that in machairodont felids real morphospace stabilization is never achieved until the Pleistocene, with the total representation of the Eumachairodontia. On the evolutionary level, the general group history seems to show a true Plio-Pleistocene radiation, identified by hyper-specialization, which led to a positive peak in disparity. The evolution of cranial disparity in machairodont felids can be included in the category of 'top-heavy clade', i.e. those groups who show a real radiation relatively late in their history.

Keywords: diversity; disparity; morphospace; sabertoothed felids; Cenozoic.

1. INTRODUCTION

Sabertoothed felids are among the most iconographic carnivorous mammals, known for the evolution of peculiar cranial characters among the most striking of which is the presence of flattened (laterally compressed, bladelike) hypertrophied upper canines. Sabertooth specializations evolve several times (at least four in the Cenozoic) amongst mammalian carnivores including marsupials, Creodonta, Nimravidae, and Felidae (Riggs, 1934; Simpson, 1941; Emerson and Radinsky, 1980; Turner and Antón, 1997; Van Valkenburgh, 2007; Slater and Van Valkenburgh, 2008), probably indicating a successful and alternative killing prey mode in comparison with modern carnivores (Emerson and Radinsky, 1980). For the really pecualiar hypertrophied upper canines, and the inferred narrow feeding niche, sabertooths have been considered as the most specialised among mammalian carnivores (Binder and Van Valkenburgh, 2010; Emerson and Radinsky, 1980; Goswami et al., 2011; Randau et al., 2013; Piras et al., 2018). Piras et al. (2018) found that in sabertooths the average extinction rate is 50% higher when compared to the condition in conical tooth mammals. According to the authors, the combination of

extremely peculias dental structures, along with a very narrow feeding niche, could represent the reason why sabertooths are generally characterised by relatively short duration in the fossil record (Piras et al., 2018).

The extreme specialization of the teeth could be linked to different biological phenomena among which are visual signals for display for access to females (sexual selection) and in agonistic encounters, or in kleptoparasitism (see Slater and Van Valkenburgh, 2008 for a complete discussion on this topic). Other suggested processes are sexual selection on the basis of only limited dimorphism in canine proportions (see Van Valkenburgh and Sacco, 2002; Salesa et al., 2005; Slater and Van Valkenburgh, 2008), and interference competition as a major driver in evolution of hypertrophied upper canines (see Slater and Van Valkenburgh, 2008). Recently, O'Brien (2019) analyses and discusses the static intraspecific scaling relationship between the size of saber-tooth canines and body size, to investigate if such peculiar structures can be interpreted as sexually selected signals. Following the same procedure found in O'Brien et al. (2018), expectations are that if the size of canine are really the result of strong sexual selection, then a significantly steeper scaling relationship between canine size and

body size should be obtained, compared to those of the reference traits and body size. On the base of 25 *Smilodon fatalis* skulls measured from The Felidae of Rancho La Brea (Merriam and Stock, 1932), O'Brien (2019) found not significant differences in scaling relationship between canine size and body size, with respect to the reference traits vs. body size. Thus, the analysis suggests that in *S. fatalis* the evolution of hypertrophic canines is not linked to a strong sexual selection signal, rather the canine "*may represent a rare case of a pure weapon, where individual quality is not encoded in the relationship between canine size and body size and canine size therefore serves no signal function*" (O'Brien, 2019, p. 6).

The most probable explanation for sabre tooth development has a functional origin linked to predatory behavior (Akersten, 1985; McHenry et al., 2007; Slater and Van Valkenburgh, 2008). According to Salesa et al. (2005) the reduction of risk during hunting (bone or tooth breakage) through a very fast lethal bite performed by long flattened upper-canines, represented the major ecological constraint and trigger of the hyperspecialized cranial characters during sabertooths toothed evolution.

Cranial evolution in sabertooths is characterized by the presence of particular features among carnivorous mammals including: a more vertical occipital plane, reduction of the coronoid process of the mandible, upward rotation of the palate and jaw joint ventrally displaced. All these modifications have been accompanied by re-organization of jaw musculature (to prevent muscle over-stretching in wide gaping) and especially to increase gape (see Emerson and Radinsky, 1980; Bryant, 1996; Martin, 1998a; Salesa et al., 2005; Slater and Van Valkenburgh, 2008). According to several authors the overall body and skull construction in machairodont felids suggest a mode of hunting directed at larger prey relative to that hunted by felines (Emerson and Radinsky, 1980; Akersten, 1985; Rawn-Schatzinger, 1992; Turner and Antón, 1997; Salesa et al., 2005). In particular, the strong forepaws of machairodonts would be able to overwhelm larger mammals, and then kill them quickly via a throat cutting bite (Martin, 1980; Turner and Antón, 1997; Antón and Galobart, 1999; Sunquist and Sunquist, 2002; Christiansen, 2007; Christiansen and Adolfssen, 2007; Salesa et al., 2015). Several authors have pointed out that canine-shear bites to the throat severing vital bloodvessels is a more effective killing strategy that targeting the abdomen, offering lesser possibilities for the canines to break after coming into contact with a bone during the bite (see Emerson and Radinsky, 1980; Valkenburgh, 2001, 2007; Salesa et al., 2005). Antón and Galobart (1999) described and discussed a peculiar flexible and long neck in sabertooths, which was crucial to enable a precise orientation of the head during attack, focusing the bite on specific body areas of the prey. This structure of the neck, at the same time facilitated power and precision in attacks protecting the canines from breakage by impacting the bones of prey (Antón and Galobart, 1999).

Figueirido et al. (2018) analysed the killing behavior of the scimitar-toothed *Homotherium serum* and the dirk-toothed *Smilodon fatalis*, using a quantitative approach on skull functionality and a comparative sample of living carnivores. In the study, the authors combined the distribution of trabecular and cortical bone in coronal sections of skulls (as a proxy for skull flexibility and stiffness), and finite element analysis (3D biomechanical modeling simulation), in order to investigate the skull load under several killing strategies. The extremely thick skull, with low percentage of trabecular bone, led to the interpretation of a stabbing canine-shear bite for *S. fatalis*, indicated by a consistent investment in cranial strength. In fact, in the modeling simulation, *S. fatalis* shows the least stress during a stabbing bite, and the large percentage of cortical bone indicates a skull structured to better resist larger and more localized stresses, with respect to the condition found in the scimitar-toothed *H. serum* and in the lion. Differently, the skull of *H. serum* is characterised by more trabecular bone, providing greater flexibility and greater resistance to compression and shear (see Carter and Hayes, 1977; Reddy et al., 2009; Guede et al., 2013; Mostakhdemin et al., 2016), with an inferred predatory behavior in between the canine-shear bite of *S. fatalis* and the clamp-and-hold technique characterizing extant lions (Figueirido et al., 2018).

Chimento et al. (2019) on the base of two *Smilodon populator* specimens from the upper Pleistocene Guerrero Member of the Luján Formation, and from the Corralito locality (Río Tercero department, Córdoba province) of Argentina, discuss some interesting aspects of the species autoecology and about the possible utility of the hypertrophic upper canines in the taxon. In particular, the two specimens are characterised by an opening at mid-width within the rostral end of the frontals, close to the suture between the nasals. The opening in one specimen can be interpreted as a peri-mortem damage, since the principal hole is surrounded by small depressed fractures; conversely, in the second specimen the hole shows bone healing, remodeling, and periosteal reactivity, thus indicating a pre-mortem damage and the survival of the individual for a quite long period. On the base oh hole shape and size, Chimento et al. (2019) ascribe the injuries to another *Smilodon* specimen during agonistic interactions, as already suggested by Geraads et al. (2004) for the hole found on the skull of machairodontine *Machairodus* and interpreted as made by a specimen of the same taxon. According to some authors (Bohlin, 1940; Kurtén, 1952), canines in saber-toothed cats were not useful for prey attack, with a very weak bite; however, such hypothesis is contrasted by Chimento et al. (2019), who stressed that canines in *Smilodon* were strong enough to penetrate bone and could be used in both interspecific and interspecific fighting. On the base of this new evidence, and on the cranial hole described for *Machairodus*, Chimento et al. (2019) concluded that intraspecific combat had to be a fairly common behavior within machairodontines,

with intraspecific fighting between males for mates and territory. Similar intraspecific injuries in extant mammals are known for example in *Acinonyx jubatus, Leopardus pardalis, Panthera onca* and *Puma concolor* (Azevedo et al., 2010; Galantine and Swift, 2007; Thompson, 2011), with combats that frequently led to the death of one of the individuals (Hunter and Skinner, 1995; Amstrup et al., 2006; Lourenço et al., 2014).

Recently, Paijmans et al. (2019) present partial mitogenome sequences from two lineages of Machairodontinae, *Smilodon* and *Homotherium*, based on one *S. populator* sample and three *Homotherium* sp. samples. The analysis confirmed that the Machairodontinae constitute a strongly supported clade, well differentiated from all living felids. The mitogenome indicatates that *Homotherium* occurred in Europe over 200,000 years later with respect to previous interpretation. In addition, a deep divergence between *Smilodon* and *Homotherium* of about 18 million years is detected, thus with an Early Miocene separation into the tribes Smilodontini and Homotherini. An interesting finding by Paijmans et al. (2019) is that all Late Pleistocene *Homotherium* should be referred to a single species, *H. latidens*, as indicated by a low genetic diversity in the analysed mitogenome sequences; a similar conclusion had already previously been proposed on the base of morphological evidences (Ballésio, 1963; Jefferson and Tejada-Flores, 1993; Koot, 2007; Koot et al., 2009).

Despite the machairodont felids being the subject of numerous research publications (e.g. Radinsky and Emerson, 1982; Turner and Antón, 1997; Sardella, 1998; Geraads et al., 2004; Barnett et al., 2005; Christiansen, 2006, 2008a, 2008b, 2008c; Salesa et al., 2010; Werdelin et al., 2010; Rincón et al., 2011; Paijmans et al., 2017; de Bonis et al., 2018; Figueirido et al., 2018; Manzuetti et al., 2018; Piras et al., 2018; Vislobokova, 2018; Chimento et al., 2019; Damián Ruiz-Ramoni et al., 2019; Janssens et al., 2019; O'Brien, 2019; Reynolds et al., 2019), with new specimens also being recently described (e.g. Wallace and Hulbert, 2013; Antón et al., 2014; Madurell-Malapeira et al., 2014; Monescillo et al., 2014; Siliceo et al., 2014; Zhu et al., 2014; Deng et al., 2016), there are few cladistic analysis based on parsimony for the group. Traditionally phylogenetic relationships between the various taxa were based on phenotypic approaches (see Christiansen, 2013). Christiansen (2013) undertook the first phylogenetic analysis of Machairodontinae based on parsimony. This included 18 ingroup taxa and four outgroups for character polarization, and was based on a matrix of 50 craniomandibular and dental characters. The most important result of the new analysis is that the traditional phenetically inferred group including Metailurini (*Metailurus, Dinofelis*), Smilodontini (*Promegantereon, Megantereon, Smilodon*) and Homotherini (*Machairodus, Amphimachairodus, Homotherium, Xenosmilus*) (see Martin, 1998b; Kurtén and Werdelin, 1990; Turner and Antón, 1997; Sardella, 1998; Antón and Galobart, 1999; Werdelin et al., 2010; Rincón et al., 2011) is

not recognized by the cladistic parsimony analysis, and these taxa are in fact paraphyletic. In addition, *Megantereon* and *Smilodon* are not in a sister taxon relationship, as traditionally inferred on basis of overall similarity. A second important outcome of the analysis is the recognition of a well-supported monophyletic group of felids comprising *Megantereon, Smilodon, Amphimachairodus, Homotherium* and *Xenosmilus*, and is characterized by true "saberteeth" (see Christiansen, 2013). For this group Christiansen (2013) proposed the name Eumachairodontia which incorporates true sabercats with hypertrophied, greatly flattened upper canines.

Over the last few decades several studies relating to skull anatomy and morphometry in sabertoothed felids were conducted (e.g. Emerson and Radinsky, 1980; Duckler, 1997; Antón and Galobart, 1999; Salesa et al., 2005; Therrien, 2005; Christiansen, 2007, 2008d; Slater and Van Valkenburgh, 2008; Prevosti et al., 2010). Recently, Piras et al. (2018) analyse the rates of taxonomic and phenotypic diversification in the mandible of sabertooths, with comparisons with both extinct and extant conical toothed cats. The study shows that sabertooth evolved at consistently higher rates with respect to the rest of the considered felids. In general, geometric morphometrics applied to mandible shape shows a clear separation between sabertoothed and conical toothed cats. However, an analysis that takes into account the quantitative trend of occupied cranial morphospace through their evolutionary history has still not be undertaken. In this contribution, I use the dataset presented by Christiansen (2013) to conduct the first exploratory study on the relationship between disparity (i.e. occupied morphospace) and diversity (expressed as the number of taxa) in machairodont felids.

Studies on the relationship between diversity and disparity during the evolution of a group have led to very interesting results in the macro-evolutionary field, both for invertebrates (e.g. Lofgren et al., 2003; Villier and Eble, 2004; Scholz and Hartman, 2007; Glaubrecht et al., 2009; Whiteside and Ward, 2011; Hopkins, 2013; Romano et al., 2018a) and vertebrates (e.g. Brusatte et al., 2008; Slater et al., 2010; Prentice et al., 2011; Benson et al., 2012; Ruta et al., 2013; Hipsley et al., 2014; Larson et al., 2016; Romano, 2017; Romano et al., 2017, 2018b). Amongst the most interesting trends recognized is a possible extended decoupling between disparity and diversity (e.g. Hopkins, 2013; Ruta et al., 2013; Halliday and Goswami, 2015; Marx and Fordyce, 2015) and recognition of a trend to great initial disparity in several clades, followed by a stabilization or decrease in occupied morphospace (see Gould et al., 1987; Foote, 1994, 1995, 1999; Eble, 2000; Huntley et al., 2006; Marx and Fordyce, 2015).

In this contribution, the discrete character dataset of Christiansen (2013) is used to quantitatively study whether disparity and diversity are coupled in machairodont felids during evolution of the group or if, the explored morphospace and the number of taxa follows a different

trend from Miocene to Pleistocene. Similarly, I have also investigated whether a basal radiation is found also in this calde, in connection to key innovations and new available niches explored, or if otherwise the occupation of the morphospace coincides with the half of the history of the group (absence of temporal asymmetry, see Gould et al., 1987), or with its terminal part ('top-heavy clade' *sensu* Gould et al., 1987).

2. MATERIAL AND METHODS

For the disparity analysis, the original matrix by Christians (2013) was used, however, obviously not considering the outgroups. The in-group taxa are: *Amphimachairodus giganteus, Dinofelis barlowi, Dinofelis cristata, Dinofelis petteri, Homotherium crenatidens, Homotherium latidens, Homotherium serum, Machairodus aphanistus, Megantereon cultridens, Megantereon nihowanensis, Megantereon whitei, Metailurus major, Metailurus parvulus, Nimravides* ssp., *Promegantereon ogygia, Smilodon fatalis, Smilodon populator* and *Xenosmilus hodsonae*. Since the publication of the work of Christiansen (2013) new taxa have been described. Accordingly the current taxonomic diversity of the group is slightly greater with respect to that considered in the present work. However, for the disparity the taxa present in the original matrix were used for compliance with the original dataset. The matrix, comprising 18 taxa and 50 discrete characters, is provided in Appendix 1. To be consistent with the original analysis and for compliance with the original dataset, the disparity-diversity analysis was conducted at the species level. Some authors consider the species level approach to be preferable for disparity (Smith and Lieberman, 1999). Other studies have empirically demonstrated that equivalent signals can be obtained by sampling at the genus and species levels (see Foote 1995, 1996). It must also be stressed out that disparity calculation depends also on sampling recovery and on phenotypic diversity within genus.

The new matrix was subjected to a Principal Coordinates Analysis with the software PAST 3.10 (Hammer et al., 2001), by using the 'Gower' similarity index (c=2 Transformation Exponent), usually preferred with respect to the Euclidean distance (Hammer, 2013). The resultant score values (Appendix 1) were used to calculate the disparity for each time bin (see below), calculated both as the sum of variance and as the sum of the ranges. According to some authors (Wills et al., 1994; Prentice et al., 2011) the sum of ranges essentially measures the amount of overall morphospace occupation, and is empirically more robust in relation to taxonomic lumping and splitting (Wills et al., 1994, Brusatte et al., 2012). Differently, the sum of variance can be considered as an indication of the dispersal of considered taxa within the morphospace (Foote, 1997; Erwin, 2007; Ruta, 2009; Prentice et al., 2011), and is robust with respect to irregular sampling over time (Wills et al., 1994; Butler et al., 2012; Brusatte et al., 2012).

The variance obtained for each time bin results as the sum of univariate variances, being essentially equivalent to the sum of the eigenvalues (Van Valen, 1974, 1978) and to the mean squared Euclidean distance between the centroid and each point in the analysis (Eble, 2000).

For the analysis of disparity and diversity through time, six time bins were selected using the time calibrated tree of Christiansen (2013, p. 548, Fig. 2). The time bins are: 12-10 Ma, 10-8 Ma, 8-5.33, 5.33-4, 4-2.58, and Pleistocene (from 2.59 Ma). The time bins have been selected to have an average duration of about 2 million years, and in order to have the occurrence of at least two taxa for each time bin necessary for the diversity analysis. The disparity calculated, both as the sum of ranges and variance, has been plotted along with diversity (the latter calculated simply as the number of taxa for each time bins) and the results are shown in figures 1 and 2. The matrix has been subjected to analysis of Principal Coordinates in PAST 3.10 (Hammer et al., 2001), by using the 'Gower' similarity index (c=2 Transformation Exponent), which is preferred to the simple Euclidean distance (see Hammer, 2013). The first two principal coordinates account for about the 79% of the total detected variance. The scatter plots of the Principal Coordinates analysis are also shown in figure 3, with convex hulls connecting the taxa both according to the classical scheme in Metailurini (*Metailurus, Dinofelis*), Smilodontini (*Promegantereon, Megantereon, Smilodon*) and Homotherini (*Machairodus, Amphimachairodus, Homotherium, Xenosmilus*), and using the new group Eumachairodontia (*Megantereon, Smilodon, Amphimachairodus, Homotherium* and *Xenosmilus*) identified by Christiansen (2013).

A graphic representation of the morphospace of machairodont felids through time is provided in figure 4, with the highlighted area indicating the explored morphospace for each time bin. The sum of ranges and variance was calculated separately for the individual groups of Metailurini, Smilodontini, Homotherini and Eumachairodontia, including all taxa considered in the study, regardless of the time bins identified. The results are shown in figure 5.

3. RESULTS

In figure 1, the trend of the disparity calculated through the sum of the variance is shown in relation to diversity. The curves show how diversity had an absolute minimum at the beginning of the evolutionary history of the group (12-10 Ma) and continually increased to reach its maximum in the Pleistocene. Diversity plateaus between 10 and 5.33 Ma, and an 'acceleration' in the appearance of taxa is observed from the Pliocene-Pleistocene boundary (2.58 Ma). Disparity as sum of variance was quite high at the beginning of the evolutionary history, reaching a maximum between 10 and 8 Ma. From this point onwards it shows a general decline trend throughout the evolutionary history of the group, with a minimum at the Pliocene-Pleistocene boundary, and then rising again in

the Pleistocene. The values of the Pleistocene are always lower than those characterizing the Miocene time bins.

Figure 2 shows the relationship between disparity, which is calculated as sum of the ranges compared to diversity. In this case the smaller disparity determined coincides with the first time bin considered, and the occupied morphospace appears to grow throughout the evolutionary history of the group. As for diversity, this reaches a peak in the Pleistocene. In the third time bin (8-5.33) the disparity shows a slight decline, whereas between 5.33 and 2.58 Ma the increase in occupied morphospace undergoes a slight deceleration.

Scatter plots of the Principal Coordinate Analysis are provided in figure 3. The scatter plot in Figure 3A shows the arrangement of the taxa considered subdivided the groups Metailurini, Smilodontini and Homotherini according to classic phenetical classification. Species of the genus *Homotherium* fall very close to each other in the graph, indicating a very compact cranial morphospace for the group. The same is observed for the genera *Smilodon* and *Megantereon*, which form an equally compact cluster.

Homotherini (blue) and Smilodontini (red) occupy a large area of morphospace, especially along the Principal Coordinate 1.

Conversely the Metailurini (green) is very compact, with significantly lower explored morphospace when compared to the Homotherini and Smilodontini. While there is no overlap between the morphospaces of Homotherini and Smilodontini, a small overlap is found between Metailurini and Homotherini, as the species *Metailurus parvulus* falls completely within the morphospace explored by the Homotherini.

The change in morphospace occupation through time is shown in Figure 4. Starting from the first time bin, a progressive increase in morphospace is observed, and a general shift towards the right portion of potential morphospace. The increase is found both along the Principal coordinates 1 and 2, even though throughout the Miocene the extension along Principal Coordinate 2 is quite low. The first major extension of morphospace is observed in the Pliocene two time bins, and the greatest explored morphospace is found in the Pleistocene,
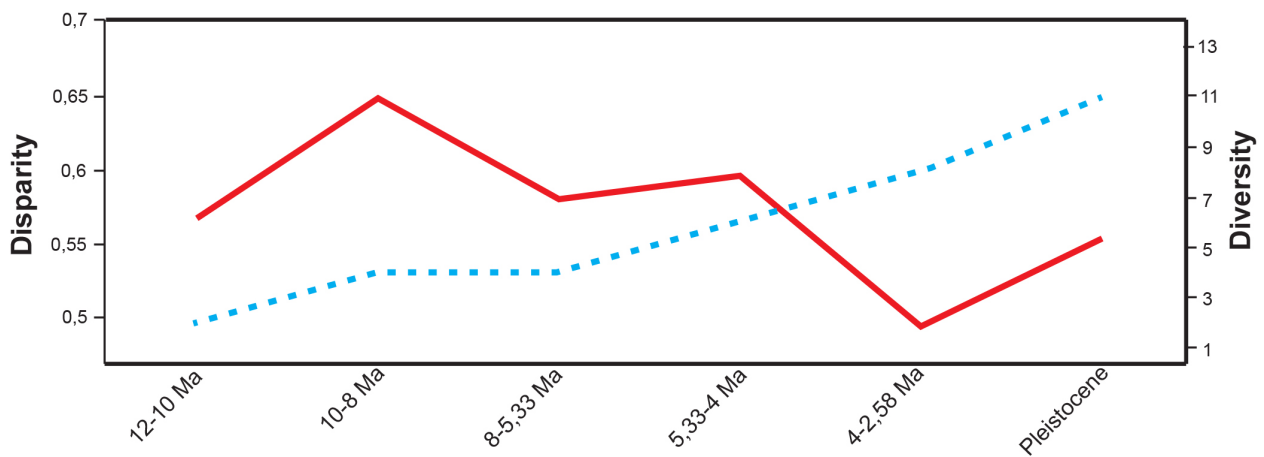

Fig. 1 - Scatter plot of diversity vs. disparity as total variance. Diversity: dotted blue line. Disparity: solid red line.
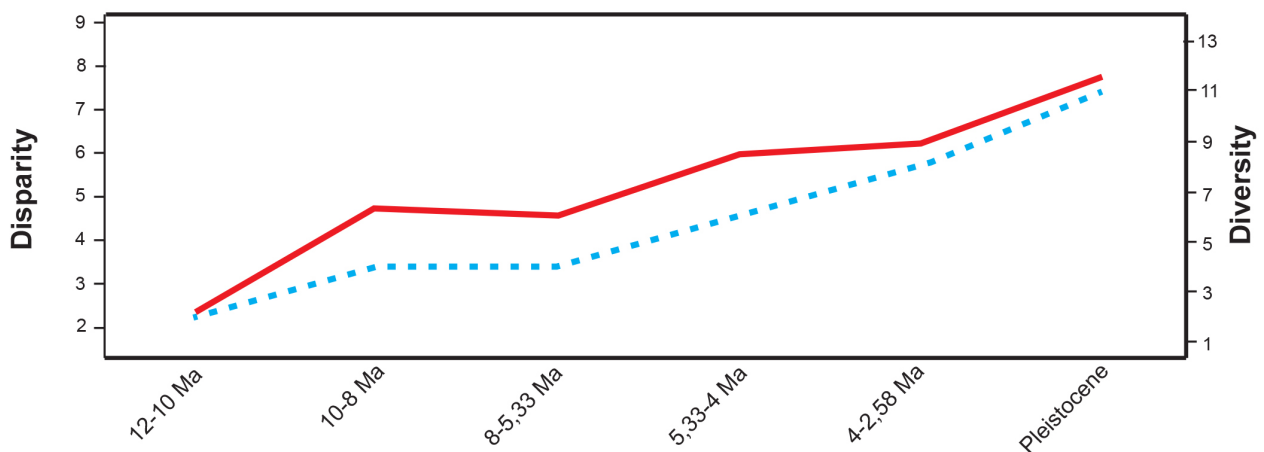

Fig. 2 - Scatter plot of diversity vs. disparity as sum of ranges. Diversity: dotted blue line. Disparity: solid red line.
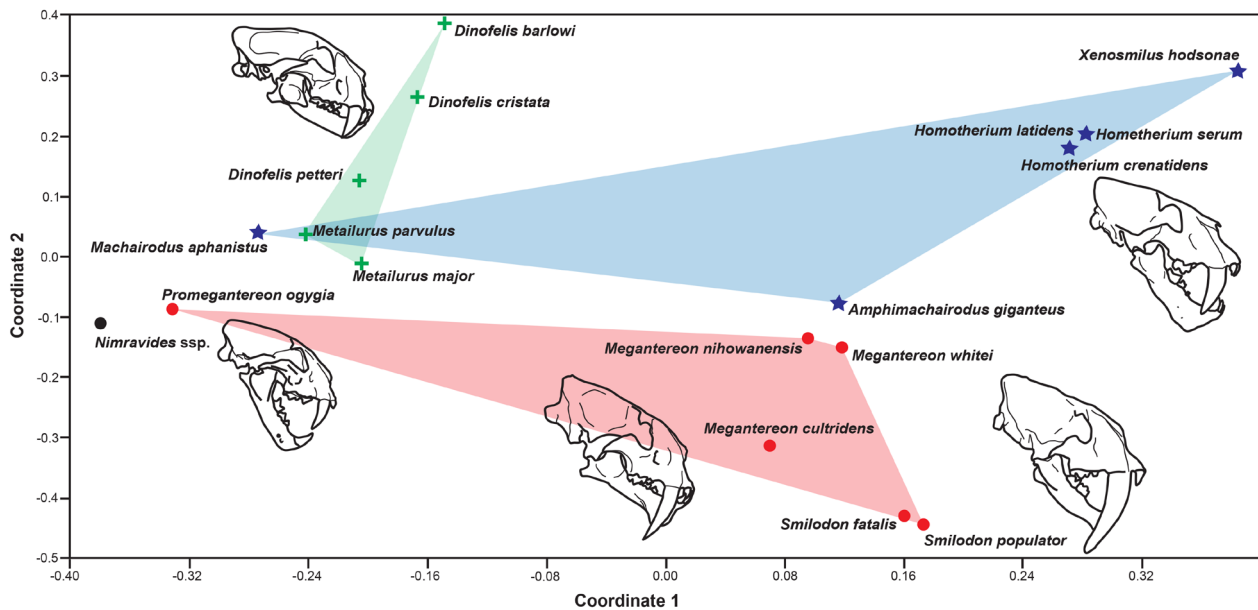
Fig. 3 - Scatter Plots of Principal Coordinaters performed on the original dataset by Christiansen (2013). Green convex hull: Metailurini; Blue convex hull: Homotherini; Red convex hull: Smilodontini.

with all Eumachairodontia represented (except for *Amphimachairodus giganteus*) and the two species *Dinofelis barlowi*, *Dinofelis cristata* of the traditional group of Metailurini (even this resulted as not strictly monophyletic in Christiansen, 2013).

4. DISCUSSION AND CONCLUSIONS

This contribution presents the first quantitative analysis of sabertoothed felid cranial disparity in relation to diversity through time. Even though taxon sampling is not exhaustive, the contribution represents a first preliminary macro-evolutionary analysis to detect major evolutionary trends in this iconic clade of mammals. Other contributions, (as Slater and Van Valkenburgh, 2008) using geometric morphometrics, have been based on only 12 machairodont species, however, obtaining convincing results about the evolution of overall shape in the skulls.

The present study manifests how the diversity of the group continuously increases from the Miocene (12 Ma), reaching a maximum peak in in the Pleistocene, after reaching a plateau of slow increase in the Pliocene. Of interest are the different, and mostly opposing, disparity trends when calculated as the sum of ranges and variance. Disparity, as the sum of ranges, is totally coupled with diversity. The minimum value is observed at the beginning of the history of the taxonomic group and the maximum reached during the Pleistocene. Differently, the disparity according to the variance is essentially decoupled with respect to diversity with a maximum at the beginning of the evolutionary history of the group (between 12 and 8Ma), and a decreasing

trend reaching the minimum in the late Pliocene, and a subsequent slight increase in the Pleistocene. Considering variance as a measure of dispersion (see Foote, 1997; Erwin, 2007; Ruta, 2009; Prentice et al., 2011), the results indicate that in machairodont felids the Miocene taxa are much more dispersed in morphospace, whereas in the late Pliocene the dispersion reaches a minimum. A different signal in the two disparity measures has already detected in stegosaurs (Romano, 2017), while totally overlapping trends of the two measures have been found in captorhinids (Romano et al., 2017), and cyrtocrinid crinoids (Romano et al., 2018a). In stem-gnathostomes pteraspidiformes heterostracans, Romano et al. (2018b) found a perfect coupling for the disparity calculated as total variance and as sum of ranges in the classical discrete characters, whereas in the continuous characters the two measures result quite decoupled (see Romano et al., 2018b). As in the stem-gnathostomes pteraspidiformes heterostracans (continuous characters), also in sabertoothed felids the disparity as total varience reaches a maximum at beginning of the evolutionary history of the group. This discrepancy in the two signals could be probably explained by the "early burst" scenario proposed by Mongiardino Koch et al. (2017). In particular, the authors stress that such early peak in morphological total variance can be obtained with cladistic discrete characters, since those characters can be biased due to autapomorphic characters overestimating evolution at the base of a clade (see also Romano et al., 2018b).

When interpreting the sum of the ranges as an index of occupied morphospace (see Wills et al., 1994; Prentice et al., 2011), the curves obtained show how morphospace exploration gradually increases throughout the history
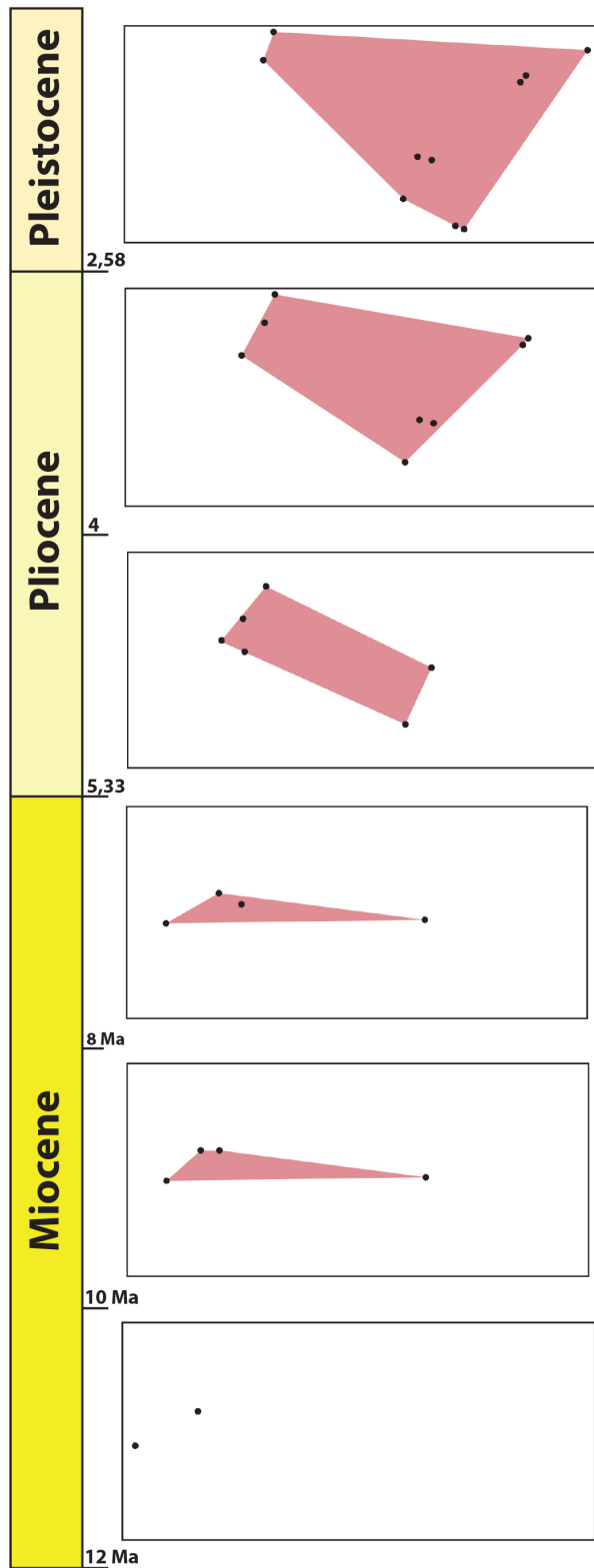
Fig. 4 - Graphic representation of the morphospace of machairodont felids through time. The highlighted area in red indicates the explored morphospace for each time bins. Each graphs represent the two first coordinates.

the group, reaching a maximum in the late Pliocene and Pleistocene. Coincidently these last time bins coincide with the appearance of all the Eumachairodontia (except for *Amphimachairodus*), or true "saberteeth" (*sensu* Christiansen, 2013). This increase in morphospace exploration is probably linked with major cranial changes related to the evolution of the characteristic hypertrophied and flattened upper canines. In particular, according to Emerson and Radinsky (1980), all the clades which have very long canines show an evolutionary convergence in general cranial morphology (see also Salesa et al., 2005). This essentially relates to increase gape (about 90?-95? in sabertoothed felids 65?-70? in modern felids according to the Authors), but at the same time retaining bite strength at the carnassial. Typical features resulting from such convergent evolution of cranial traits are: facial skull more upwardly rotated with respect to the braincase, skulls relatively narrow across the zygomatic arches, short distance from mandibular condyle to carnassial, smaller orbits, reduced coronoid process, temporomandibular joint and mastoid process more ventrally located, laterally displaced angular process, shorter and narrower temporal fossae, smaller masseter and temporalis moment arms and longer tooth row lengths (Emerson and Radinsky, 1980). According to Salesa et al. (2005) the reduction of the coronoid process and its dorsal placement typical of sabertoothed felids lead increasing maximum gap, while the backward projection of the atlas wings, and a well-developed mastoid process enabled expansion of the cranial flexor muscles and which proportionately increased the leverage arm.

A constant increase in occupied morphospace in the course of evolutionary history is evident in figure 4. Starting from the lower Pliocene the area identified by the taxa in Principal Coordinates scatter plots begins to be consistent, reaching the maximum extension in the Pleistocene ('late saturation', see Hughes et al., 2013). The continuous increase in occupied morphospace indicates that in the machairodont felids morphospace stabilization (*sensu* Villier and Eble, 2004) is not reached, if not in the Pleistocene with the total representation of the Eumachairodontia. Thus, although the evolution of the sabertoothed felids tends towards a compact and common general cranial structure as stressed by Emerson and Radinsky (1980), the results of the disparity indicate great morphological variability at the end of the evolutionary history of clade. This aspect was highlighted by Emerson and Radinsky (1980, p. 309), who stress *"Although sabertooths show a high degree of convergence in cranial morphology, there is also a considerable amount of variation among sabertooths".* Emerson and Radinsky (1980) connect this variability with the different degrees of canine enlargement, even though some differences may not be directly linked to the principal adaptations to increase gape. In this regard, they consider the genus *Smilodon "one of the more unusual genera with respect to cranial morphology"* (Emerson and Radinsky, 1980, p. 309). In their morphometric analysis Slater and Van

Valkenburgh (2008) detected an evolutionary trajectory in morphospace for Smilodontines, which they attribute to more vertical occiputs and increasingly deeper rostra.

The histograms in figure 5 show the distribution of the sum of ranges and variance in the individual groups, regardless of the selected time bins. Disparity in sum of variance in the Metailurini and Smilodontini is equally low, with increases in the Homotherini indicating that taxa in this group are more dispersed in their morphospace, and results are again low in the Eumachairodontia. Disparity as sum of ranges is minimal in Metailurini, indicating a compact explored morphospace. The occupied morphospace increases in the Smilodontini and Homotherini, peaking very significantly in the Eumachairodontia. Among the three classic groups, the greater dispersion and the widest explored morphospace is found among the Homotherini, as shown in figure 5. This result can be related to the fact that an increase in relative canine length is detected in scimitar-tooths throughout their evolutionary histories, leading to continuous increases in gape-related adaptation; an evolutionary trend that, according to Slater and Van Valkenburgh (2008), is particularly marked in the Homotheriini.

The Eumachairodontia are very little dispersed in the morphospace, a result most probably linked to the exclusion of *Machairodus* (traditionally included in the Homotherini) and of *Promegantereon* (traditionally included in the Smilodontini). Thus, the new group of true "saberteeth" are ultimately quite compact as regards dispersion in morphospace. On an evolutionary level the group seems to manifest a true late Plio-Pleistocene radiation, identified by a hyper-specialization (including surely hypertrophied upper canines) which has led to a maximum peak in disparity, i.e. in the explored morphospace.

Based on this evidence, and using the sum of the ranges as an indication of occupied morphospace, the evolution of cranial disparity in machairodont felids can be included in the classic category by Gould et al. (1987) of a 'top-heavy clade', i.e. those groups that show

a true radiation relatively late in their history. Although the original categories of Gould et al. (1987) were based only on the trend of diversity (i.e. number of taxa), in this contribution the category 'top-heavy clade' is used also to indicate clades where the explored morphospace results maximum close to the end of evolutionary history of the group. According to Hughes et al. (2013) considering a homogeneous birth–death model and evolution of characters in a Brownian fashion, a trend toward top-heaviness is totally expected (see also Foote, 1991).

The scatter plots of the Principal Coordinates analysis show how the genera *Homotherium Smilodon* and *Megantereon* are extremely compact, indicating an occupied morphospace capable of identifying and separating the groups. The large morphospace occupied using the classic divisions in Metailurini, Smilodontini and Homotherini (especially in the last two groups) is due to the choice of paraphyletic groups, not supported in the cladistic analysis by Christiansen (2013). In fact, the phylogenetically unsupported inclusion of *Machairodus aphanistus* in the Homotherini and *Promegantereon ogygia* in the Smilodontini artificially expanded, in a consistent way, the morphospace occupied by the groups towards the left portion of the scatter plot (Fig. 3A).

The opposite trend obtained by using respectively the sum of the variance and ranges as an indication of disparity in a group, clearly indicate how it can be dangerous to use just one of the two proxies for macroevolutive analysis, even though in some cases it has been shown empirically as the total range and total variance tend to correlate (see Foote, 1992). Thus the present empirical study encourages the calculation and presentation of both measures of disparity derived from ranges and variance, trying to interpret their possible conflict or concordance.
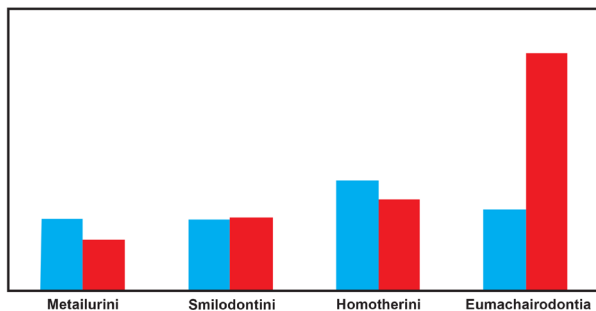
Fig. 5 - Sum of ranges (red) and total variance (blue) calculated separately for the individual groups of Metailurini, Smilodontini, Homotherini and Eumachairodontia, including all taxa considered in the study and regardless of the time bins identified.

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