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Evolution, morphological diversity and dietary signal in the carnassial teeth of Pan-Carnivorans

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Abstract

Title: Evolution, morphological diversity and dietary signal in the carnassial teeth of Pan-carnivorans.

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Mammalian dental morphology is remarkably diverse and complex, providing key insights into various aspects of their biology, including diet, phylogeny, and ontogeny. Within this considerable diversity, some species exhibit morphologies that are strongly derived toward increased sectorial efficiency; these teeth are known as carnassial teeth. This master thesis focuses on the morphology of carnassial teeth of Pan-carnivorans and (1) aim to quantify their morphological diversity and (2) the evolution of this diversity through time as well as (3) to assess the dietary signals they contain. To achieve this, we used high-density landmarking methods on 3D models of carnassial teeth from 250 species of extant and fossil animals. Surface scans of more than 100 specimens were realised exclusively for this thesis, while the remaining models were shared with us by institutions from all over the world. Our results show that carnassial teeth carry significant dietary information, although the precision of possible dietary inferences is clade-specific. We also describe how the 'Grande Coupure' and associated Oligocene migration events caused remarkable perturbations in the dental phenotypes of large predators, leaving lasting effects that are still visible in modern ecosystems with the dominance of canids and felids in hypercarnivores guilds. Furthermore, we demonstrate that highly derived dental morphology associated with hypercarnivory – so called 'hypercarnassialised' teeth - has been a consistent feature of mammalian diversity since the Eocene, evolving independently in multiple lineages with no discernible temporal gaps. This study advances our understanding of the evolutionary dynamics of Pan-carnivorans and provides valuable insights into the paleoecology and predator-prey dynamics throughout the Cenozoic era.

Résumé

Titre: Evolution, diversité morphologique et signal alimentaire des dents carnassières chez les Pan-carnivora.

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La morphologie dentaire des mammifères est remarquablement diversifiée et complexe ; elle permet l'extraction d'informations précieuses sur divers aspects de leur biologie comme leur régime alimentaire, leur statut phylogénique ainsi que leur ontogénie. Au sein de cette diversité considérable, certaines morphologies dentaires fortement spécialisées permettent une amélioration de la capacité à sectionner des tissus ; ces morphologies particulières sont connues sous le nom de dents carnassières. Ce mémoire se concentre sur l'étude morphologique des dents carnassières au sein des Pan-carnivora et vise à (1) quantifier leur diversité morphologique et (2) l'évolution de cette diversité dans le temps, ainsi qu'à (3) évaluer la qualité des inférences alimentaires qu'elles permettent. Pour ce faire, nous avons utilisé des méthodes de landmarking de haute densité sur des modèles 3D de dents carnassières appartenant à 250 espèces actuelles et issues du registre fossile. Des scans surfaciques de plus de 100 spécimens ont été réalisés exclusivement pour ce mémoire, tandis que les modèles restant nous ont été partagés par des institutions du monde entier. Nos résultats montrent que des inférences alimentaires solides peuvent être faites à partir de la morphologie des dents carnassières bien que la précision de ces inférences soit variable selon le clade auquel appartient l'espèce étudiée. Nous décrivons également comment la "Grande Coupure" et les événements migratoires associés au cours de l'Oligocène ont provoqué des perturbations remarquables dans les phénotypes dentaires des grands prédateurs, laissant des traces encore visibles dans les écosystèmes modernes avec la domination des canidés et des félidés au sein des guildes d'hypercarnivores. En outre, nous démontrons que la présence de morphologie dentaire hautement dérivée associée à l'hypercarnivorie - les dents dites "hypercarnassialisées" - est une caractéristique constante de la diversité des mammifères depuis l'Éocène et a évolué indépendamment dans de multiples lignées sans exception temporelle perceptible.

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1. Introduction

Within the animal kingdom, the class Mammalia is characterised by many physiological and morphological features. Of particular interest is the complexity and diversity of their dental morphology: in addition to a generally high degree of heterodonty, the interspecific morphological diversity of dental crowns is also unique among vertebrates (Berkovitz & Shellis, 2018; Pineda-Munoz et al., 2017; Yamanaka et al., 2015).

This rich variety of shapes can be related to many other aspects of mammalian biology; if certain dietary information can be inferred (Croft et al., 2018; Melstrom, 2017; Pineda-Munoz et al., 2017), phylogenetic or ontogenetic information can also be extracted from dental shape (Bryant, 1988; Peterkova et al., 2006; Rodrigues et al., 2019). Their ability to withstand erosion, transport and diagenesis (Cuy et al., 2002; Schmidt et al., 2017) also makes teeth an essential fossil record for the study of ancient mammalian diversity.

A series of mammalian clades have evolved a ‘carnassial’ molar morphology, ideal for cutting flesh and tendons. These carnassial teeth have attracted the attention of the scientific community both for the phylogenetic signal they can carry and for their morphological and functional versatility (Pineda-Munoz et al., 2017; Van Valkenburgh, 1989, 2007). However, quantification of the morphological diversity of carnassials teeth and the strength of their dietary signal remains rare. Furthermore, studies focusing on the competition and replacement dynamics among their bearers, known as Pan-carnivorans (*sensu* Queiroz et al. (2020)), are still sporadic. A more comprehensive large-scale analysis of the morphology of carnassial teeth in these placental predators could provide valuable insights into the palaeoecology and the predator-prey dynamics throughout Cenozoic. It could also provide a clearer picture of the evolutionary processes that gave rise to modern predator guilds and their ecological functions.

1.1 Pan-Carnivora: clade phylogeny and diversity

From small mustelids weighing just a few dozen grams to large phocids weighing several tonnes, the order Carnivora represents one of the most diverse clades of placental mammals today (Burgin et al., 2018; Friscia et al., 2007). With 16 families currently distinguished (Burgin et al., 2018), carnivorans have colonised every continent and most ecosystems. Despite their name, they have explored numerous dietary niches (Van Valkenburgh, 2007); while carnivory remains the most common, several groups have adopted omnivorous diets, such as many ursids and mustelids (Bojarska & Selva, 2012; Clevenger et al., 1992; Sacco & Van Valkenburgh, 2004; Selig, 2023). Sea otters have specialised in molluscivory (Doroff et al., 2012), while insectivory is common in mongooses and many other species (Friscia et al., 2007; Nel & Kok, 1999). Some, such as giant pandas and olingos, have even adopted an exclusively vegetarian diet (Figueirido et al., 2010; Jiangzuo et al., 2024; Kays, 2000; Xue et al., 2015). This dietary flexibility goes hand in hand with the plasticity of their dental morphology, which is sometimes seen as one of the key factors in their remarkable evolutionary success (Van Valkenburgh, 1999).

Carnivorans appear to have emerged during the Palaeocene, at least 42my ago (Arnason et al., 2007; Polly et al., 2006), from an older group of small insectivorous hunters known as ‘**miacids**’. The phylogenetic classification of this group has been widely debated and has undergone numerous revisions; if they have long been considered as a separated family, it is now generally accepted that this group forms the stem group of Carnivora (Wesley & Flynn 2005; Spaulding & Flynn, 2012). ‘Basal carnivoraforms’ is undeniably a more suitable term for species formerly classified in this family; however, the persistence of ‘miacids’ owes to its historical origins and pragmatic utility. ‘Miacids’ or ‘miacoids’ were mostly comparable in size and morphology to civets and, like them, predated on land or in trees in Europe, Asia and North America (Jenkins & Camazine, 1977; Solé & Smith, 2013). Together, carnivora and its stem group form the clade **carnivoraforms** (Flynn et al., 2010).

Carnivorans can be subdivided into two suborders: **Caniformia** and **Feliformia** containing respectively 9 and 7 extant family. They can be distinguished by multiple features such as the common reduction of the dental formula in feliformians, the inability to retract claws in most caniformians, the generally shorter snouts in feliformians among others (Ewer, 1973; Turner & Antón, 1997). However, the main synapomorphy lies in the morphology of the auditory bullae: feliformians have a double-chambered bullae while it is uni-chambered (or falsely double-chambered) in caniformians (Ewer, 1973). When considering the fossil

record, Caniformia and Feliformia exhibit even greater diversity, encompassing far more families than the 16 extant ones. Among those numerous families, Nimravidae stands out due to its extremely developed carnassial teeth and uncertain phylogenetic placement.

Sometimes placed as basal feliformians (Barrett et al., 2021) and sometimes as an extra clade among carnivoraforms (Spaulding & Flynn, 2012), nimravids form an extinct family of carnivorous mammals exhibiting many evolutionary convergences with felids (Chatar et al., 2022, 2024). This family appeared in the Eocene and lasted to the middle Miocene of America, Asia and Europe (Barrett et al., 2021). They are known for their cat-like silhouette as well as their tendencies to show elongated canines giving them the common label of ‘False saber-toothed cats’. Their simplified dentition as well as their canine and carnassial morphology indicate a probable hypercarnivorous diet (Poust et al., 2022; Van Valkenburgh, 1989, 1999, 2007).

Parallel to carnivoraforms, **viverravids** forms an early group of carnivorous mammal and likely constitute a monophyletic family characterized by the lack of upper and lower 3rd molar (Flynn, 1998; Flynn et al., 2010). They are known from North America, Europe, and Asia from the Middle Paleocene to Late Eocene (Gingerich and Winkler, 1985; Polly, 1997; Flynn, 1998; Meehan and Wilson, 2002) where they formed a diverse group of small-sized insectivorous and carnivorous animals. Viverravids arose simultaneously to ‘miacids’ and probably originate from North America as suggested by their rapid radiation in this region during the Paleocene (Solé & Smith, 2013). The clade grouping carnivoraforms and viverravids is called **Carnivoramorpha**, adapted from Wyss & Flynn, 1993.

The most striking synapomorphy of this clade is the presence of a highly modified dental complex formed by the 4th upper premolar (abbreviated as P4: the uppercase referring to the upper jaw) and the 1st lower molar (abbreviated as m1: the lowercase referring to the lower jaw) (Matthew, 1909; Wyss & Flynn, 1993). This pair of interacting teeth P4/m1 is known as the "carnassial complex" or "carnassial teeth" which efficiency lies in the scissor-like interaction between the m1 and the P4 during jaw occlusion (see Fig 5.).

While this carnassial complex likely first evolved to efficiently slice flesh (De Muizon & Lange-Badré, 1997; Pineda-Munoz et al., 2017; Van Valkenburgh, 1999), its morphological plasticity remains noteworthy (Lang et al., 2022; Selig, 2023; Van Valkenburgh, 1989).

For several million years, carnivoramorphan had to share the higher stages of the food chain with other groups such as Mesonychidae, a group of carnivorous ungulates lacking a

carnassial complex (Solé et al., 2011; Solé & Smith, 2013; Van Valkenburgh, 1999) as well as '**Creodonta**', a polyphyletic clade of Ferae, spanning from the Palaeocene to the Miocene across Africa, Europe, Asia and North America (Borths & Stevens, 2019; Morales et al., 2010; Yans et al., 2014). Like carnivorans, creodonts have evolved a wide range of size, with some species barely exceeding the size of a weasel, while others may have been larger than a polar bear (Borths & Stevens, 2019; Morlo & Gunnell, 2003). These animals, whose general morphology resembles that of carnivoramorphans, also possessed carnassial teeth (Butler, 1946; Lang et al., 2022). As dominant carnivores in many ecosystems during most of the Palaeogene, these animals experienced considerable evolutionary success for several millions of years before vanishing (Frischia & Valkenburgh, 2010; Solé & Smith, 2013; Van Valkenburgh, 1999). It is commonly suggested that their ultimate decline may have been exacerbated by the escalating competition with carnivorans during the Neogene (Frischia & Valkenburgh, 2010) although their initial major decline in diversity during the Paleogene cannot be solely attributed to this event, given that its diversity had already begun to decrease before the radiation of carnivorans (Van Valkenburgh, 1999).

The '**Creodonta**' clade initially encompassed the family '**Hyaenodontidae**' and the family '**Oxyaenidae**'; the current consensus is that the ecomorphological similarities between the two families arose through convergence, relegating this clade to a polyphyletic nature (Polly, 1994; Solé et al., 2022; Wesley-Hunt & Flynn, 2005). These two clades are therefore sometimes classified at the order level (as **Hyaenodonta** and **Oxyaenodonta**) to reflect this consideration. Although the phylogenetic position of some creodont species is still debated, **Oxyaenodonta** can generally be distinguished from **Hyaenodonta** by the loss of the upper and lower 3rd molars (like viverravids) (Butler, 1946; De Muizon & Lange-Badré, 1997; Gingerich, 1980; Solé et al., 2011; Solé & Smith, 2013).

The term **Pan-Carnivora**, proposed by Flynn et al. 2020, aims to bring together all the Carnivoramorpha and "**Creodonta**" under a monophyletic envelope (Fig. 1) (Queiroz et al., 2020). This clade therefore includes the common ancestor of these two groups as well as all their descendants, although the intern phylogeny of its constituent clades is still strongly debated.

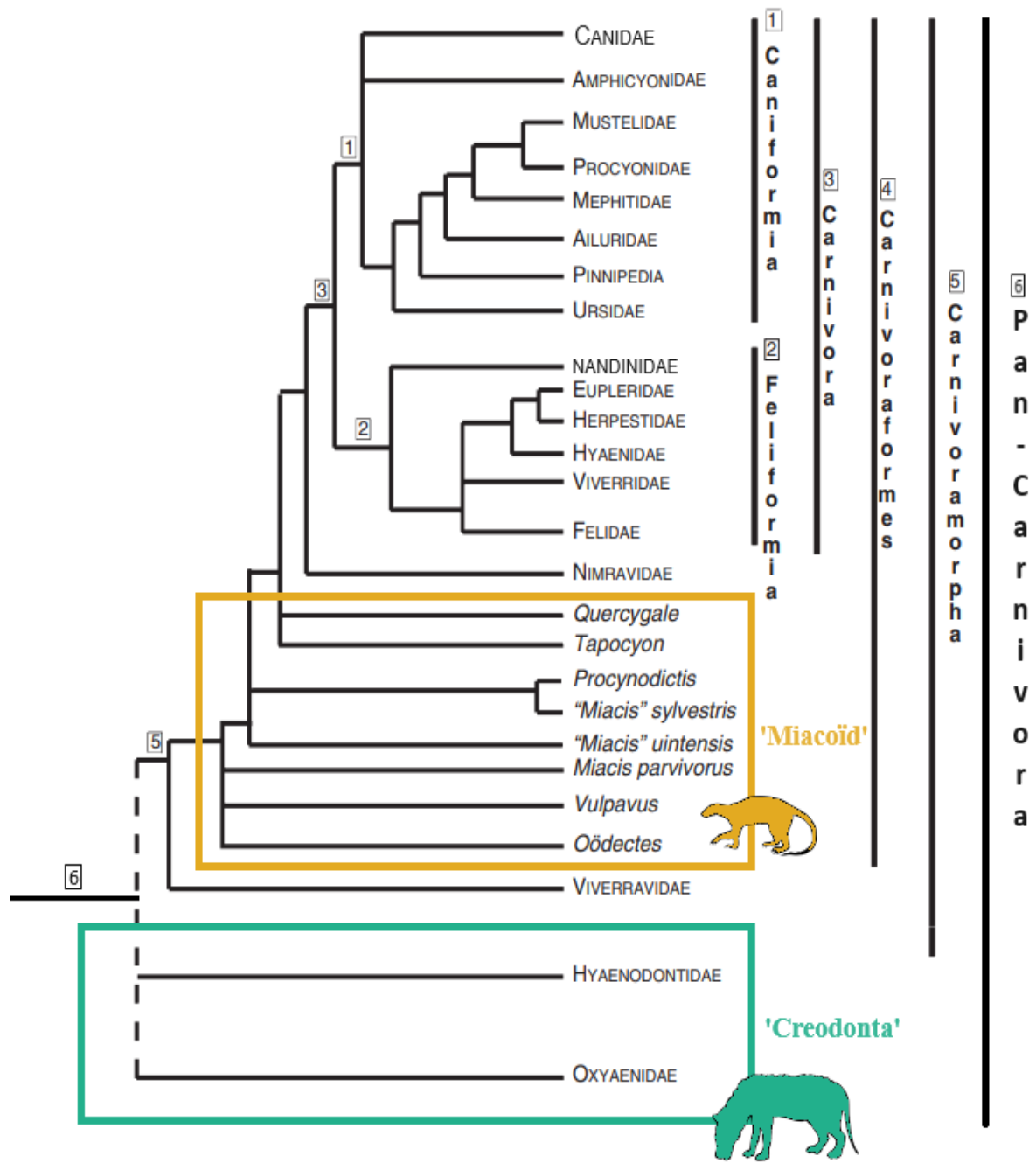


Figure 1. Phylogeny of Pan-Carnivora, Modified from John J. Flynn, John A. Finarelli & Michelle Spaulding 2010

1.2 The dentition of carnivorous mammals

Mammalian dentition is constituted of several tooth types with clearly defined positions and functions (Berkovitz & Shellis, 2018).

There are (Fig. 2):

Incisors, located at the front of the jaw, generally labio-lingually flattened, and used to acquire food by grasping, cutting, or gnawing.

Canines, located on the edge distally to the incisors, are sharp, conical, and generally show a relative degree of curvature. They serve a variety of roles such as killing prey, grooming or in intra- and interspecific communication.

Premolars: located distally to canines, variable in shape and used to process food.

Molars: located at the distal end of the dental row, with an extremely variable shape but commonly flattened in the baso-occlusal axis and widened labio-lingually and used for grinding, chewing, or cutting the food bowl.

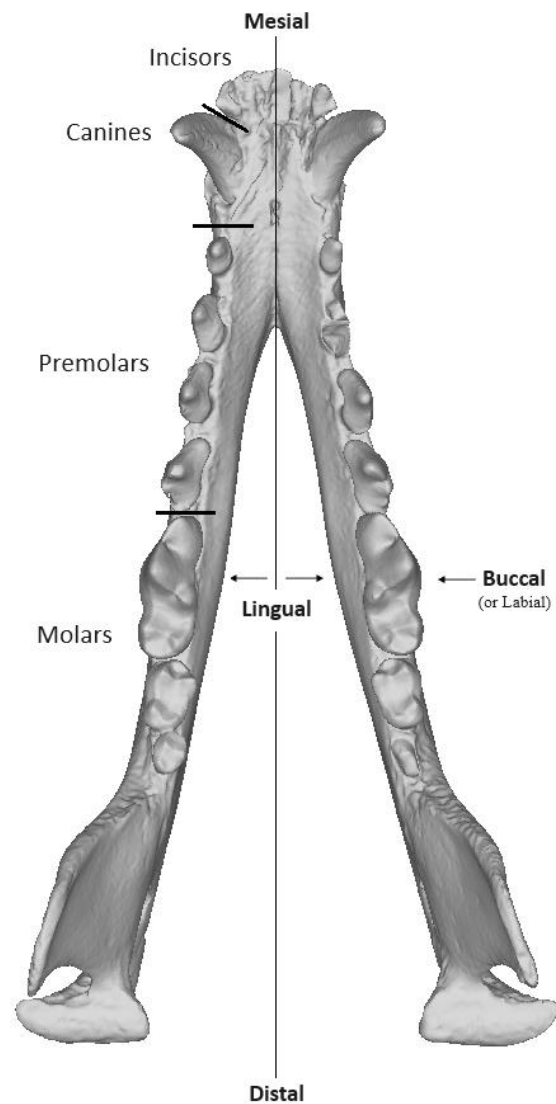


Figure 2. Mandible anatomy on a 3D model of *Crisocyon brachyurus* (RBINS-27342). Occlusal view

The number and type of teeth carried by an animal species is known as ‘dental formula’ and is generally given per upper and lower half jaw according to the following formula:

$$\frac{N}{n}I + \frac{N}{n}C + \frac{N}{n}PM + \frac{N}{n}M$$

In this formula, expressed as a fraction, the 'N' numerator indicates the number of teeth of the corresponding type on the upper jaw (maxilla) and the 'n' denominator, the number on the lower jaw (dentary). The letters following these fractions express the tooth type in question (I = incisor, C = canine, PM = premolar, M = molar).

For a dog, who possess 6 incisors, 2 canines, 8 premolars and 4 molars on the upper jaw and 6 incisors, 2 canines, 4 premolars, and 6 molars on the lower jaw (total 42 teeth), the dental formula is, for example:

$$\frac{3}{3}I + \frac{1}{1}C + \frac{4}{4}PM + \frac{2}{3}M$$

Although the dog's dental formula is shared with many carnivorans and hyaenodontids, it is not uncommon for certain clades to lose premolars or molars secondarily such as felids, nimravids and oxyaenids for example (Butler, 1946; De Muizon & Lange-Badré, 1997; Van Valkenburgh, 1989).

1.3 Carnassial teeth

This Master thesis is focusses on the morphological complexity of the carnassial teeth. This name can be viewed from two angles:

From an analogical point of view, a tooth is said to be carnassial if its shape is characterised by enlarged cutting edges and an angular shape for efficient meat cutting (De Muizon & Lange-Badré, 1997; Lang et al. 2021). This approach applies equally to carnivorans and creodonts. More surprisingly, teeth with this set of characteristics have also been found in some teleosts (Matsui & Kimura, 2021).

From a homological point of view, the approach is different: as one of the synapomorphies of Carnivoramorpha is the presence of a so-called "carnassial complex", all the 4th upper premolar and 1st lower molar of carnivoramorphans can be referred to as carnassial teeth. However, some species have secondarily lost the carnassial function of these teeth and have undergone profound secondary modifications to their morphology (Van Valkenburgh 1989). For example, ursids and some mustelids considerably reduced their carnassial traits and redeveloped a mastication/crushing form similar to the molars of other mammalian groups such as suids and primates (Berkovitz & Shellis 2018; Selig, 2023). This transformation is notably characterized by the substantial development of the more distal, flattened part of the tooth known as 'talonid'. Conversely, other families with a hyper-carnivorous diet, such as felids, have a considerably reduced talonid and exacerbated the shearing function by developing bicuspid and blade-shaped trigonids (the proximal part of the teeth) (Holliday & Stepan, 2004; Berkovitz & Shellis 2018). A few particular morphologies are shown in Fig.3.

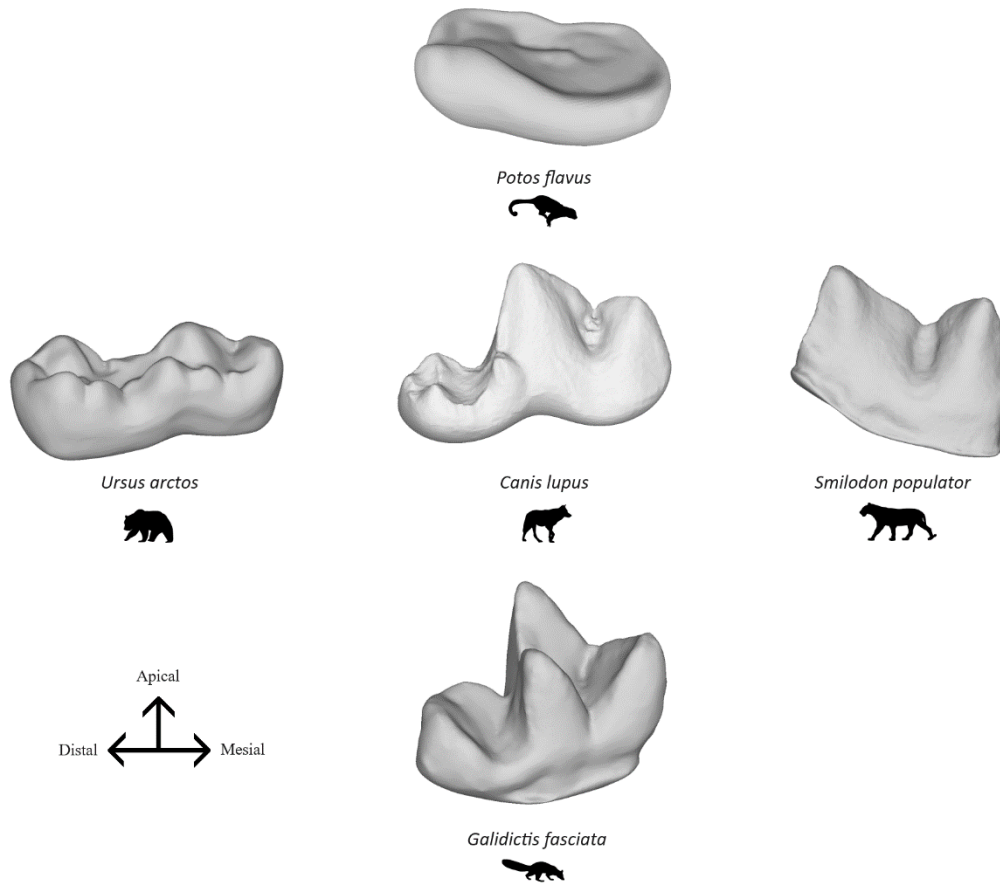


Figure 3. The diversity of carnassial crowns based on 3D models of *Potos flavus* FMNH: Mammals:68882; *Ursus arctos* IRSNB16404; *Canis lupus* IRSNB13255; *Smilodon populator* NHMUK-PV-M9374; *Galidictis fasciata* MNHN-ZM-MO 1880-1962

Many other evolutionary pathways have strongly modified the mandibular m1 morphology, such as in bone- and shell-crushing forms (Law et al., 2016; Van Valkenburgh, 1989). This vast array of functions is enabled by the differential development of the talonid and trigonid, allowing the obtention of very distinct shapes (Lang et al., 2022). In addition, the carnassial complex can also differ in the position and number of teeth involved. In hyaenodontids, this complex is formed mainly by the M2/m3 pair but is also supported by the M1/m2 (and partially by P4/m1) (Butler, 1946). Similarly, in oxyaenids, carnassials are also not formed by the P4/m1 pair like in carnivorans but by the M1/m2 pair (Butler, 1946; Matthew, 1909; De Muizon & Lange-Badré, 1997). Although these teeth are analogous to the carnassial teeth of carnivorans, they are thus generally not biologically homologous. A major difference between Carnivora and Creodonta should be noted: in the former, only one tooth per half jaw can be described as 'carnassial', whereas in 'Creodonta', all the molars can be defined as such. This 'hyperspecialisation' of their dental formula is sometimes suggested to have led to limited

dietary plasticity, potentially contributing to their extinction in favour of carnivorans (Frischia & Valkenburgh, 2010; Van Valkenburgh, 1989, 1999).

1.4 Morphology of the lower molars:

Nomenclature adapted from Hartstone-Rose & Stynder, 2013, Osborn, 1907, and Szalay, 1969.

On the dental crown (enamel-covered area of the tooth), molars possess two distinct functional regions: the trigonid and the talonid (Fig. 4). The trigonid is the most mesial part of the tooth. It consists of three main cusps, the protoconid situated buccally and generally the most prominent, the paraconid mesially and the metaconid disto-lingually (Osborn, 1907; Szalay, 1969). The protoconid and paraconid are linked by a sharp ridge called the *paracristid*. Between the protoconid and the paraconid, there is a pronounced depression called the 'carnassial notch' which helps soft food (like meat) to remain trapped on the cutting edges of the tooth during occlusion (Hartstone-Rose, 2011; Hartstone-Rose & Stynder, 2013). The 'keyhole' shape of the end of the notch is also thought to be able to dissipate pressure, thereby reducing fracture events in the tooth (Hartstone-Rose & Stynder, 2013).

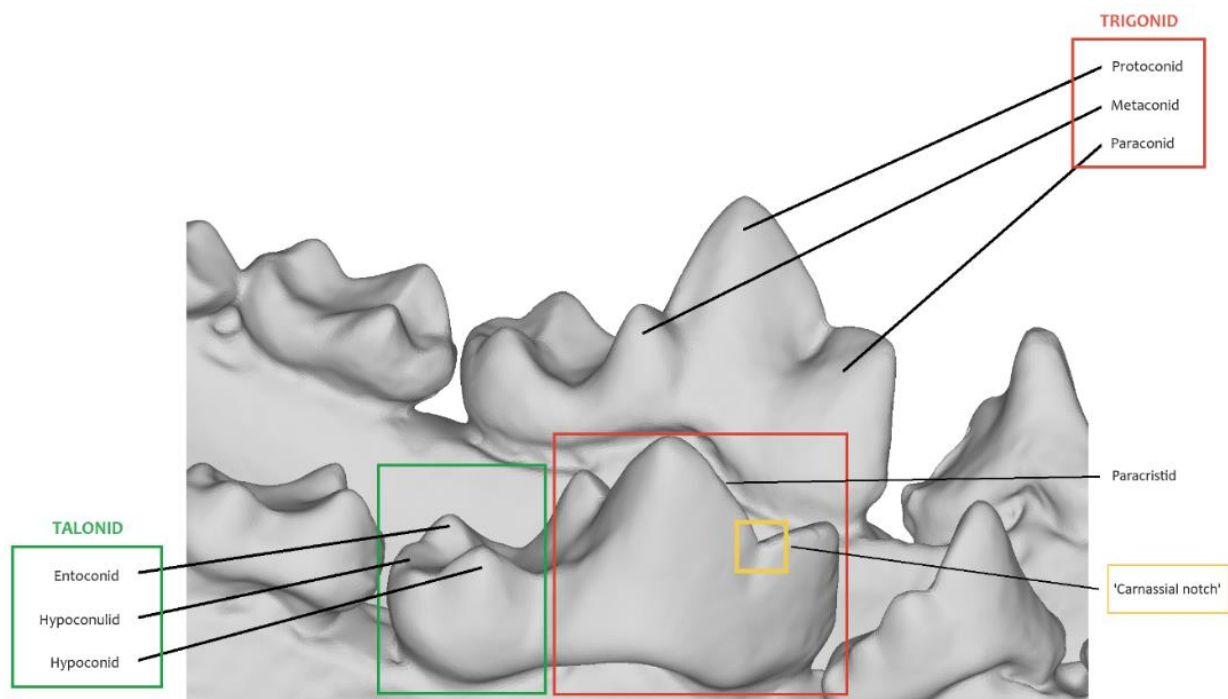


Figure 4. Lower 1st molar anatomy on a 3D model of *Crisocyon brachyurus* (RBINS-27342).

In Carnivoramorpha, the trigonid of the lower carnassial jaw interacts with the 4th upper premolar during occlusion of the jaw to enable the alimentary bolus to be cut. More specifically, it is the interaction between the "V" formed by the "protoconid-paracristid-paraconid" segment of the m1 and the "paracone-metastyle" segment of the P4 that traps the food in the carnassial-notch and causes it to be sliced cleanly (Fig.4) (De Muizon & Lange-Badré, 1997; Hartstone-Rose & Stynder, 2013). This function is performed similarly by the M2/m3 complex in most hyaenodonts and by the 1/m2 in most oxyaenodonts (Butler, 1946; De Muizon & Lange-Badré, 1997; Gingerich, 1980a), although all molars likely participate in the carnassial function.

The distal part of the tooth is formed by the talonid. The talonid is a tooth crown flare of highly variable amplitude. A series of cuspids can also be recognized, the most commonly discussed being the entoconid lingually, the hypoconulid distally and the hypoconid buccally (Osborn, 1907; Szalay, 1969). This less angular part meets the 1st upper molar during jaw occlusion, enabling food to be broken, crushed, and more generally processed (Fig. 5). This increased occlusal area afforded by an enlarged talonid is a key element in the morphological adaptation of the diet of herbivores, particularly when they lack the physiological capacity to digest plant matter efficiently (Gudinho & Weksler, 2021; Jiangzuo et al., 2024; Lucas, 2004). Therefore, it is not surprising that the most herbivorous carnivoran lineages, such as ursids and procyonids tend to exhibit a smaller trigonid/talonid surface ratio (Lang et al., 2022; Van Valkenburgh, 1989). In contrast, in many 'creodonts', as well as in felids, nimravids, and hyaenids, the talonid is extremely reduced or has completely disappeared (Berkovitz & Shellis, 2018; De Muizon & Lange-Badré, 1997; Van Valkenburgh, 1989). Additionally, it is not rare that the metaconid also disappears in the process. Modern taxa with such secondary modifications tend to be hypercarnivorous, like felids, and or may present some degree of osteophagy like hyaenids (Pineda-Munoz et al., 2017; Van Valkenburgh, 1989, 1999). As the first lower molar bears both the crushing and the shearing function, the analysis of this tooth is more informative than the analysis of the upper fourth premolar which is not involved in the crushing function (Lang et al., 2022).

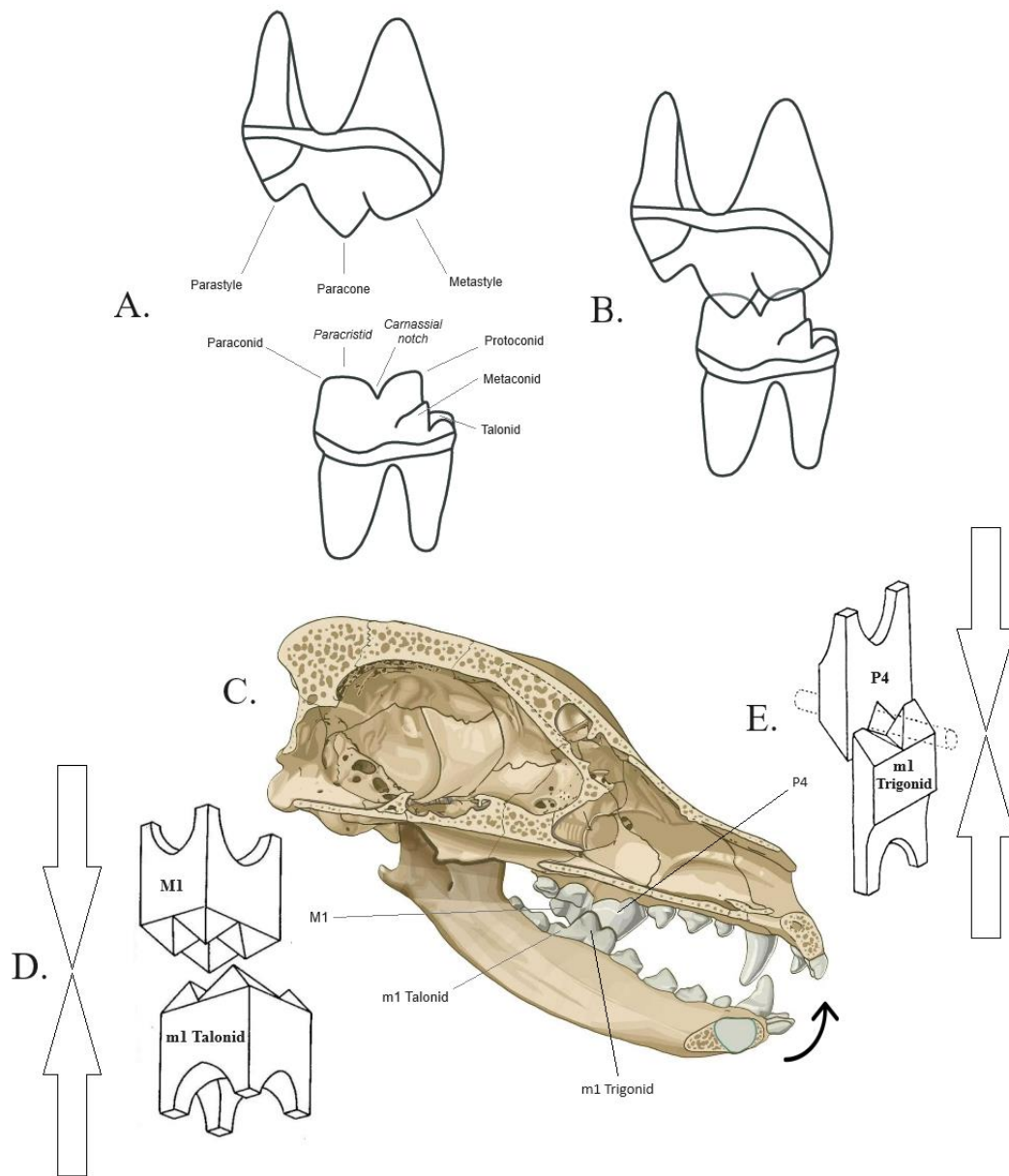


Figure 5. Trigonid shearing function & talonid crushing function mechanics modified from Harstone-Rose 2008, Micheau et al. 2018 & D G Mackean Biology Education resources. A. carnassial complex functional anatomy; B. visual of P4/m1 complex interaction; C. Lingual view of the M1/m1 - P4/m1 interactions on a sagittally cut dog cranium; D. M1/m1 talonid interaction analogy; E. P4/m1 trigonid interaction analogy.

1.5 Morphometric analyses

Morphometry (from Greek 'morphē' = shape, and 'metria' = measurement) is the discipline of science focusing on the quantitative analysis of the size and shape of objects (Rohlf & Bookstein, 1990). While the term was not used until the latest stages of the 20th century, the roots of classical morphometry, consisting of measurements of lengths, areas, angles, ratios and volumes, are much older (D'Arcy, 1917; Dürer, 1532; Richards, 1955). However,

morphometry has evolved considerably since then, and new methods have emerged in parallel with the development of computer technologies (Bookstein, 1992; Rohlf & Bookstein, 1990). Two- and three-dimensional morphometric analyses have notably benefited from new horizons with the introduction of morphometric geometry techniques. These techniques involve positioning ‘landmarks’ on homologous structures, recognizable between different specimens, in order to extract cartesian coordinates that can be compared (Bookstein, 1992; Goswami et al., 2019; Mitteroecker & Gunz, 2009). Now widely used (e.g. Fischer et al., 2022; Francoy et al., 2011; Frederich et al., 2008; Klingenberg & Gidaszewski, 2010), these methods can be useful to study the evolution of forms along ontogenetic (Frederich et al., 2008), phylogenetic (Catalano et al., 2015) or environmental gradients (Monteiro et al., 2005). These same techniques can also be used to assess morphological diversity between a set of fossil and extant taxa alike, enabling the identification of divergence and convergence events between them (Chatar et al., 2021; Fischer et al., 2022; Scavezoni & Fischer, 2023). Landmarks can also be associated with ‘semilandmarks’ designed to capture the shape of curves and surfaces and whose initial position is relative to standard landmarks (Goswami et al., 2019; Mitteroecker & Gunz, 2009; Zelditch et al., 2012). More recently, the advent of high-density landmarking methods has enabled further advances in the accuracy of information that can be recorded on biological structures, especially with the addition of new tools such as ‘pseudolandmarks’ who are automatically placed to sample a surface without homological reference (Boyer et al., 2015; Cardini, 2020; Goswami et al., 2019). These methods now make it possible to account for an unprecedented amount of geometric information, opening the door to new horizons, particularly in the study of complex structures or those on which determining homology is impossible or hazardous (Cardini, 2020).

In many areas, such as large-scale comparative morphology studies or evolutionary trajectories studies, high-density approaches (i.e. sampling a large amount of surface points) can be beneficial and have already proven their worth (Felice et al., 2019; Felice & Goswami, 2018; Fischer et al., 2022). However, as all these techniques are geometric in nature, it is necessary to be able to exclude the size factor to only retain the shape factor in the analysis. To this end, the most commonly used method for processing geometric morphometric data is the Procrustes superposition (Mitteroecker & Gunz, 2009). Like its mythological namesake, this method allows each sample to be standardised by removing geometric information that does not reflect a form factor (Rohlf & Slice, 1990).

1.6 Research goal

As evident from the state of the art above, Pan-carnivorans have evolved carnassial teeth multiple times, with a diversity of forms and positions. In parallel, a series of clades exhibit evolutionary trajectories likely diverging from the flesh-cutting function. Carnassial teeth thus provide a fertile cradle to analyse diet–shape relationships, cases of convergences, and evolution of ecological disparity over time and place. This Master thesis inserts within this broad research topic by aiming to answer three main questions:

- 1) What is the range of morphological diversity in the first lower molars of carnivoramorphans?
- 2) What is the relationship between first lower molar morphology and the diet in extant carnivorans?
- 3) What are the morphological signatures of the carnassial teeth of large carnivorous mammals throughout the Cenozoic?

2. Materials and methods

2.1 Model acquisition and scanning

The lower carnassial meshes were acquired through surface scanning, either using 3D models created exclusively for this master thesis or previously scanned specimens. During this project, various institutions were visited, and the objects of interest were digitized using different technologies. For most of the specimens, the Artec Space Spider 3D scanner (3D point accuracy of 50 μ m & 3D resolution of 100 μ m) was used. A limited number of specimens, especially small miacids and viverravids, were also digitized using the Artec Micro II scanner (3D point accuracy of 5 μ m and repeatability of 2 μ m). Additionally, numerous meshes were recovered from scans conducted beforehand or in parallel using different models of surface, medical or CT scanners by universities and research institutes around the world. Many of these scans were shared by researchers, but others were downloaded from two 3D sharing platforms: Sketchfab and Morphosource. Due to the variety of technologies used and the varying state of preservation of the specimens, the quality of the meshes obtained varies. However, considering the large morphological diversity in the final dataset, the analyses performed (see 2.4, 2.5) do not require a high-resolution model to comprehensively capture the disparity. For practical reasons, mephitids and pinnipeds were excluded from our study because of their very particular ecological niche and/or dental morphology. All the species sampled for this study alongside their identifiers and metadata can be found in supplementary material (Supplementary material S.9).

2.2 Model processing

Some teeth were isolated, others were not. In this last case, teeth were first extracted from the mandible or fragment of mandible using the ‘lasso’ selection tool in Geomagic Wrap. These teeth then underwent different treatments depending on the quality of the material. Teeth with a perfectly preserved structure only underwent filling of the lower and/or anterodistal holes resulting from their extraction from the mandible. Since the root of the tooth is not considered in this study, it was erased, leaving a hole. Similarly, when teeth are present in a complete mandible, they are usually in direct contact with the proximal and/or distal tooth/teeth, the extraction of the tooth results therefore in a small hole that needs to be filled. If the integrity of the tooth was not entirely preserved but the wear of its cusps, its fractures or other defects were of small amplitude, these were corrected based on models or photographs

of other specimens in order to re-establish the natural curvature and amplitude of the cusps of the tooth. This step was done using the hole filling tool in Geomagic Wrap by playing with different parameters (Tangent, curvature, or flat filling; complete, partial or bridge). If the defects present on the teeth were too great to be filled sparingly without altering its natural shape, or if no template existed, these models were set aside and are not included in this study. If a left carnassial in good condition was not available but a right carnassial was, the latter was taken and mirrored. All the transformations discussed above were carried out using Geomagic 2013 © version 2013.0.1.1206 or Artec Studio 18 Professional © version x64 18.1.2.25.

2.3 Landmarking

Every final model was landmarked with a limited number of points using Landmark © version 3.0.0.6. Our method consists of 12 fixed landmarks placed at strategic points throughout the surface of the tooth (Figure 6):

The 1st Fixed Landmark (hereafter referred to as “FL”) is placed at the mesial base of the tooth. The next FL will then be placed clockwise: the 2nd, 3rd, and 4th FL are placed at equidistance on the lingual part of the tooth; The 5th FL is placed on the distal base of the tooth in perfect opposition to the 1st one. The 6th, 7th, and 8th FL are placed similarly to the 2nd, 3rd, and 4th but on the buccal side of the teeth (Figure 6). Those 8 FLs are placed at the base of the enamel-covered area of the teeth, as this region serves as the basis of their functional locus.

The 9th, 10th, and 11th FL are then respectively placed on the top of the protoconid, paraconid, and metaconid. Finally, the last and 12th FL is placed at the geometric centre of the talonid (Figure 6). If these locations are well defined among many of the Pan-carnivorans, the positioning of some FL can sometimes become challenging. Among very morphologically derived taxa, 2 FL often require special treatment. The 11th FL location is less straightforward due to the loss of the paraconid in some taxa. For those specimens, the 11th FL is placed at equidistance between the 9th and the 10th FL, at half of the tooth crown height.

Finally, the 12th FL can also be tricky in taxa with reduced talonid. For those specimens, this FL is placed at equidistance between the 5th and the 9th FL on the distal edge of the tooth. Then, the same 12 fixed landmarks were placed on a template (Fig 7.1).

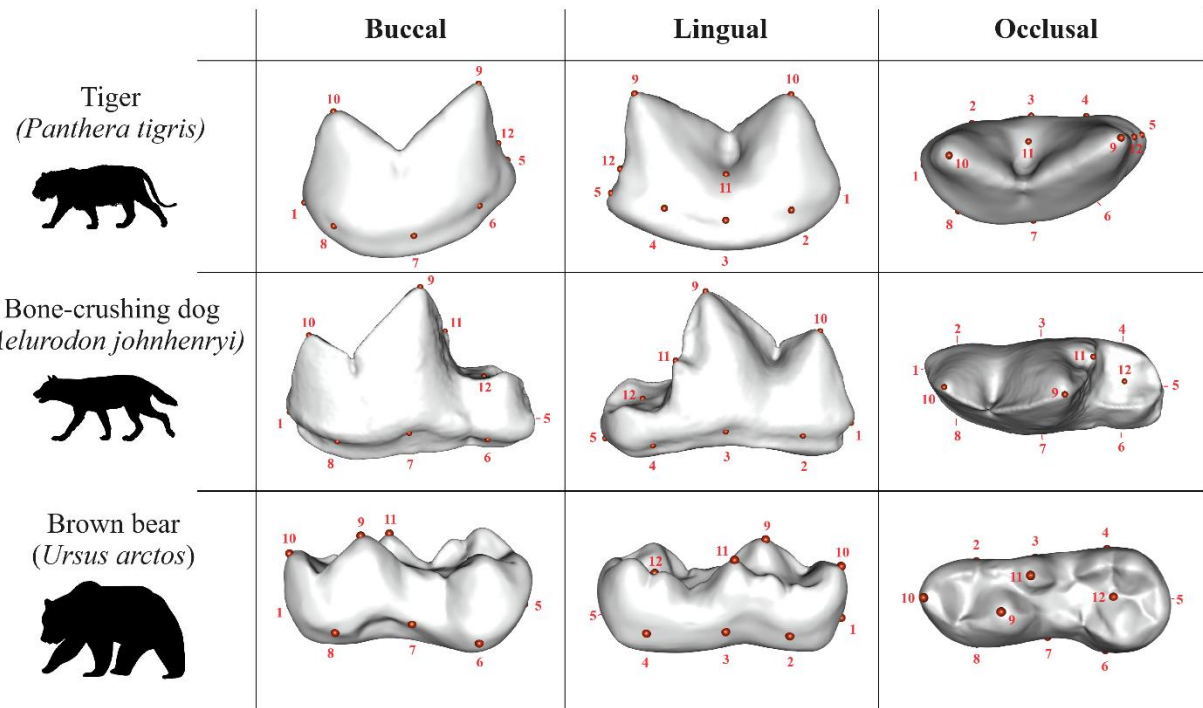


Figure 6. Landmarking method on 3 different morphotypes. 1-8: base of the teeth, 9: protoconid apex, 10: paraconid apex, 11: metaconid apex, 12: geometric center of the talonid

2.4 High Density 3D Geometric Morphometry

After the placement of the fixed landmark, 1500 ‘pseudolandmarks’ were automatically generated on the surface of a template in R by randomly selecting 1500 elements of the point clouds forming the mesh. This template with the 12 fixed landmarks and the 1500 *pseudolandmarks* were combined in the ‘createAtlas’ function of the ‘Morpho’ package in R to create an atlas (Fig. 7.2). These points were then projected on each specimen using the ‘placePatch’ of the ‘Morpho’ package as described in Fischer et al. (2022) (Fig. 7.3). These projected points generated by the ‘placePatch’ function are described as surface semilandmarks. As the interspecific morphological variation among pan-carnivoran’s carnassial is consequent, we used a simple template as suggested by Souter et al. (2010); in this case, a half-ellipsoid. Various configurations of fixed landmarks and templates were tested; however, the arrangement of 12 landmarks on the half-ellipsoid proved to be the most accurate for capturing shape variation in my dataset. For all the data treatment and analyses, R version 4.3.1 was used on the RStudio interface.

2.5 HD3DGM data analysis

A Generalised Procrustes Analysis (GPA) was then performed using the ‘gpagen’ function of the ‘geomorph’ package (Adams et al. 2022) on the whole set of coordinates (1,512 points) with 1500 semilandmarks defined as sliders in through the ‘surface’ argument of the ‘gpagen’ function. This transformation translate the coordinates to a common origin, scale the landmark configuration according to their centroid size and rotate the coordinates to minimise the Euclidean distance between points (Mitteroecker & Gunz, 2009)

Although this alignment scales all the specimens to the same centroid size this information is not lost and is stored in one of the arguments of the object resulting from the GPA (Rohlf & Slice, 1990). The Procrustes coordinates from the GPA were then subjected to a Principal Component Analysis (PCA) using the function 'gm.prcomp' to represent the main axes of variation in carnassial shape and to construct the morphospace (Principal Components 1, 2 and 3). The 'geomorph' package in R studio (Adams et al., 2022) contains all the function that were used here above for 3D analysis.

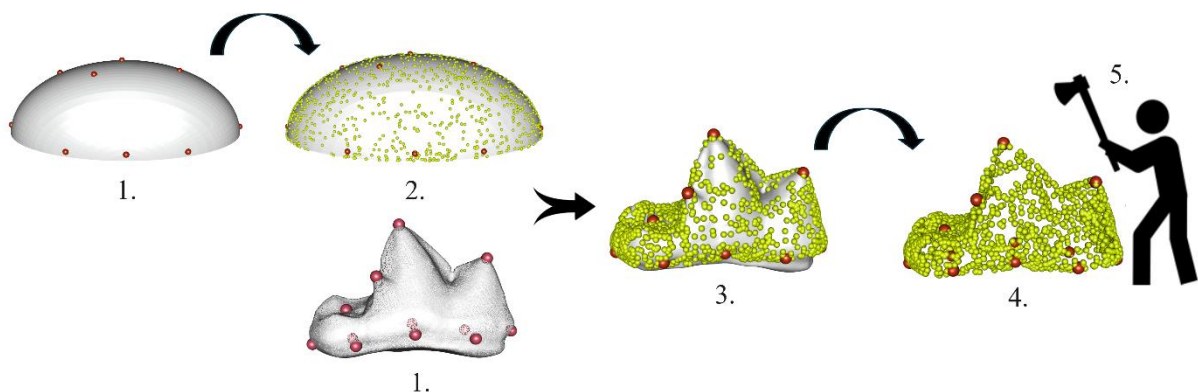


Figure 7. High Density 3D Geometric Morphometry method adapted from Fischer et al. (2022). 1. Placement of the 12 fixed landmarks on the template and on the teeth, 2. Sampling of 1500 pseudolandmarks on the template, 3. Patching of the template's pseudolandmarks on the teeth, 4. Registration of the cartesian coordinates of all the marks. 5. Procrustes transformation of the coordinates.

2.6 Stratigraphical, phylogenetic, and dietary data

2.6.1 Phylogeny and taxonomy

The phylogeny of extant carnivorans is well documented and there is a consensus, at least regarding family classification. However, the phylogenetic relationships within ‘creodonts’ and ‘miacoid’ remain poorly resolved. In this Master thesis, the creodont phylogeny employed is derived from Solé & Mennecart 2019. Following their phylogeny, I divided Hyaenodonts in 3 clades: ‘Lymnocyonoidea’, ‘Hyainailouroidea’, ‘Hyaenodontoidea’ (Fig. 8). As for ‘miacids’ and ‘oxyaenids’, they are considered at family-level (Heather, 2017) for practical reasons.

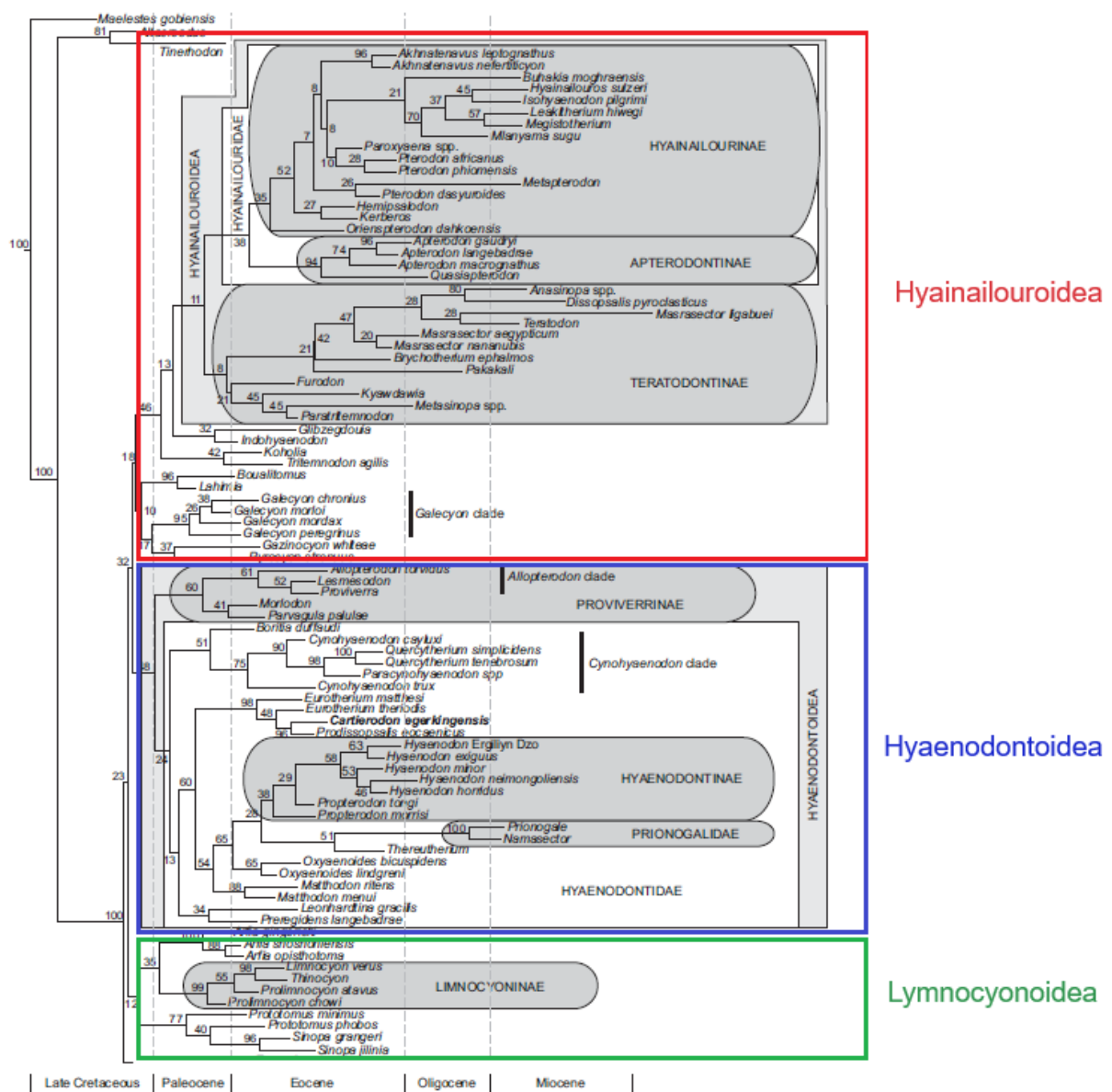


Figure 8. Hyaenodont clades extracted from Solé & Mennecart 2019.

2.6.2 Biostratigraphy

Stratigraphical information was obtained in literature revision for each species so that they could be classified by Epoch. Species spanning through multiple Epochs are listed as member of both.

2.6.3 Diets

Extant carnivorans were classified into diet categories modified from Van Valkenburgh, 2007. Those categories are established as percentage of feeding occurrence or volume of intake. When direct stomach content analysis or feeding observations were not available in the literature, we also used scats content analysis exists. The categories stand as follows:

- Hypercarnivorous: >80% of vertebrates (muscle, organs, or bones of vertebrates).
- Mesocarnivorous: 80–60% of vertebrate.
- Insectivorous: >60% land invertebrates.
- Herbivorous: >80% plants.
- Frugivorous: >80% fruits, honey, or nectar
- Omnivorous: <80% plants & <60% vertebrate flesh or invertebrates.
- Piscivorous: >60% fish.
- Molluscivorous: >60% of molluscs, crustaceans, echinoderms.

Though sometimes approximative considering that some taxa exhibit geographical and/or temporal variability in their diet, these categories stay relatively indicative and fit well for large meta-analysis.

2.7 Carnivoramorpha datasets

All recorded carnivoramorphans were studied for the first part of this thesis. However, as dietary information may remain patchy or totally unknown in extinct species and in poorly studied extant ones, only a subset of carnivoramorphans has been included in the dietary study. Of the 224 Carnivoramorpha sampled, only 108 had a sufficiently documented diet to be assigned a diet category. As all extant carnivoramorphans are carnivorans, these will be referred to as ‘Carnivora subset’ in this master thesis.

2.8 Medium to large carnivorous guild dataset

For the second part of this work consisting of the analysis of predator guilds through Cenozoic and the dynamics among Pan-carnivorans, we established a new subset where we excluded Pan-Carnivorans that did not fit within the guild of medium-to-large body sized predators exhibiting a carnassial complex. To proceed so, we excluded the following families: Mustelidae, Viverridae, Viverravidae, Ursidae, Semantoridae, Procyonidae, Herpestidae, Eupleridae, Ailuridae. These families were excluded because of ecological, morphological or physiological evidence showing either the absence of a functional carnassial complex or the low probability that they could form or have formed a substantial part of the medium to large predatory guild during any stage of the Cenozoic due to morphological, dietary, mobility, biomechanical, or ethological reasons. We also set a minimum teeth centroid-size of 150 to ensure the exclusion of small-sized animals in remaining taxa. The subset obtained contains 138 species from 10 families.

2.9 Statistical analysis

2.9.1 *Carnivoramorpha* family and diet analysis

A disparity analysis (Procrustes variance) was performed on the recorded carnivoramorphan families (224 sampled species from 19 families) using the ‘morphol.disparity’ function in the ‘geomorph’ package in R (Adams et al. 2022) in order to determine the extent of morphological diversity within and between families. The same analysis was also performed on the subset of extant carnivorans whose diet was sufficiently known to be classified (108 species from 11 families) to test the disparity between families and between diet in this subset (supplementary material S.1). These Procrustes variance analyses were complemented with hypervolume measurements for method comparison. For the two first datasets (*Carnivoramorpha* & *Carnivora* subset) an hypervolume of n dimension (with n = the number of principal components required to explain 90% of variance) was calculated for each group (diet group or clades) to compare it with results from ‘morphol.disparity’. The natural logarithm of the volumes obtained was then calculated and put into graph for comparison. This was made using ‘hypervolume_gaussian’ and ‘get_volume’ from the “hypervolume” package (Blonder et al., 2018).

On the subset of 108 extant carnivorans, a Procrustes ANOVA was also performed to evaluate the individual impact of diet and phylogeny (through family classification) as well as

their interaction on the morphology of the lower m1 as described by the Procrustes coordinates. This analysis was performed using the ‘ProcD.lm’ function in “geomorph” package (Adams et al., 2022). The linear model has been constructed as follows: $Y \sim X1 * X2$ where Y is the dependent variable (in this case the Procrustes coordinates), X1 is the diet category assigned to the observations and X2 is the family. The interaction between family and diet has been considered through the use of the multiplier instead of the addition between the two independent variable.

To compare Procrustes coordinates of each diet group to one another, the Procrustes coordinates of the Carnivora subset were transformed in a 2D data matrix using ‘two.d.array’ from ‘geomorph’ package (Adams et al., 2022) of R. This matrix was then combined with the associated diet to form a new data frame. Each diet pair was then used to form a distance matrix and tested with a PERMANOVA using ‘adonis2’ from the “vegan” package of R (Oksanen et al., 2001). The results of these pair test are found in supplementary material (S.2).

2.9.2 Medium to large carnivorous guild disparity measures

Disparity analyses were performed on the large carnivorous guild dataset to compare consecutive epochs. The first 15 principal components of the PCA (90% of explained variance) were used with 100 bootstraps to create a disparity matrix, also containing the stratigraphical information. A Shapiro test was then used on the matrix followed by a ‘leveneTest’ from the “Car” package of R (Fox et al., 2001) to test the normality of the distribution and the homoscedasticity of variances. As variances were not homogeneous between epochs and the distribution of data was not following a normal distribution, we realized a Wilcoxon pairwise test with Bonferroni correction. Boxplots were then produced to visualize the comparison of disparity between Epochs (Fig.16). The corresponding values for adjacent Epochs can be found in supplementary material (S.3).

3. Results

3.1 Carnivoramorphan families morphospace occupation

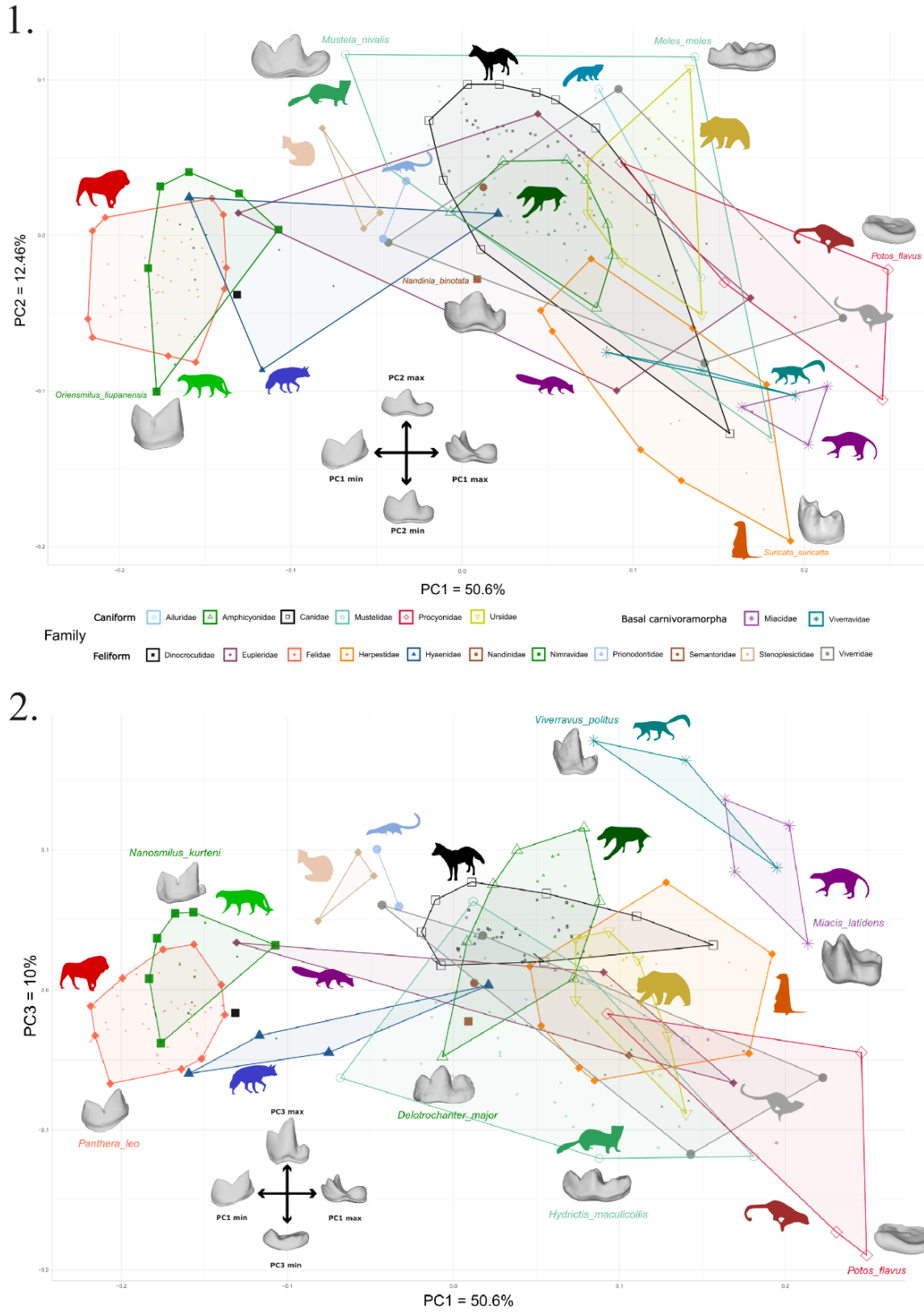


Figure 9. Morphospace of carnivoramorphan *m1* by family. 1. PC1 vs PC2; 2. PC1 vs PC3

Figure 9 contains the morphospace resulting from the PCA carried out on the ‘procrustes’ coordinates of the 224 species belonging to carnivoramorphans. The 1st principal component summarizes 50.6% of the observed variability while the 2nd summarizes 12.46%. The first five components combined explain about 80% of the total variation. The first component mainly captures the development of the talonid and metaconid as well as the rotation of the protoconid-paraconid axis. At low values of PC1, the talonid and the metaconid are extremely reduced while the protoconid-metaconid axis straightens in the anteroposterior axis. On the contrary, at high values of PC1, the talonid is more developed bucco-lingually and mesio-distally, the metaconid is well pronounced in the lingual position and the protoconid-paraconid axis undergoes a slight antero-dextral rotation.

The second component summarizes the relative bucco-lingual compression as well as the mesio-distal elongation. The teeth are more elongated mesiodistally and compressed buccolingually at high values of PC2 while the length/width ratio is more equal at low values of PC2.

The third component summarizes the relative height of the trigonid, particularly that of the protoconid.

Three main zones of high phenotypic density can be identified in the first morphospace (see supplementary material S.5). The 1st zone regroups specimens with PC1 varying from -0.25 to -0.1 and PC2 from -0.1 to 0.05, which basically correspond to the extreme left of the morphospace. This area is mainly occupied by feliforms (full forms on the morphospace). We find there the entire Felidae and Nimravidae families as well as a significant part of Hyaenidae, alongside a few other species (e.g. the hypercarnivorous euplerid *Cryptoprocta ferox* as well as the extinct dinocrocutid *Dinocrocuta gigantea*). Those taxa present a molar morphology characterized by a bicuspid, “blade-like” morphology, with a major or even total reduction of the talonid and metaconid. The paracristid is well developed and the protoconid-paraconid axis is strongly straightened in the antero-distal axis (Fig10.1).

The 2nd notable zone corresponds to PC1 values varying from -0.05 to 0.15 and PC2 values ranging from 0.00 to 0.10. This second zone contains a heterogeneous mixture of predominantly caniform observations. Canidae and Amphicyonidae are strongly represented there as well as a significant part of Mustelidae, Viverridae and Ursidae. The inter-family overlap is important in this region. The teeth associated with observations from this area present a trigonid and a talonid both well developed; the trigonid is complete with the protoconid as

the main cusp followed by the paraconid and a relatively well developed metaconid. A slight antero-dextral rotation of the protoconid-paraconid axis is discernible and the height difference between the talonid and trigonid is notable. The talonid forms a relatively large basin with more or less developed secondary cusps (Fig10.2).

The 3rd notable zone in the first morphospace can be found in PC1 values varying from 0.00 to 0.25 and PC2 varying from -0.20 to 0.00. This is a large area with a lower occupation density but high inter-family overlap. This area contains all basal carnivoramorphs (Viverravidae & Miacidae), as well as all Herpestidae. A significant part of Procyonidae and Viverridae accompanies them with some other species. This 3rd zone being the largest, the teeth morphology in this area are quite disparate. However, all these teeth have some similarities such as a large relative width as well as a very marked antero-dextral rotation of the protoconid-paraconid axis. The talonid is still present but the height of the talonid and trigonid fluctuate and is only seriously explained in the 3rd PC (Fig10.3).

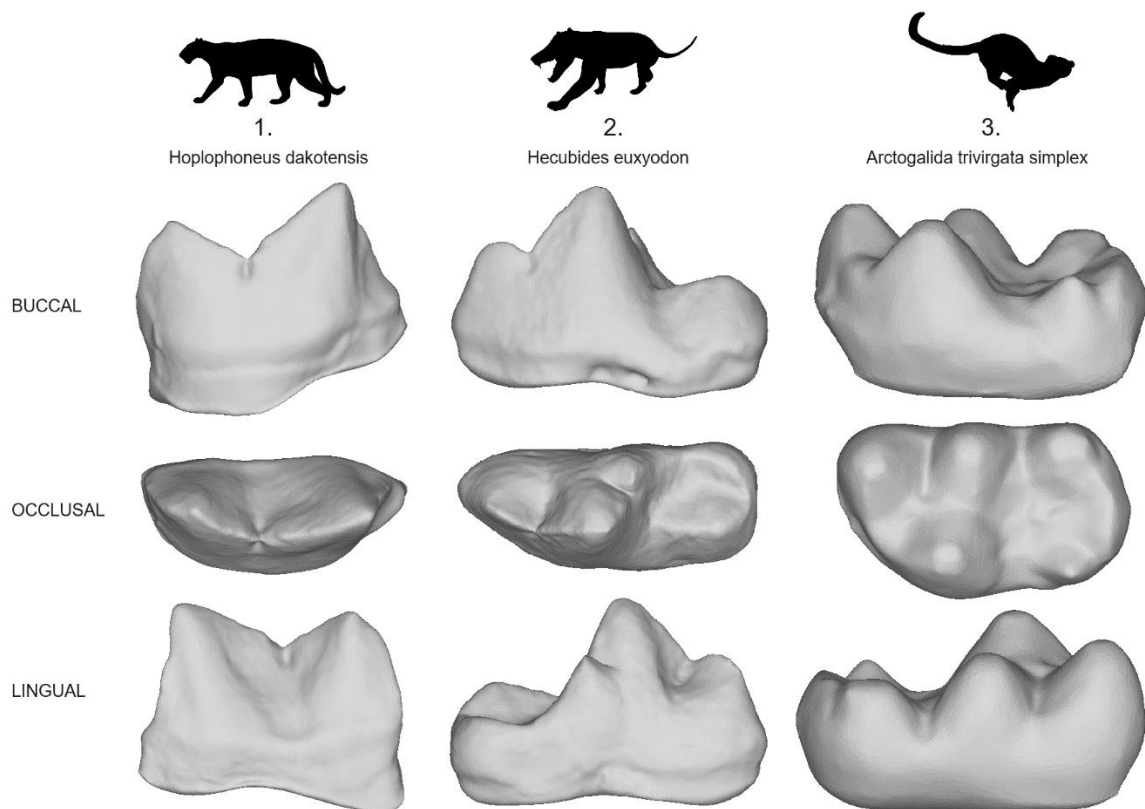


Figure 10. Visualisation of a typical example of each of the 3 morphological groups that can be observed on the PCA.

Two families stand out regarding disparity measured by Procrustes ANOVA: Eupleridae and Procyonidae with disparity values of 0.0217 and 0.0224, respectively. Ailuridae,

Herpestidae, Nimravidae, Mustelidae, Viverridae, Ursidae and Hyaenidae also have relatively high variance, greater than 0.01 (Fig. 11. 2). Concerning hypervolume measurements, although the general trend is similar, notable differences are presents with the position of some clades going up or down (Fig. 11. 1).

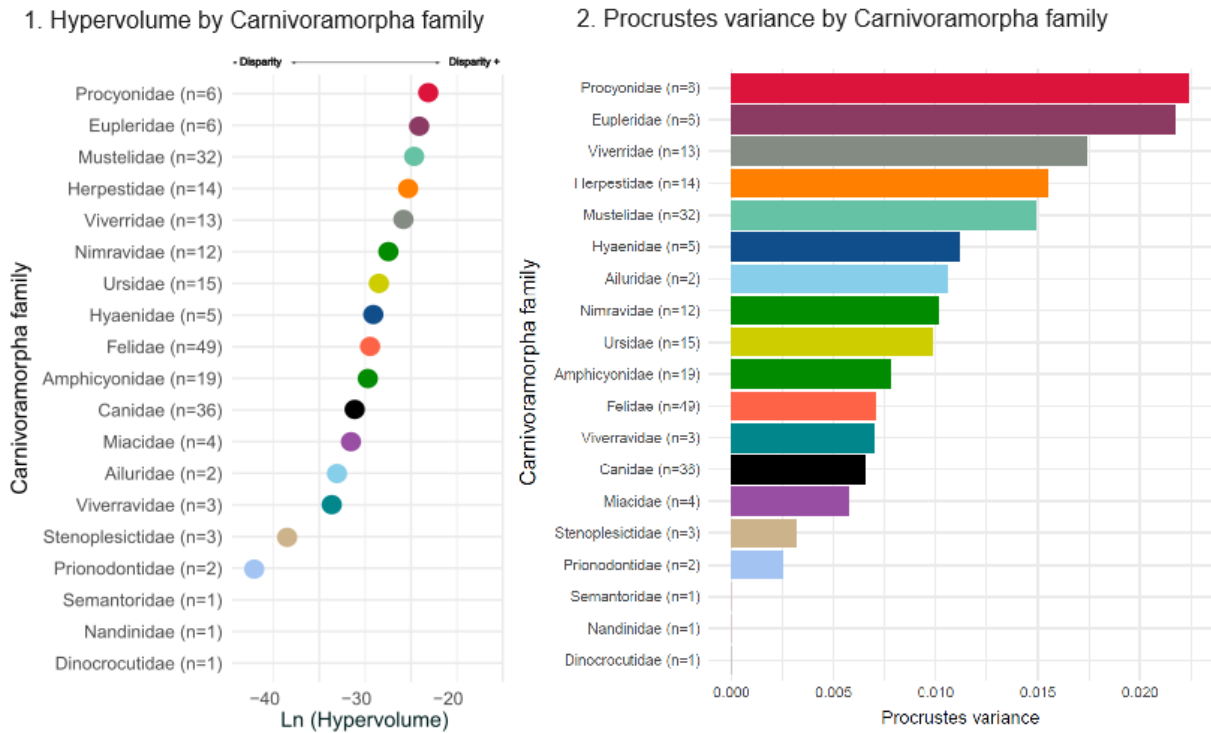


Figure 11. Histograms of family disparity measures. 1. Natural logarithm of hypervolumes measurements (lower negative values indicates higher disparity). 2. Procrustes variance.

3.2 Carnivoramorphan diets morphospace occupation

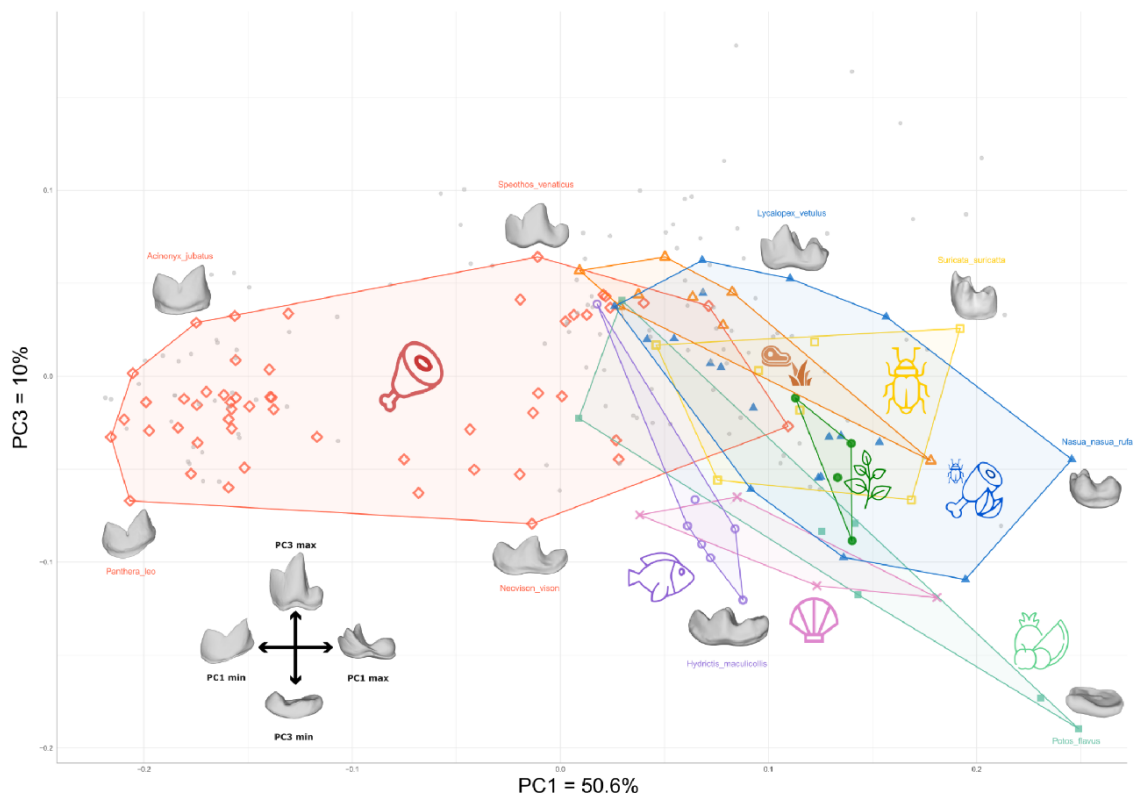
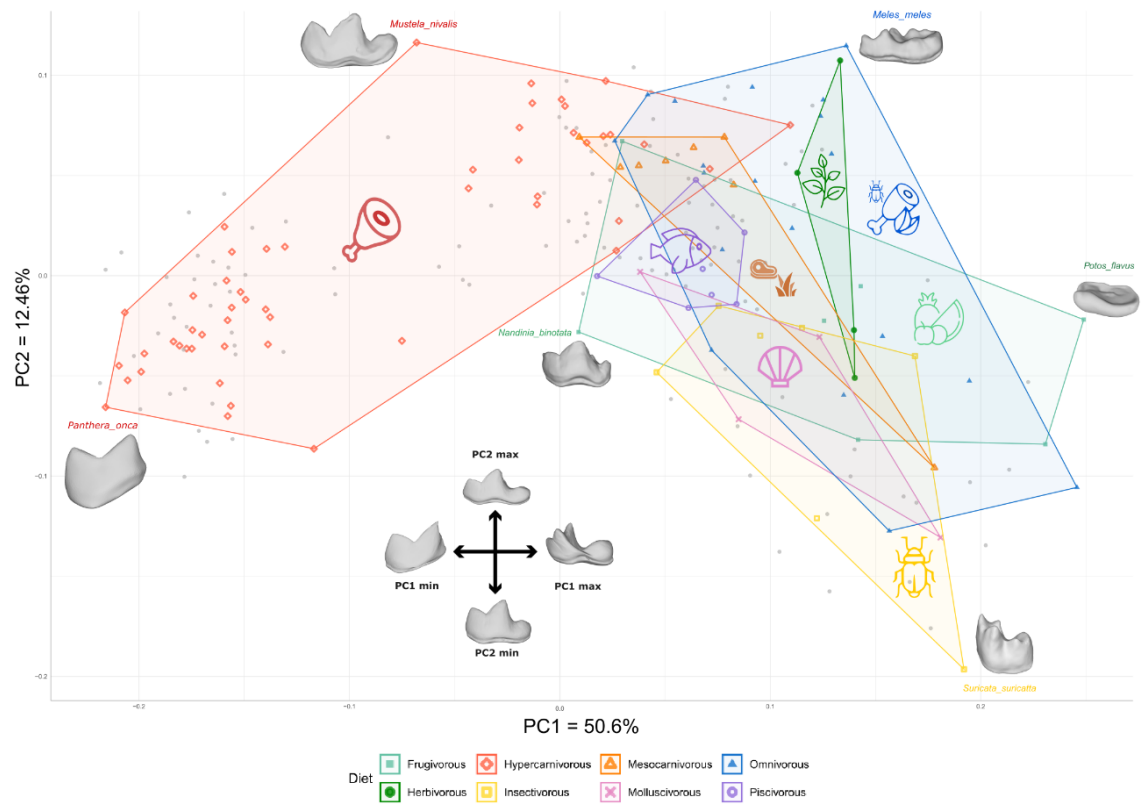


Figure 12. Morphospace of carnivoran by diet. 1. PC1 vs PC2; 2. PC1 vs PC3. The morphospace presented here is build from the same coordinates as the previous one, however it is not the families that are represented here but the diets as described in the material and method section (see 2.6.3).

The species located in the zone corresponding to negative PC1 are all categorized as hypercarnivorous. The positive zone includes the other 7 diets with significant overlap. A link seems to be observed between the progression in positive values of PC1 and the progression towards hypocarnivorous diets. Concerning the second PC, no hypercarnivorous observations are located on the lower third of the morphospace. Besides a few extreme observations in frugivores, most observations are recorded between -0.75 and +0.75 of the PC3, regardless of their diet.

Carnivora subset diet disparity:

The analysis of disparity in relation to diets was carried out on the subset of the Carnivoramorphia dataset including only the 108 extant carnivora species that could be assigned to a diet.

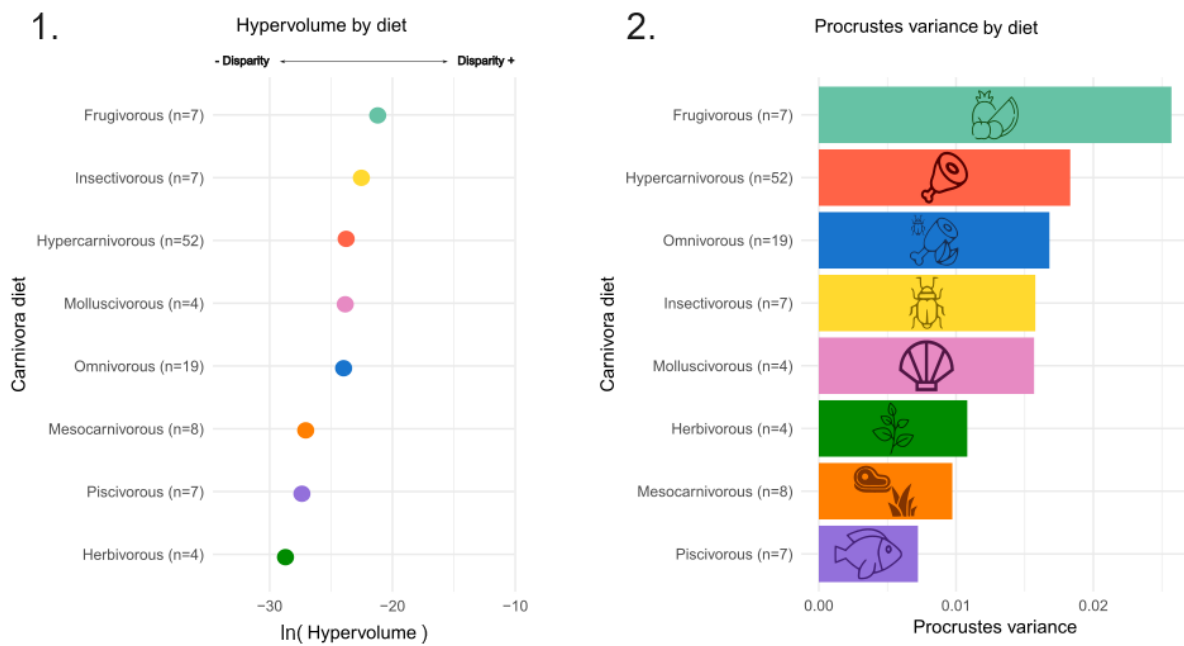


Figure 13. Carnivoran subset diet disparity measurements: 1. natural logarithm of hypervolume measurements. 2. Procrustes variance.

Figure 13 compares the ranking of hypervolumes measurement as well as the Procrustes variance. The analysis of disparity based on Procrustes variance reveals notable differences according to diets. Frugivores (n=7) stand out with a very high variance (0.0257) followed by Hypercarnivores (n=52) with (0.0183) and omnivores (n=19) with (0.0168). Insectivores (n=7) also present a certain plasticity (0.0158) as well as molluscivores (n=4) with (0.0157) and herbivores (n=4) reaching (0.0108). On the other hand, the mesocarnivorous (n = 8) present a low disparity (0.0097) similarly to the piscivores (n = 7) (0.0072). Regarding hypervolumes

measurements, the ranking is notably different. While the frugivores are still in first place, the hypercarnivores are in 3rd place, giving up their second place to the insectivores, who gain two places. Omnivores move from 3rd place in Procrustes variance to 5th place in hypervolume. Mesocarnivores come 6th, followed by piscivores, and herbivores come last.

Diet vs Family comparison on the Carnivora diet subset

The following table (Tab. 5) contains the results of the analysis of variance concerning the interaction between family and diet; the following values are indicated:

Diet and family both carry a statistically significant signal on the three-dimensional conformation of teeth (p-value < 0.001 for both factors).

With an Rsq of 0.4479, diet explains approximately 44.8% of the variance in the Procrustes coordinates of the teeth and the Z-value greater than 10 indicates a relatively large magnitude of effect. The value of F is high (22.6566) which shows that the portion of explained on unexplained variance is of notable importance.

Similarly, family explains approximately 26.9% of the variance (Rsq of 0.269), which, even if lower than diet, remains relatively high. The Z value (11.541) indicates a magnitude of effect even greater than that explained by diet and the F-score of (9.542) indicates the group means present significant differences.

The interaction between Diet and Family explains approximately 5.4% of the total variance, with an F value (2.117) and a p-value of 0.001, suggesting that the interaction between Diet and family also had a significant effect on tooth shape, although this effect was less pronounced than the main effects.

Table 1. Variance analysis using Residual Randomization on the interaction between “Family” and “Diet” for the Procrustes coordinates in the carnivoran-subset • R-squared (Rsquared): the coefficient of determination that measures the proportion of variance in the dependent variable predictable from the independent variables, indicating model fit. • F-value (F): measures the ratio of explained to unexplained variance to test if group means are significantly different. • Effect size (Z): quantifies the magnitude of the effect between groups. • P-value (P): measures how likely it is that the observed results are due to random chance.

	Rsquared	F	Z	P-value
Diet	0.448	22.657	10.005	0.001
Family	0.269	9.542	11.541	0.001
Diet:Family	0.054	2.117	2.986	0.001
Residuals	0.229			

3.3 Medium-to-large carnivorous guild

Morphospace occupation of represented clades.

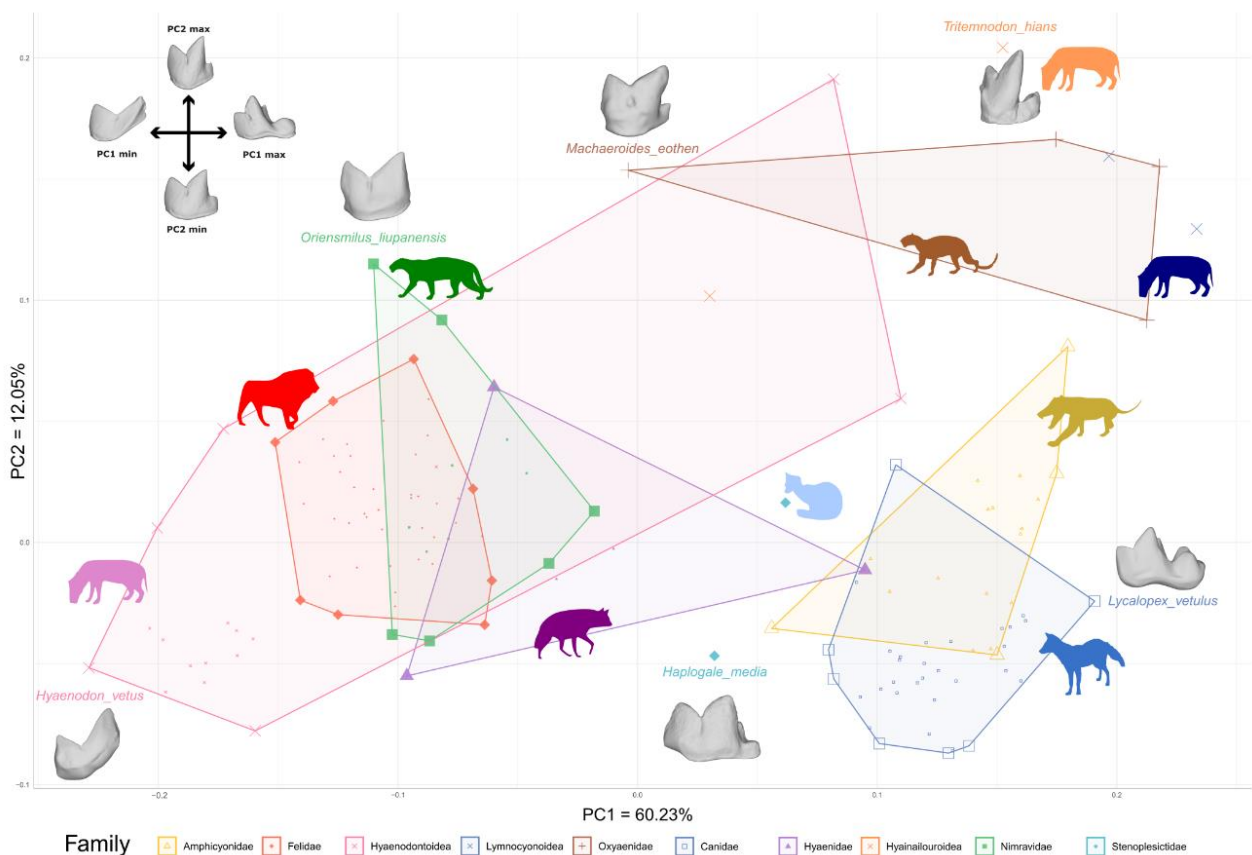


Figure 14. PCA on the family of medium to large carnassial bearing Pan-carnivorans.

Figure 14 contains the morphospace resulting of the PCA carried out on the Procrustes coordinates of the 138 species belonging to the medium to large-sized Pan-carnivora possessing morphologically analogous ‘carnassial teeth’. The 1st principal component summarizes 60.23% of the observed variability while the 2nd summarizes 12.05%. Five principal components are necessary to reach 80% of explained variation. The first component still mainly summarizes the development of the talonid and metaconid as well as the rotation of the protoconid-paraconid axis, but also the bending of the dental crown’s base. At low values of PC1, the talonid and the metaconid are vestigial if not completely reduced, the protoconid-metaconid axis straightens in the anteroposterior axis and the base of the dental crown arcs to raise the basal zone of the protoconid compared to that of the paraconid. On the contrary, at high values of PC1, the talonid remains more developed bucco-lingually and mesio-distally, the metaconid is well pronounced in the lingual position, the protoconid-paraconid axis undergoes a slight antero-dextral rotation and the base of the dental crown flattens.

The second component does not change fundamentally and still generally summarizes the bucco-lingual compression as well as the mesio-distal elongation. The teeth are more elongated mesiodistally and compressed buccolingually at high values of PC2 while the length/width ratio is more equal at low values of PC2.

Although different, species occupation in the morphospace can also be divided in 3 main zones as in Figure 9. The 1st zone is large, with PC1 values varying from -0.25 to 0.01 and PC2 values varying from -0.075 to 1.25. This first region is still occupied by all felids and nimravids as well as a significant part of the Hyaenidae with the notable addition of the majority of ‘Hyaenodontoidea’. The bicuspid, ‘blade-like’ morphology, with a major or even total reduction of the talonid and metaconid, is combined with a bending of the base of the dental crown as described above. The development of the paracristid and the antero-distal straightening of the protoconid-paraconid axis remains diagnostic.

The 2nd zone is still very similar to that observed in Figure 9, and correspond to PC1 values varying from +0.05 to + 0.2 and PC2 values ranging from 0.00 to 0.10. Except for one hyaenid and one stenoplesictid, only caniforms and more specifically canids and amphicyonids occupy this area, with notable overlap. The typical morphology is still characterized by a well-developed and complete trigonid and talonid. The slight antero-dextral rotation of the protoconid-paraconid axis is notable and the difference in height between the talonid and the trigonid remains clearly visible.

A 3rd debatable zone in this PCA can be drawn in PC1 values varying from -0.025 to 0.25 and PC2 values varying from +0.075 to +0.225. This area with more disparate observations contains virtually only creodonts including all oxyaenids. The morphologies represented there present a trigonid of a significant height relative to the length of the tooth as well as a clear talonid although of variable size.

Variation of carnassial shape density peaks throughout Cenozoic

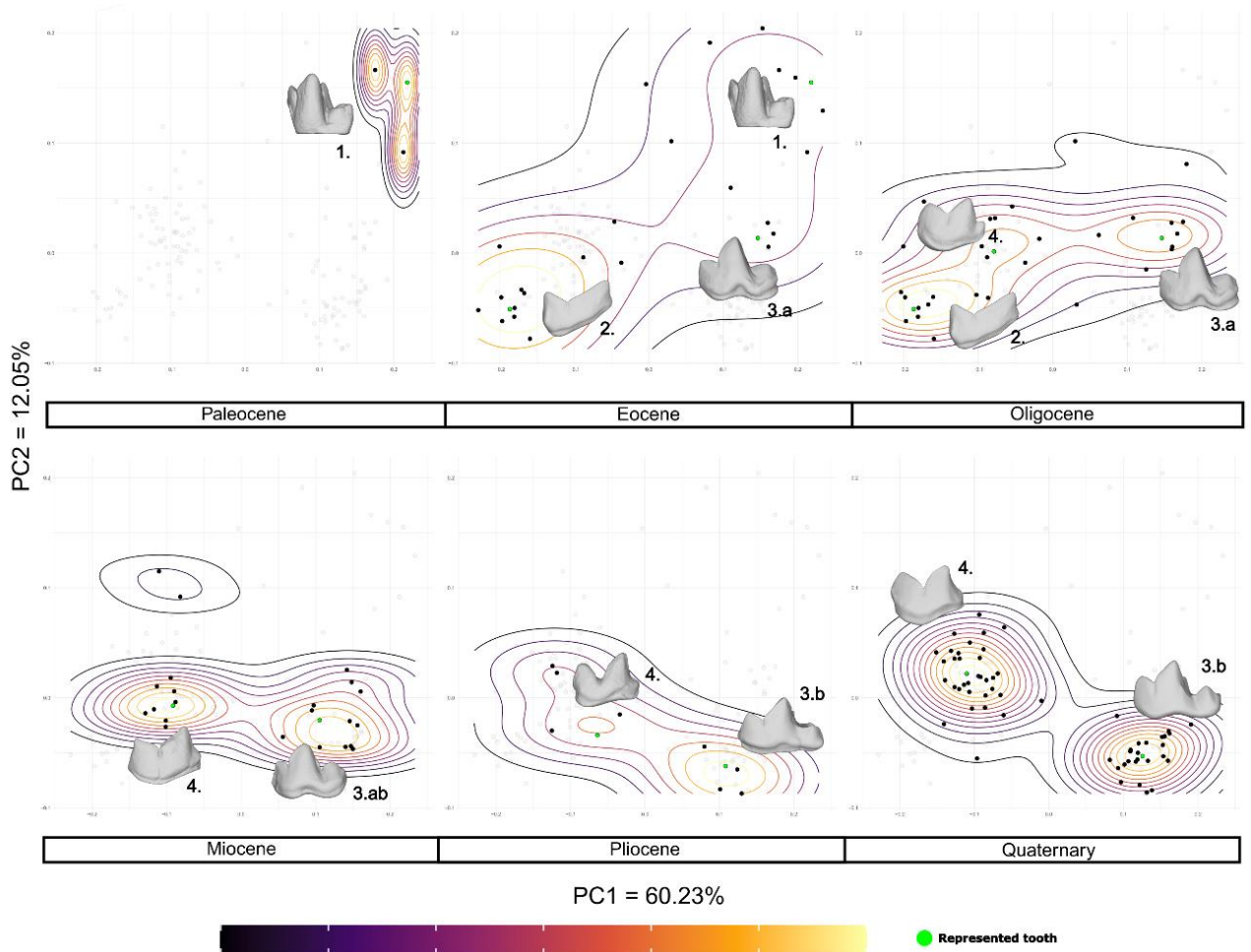


Figure 15. Cenozoic sequence of carnassial shape density. 1. Primitive carnassial, 2. Elongated bicuspid carnassial, 3. Canimorph carnassial, 4. Felimorph bicuspid carnassial.

The 15th figure represents the variation of the carnassial morphological landscape in medium to large sized predator throughout Cenozoic. The collected sampling from the Palaeocene contains 3 specimens, all situated on the top right of the morphospace (high PC1, high PC2, see Fig. 15. 1.). Their carnassial teeth (second lower molar in most oxyaenids) are

characterized by a well-developed and complete trigonid but the paracristid is not particularly sharp. The teeth also exhibit a notable talonid, substantially lower than the trigonid, and are not bucco-lingually flattened. No other morphospace zone is occupied for this period.

In the Eocene, the previously described dental morphology is still well present new morphotypes appeared. The bottom left of the morphospace (Low PC1 and low PC2) is colonised by bucco-lingually flattened teeth with total absence of talonid and metaconid (Fig. 15. 2.). These sharp morphologies with arched enamel base (Elongated bicuspid carnassial) are not the only new morphotype appearing; teeth with a well-developed and sharp trigonid are also present on the right side of the morphospace (Low PC1, high PC2). These morphologies (Canimorph carnassial) differ from the precedent by their notable talonid development as well as the presence of a notable metaconid (Fig. 15. 3.a). Some intermediate morphotypes are also present in between those three extremes, however their lower frequency does not affect that much the density.

During the Oligocene the first morphotype disappears while the density of the second and third morphotypes became more important. The Oligocene also sees the appearance of a new morphotype, characterized by a less arched enamel base and less mesio-distal enlargement and a small but discernible talonid is also emerging (Fig. 15. 4.). A sensible variety of others morphotypes are noted around the two-to-three main one but their lower frequency does not form other density peaks.

During the Miocene, the second morphotype (Elongated bicuspid carnassial) disappears and the density peak of the 3rd drifts slightly lower on the PC2; only two main morphotypes remains: 3 (Canimorph carnassial) and 4 (Felimorph bicuspid carnassial). In the Pliocene and Quaternary, the 3rd morphotype ends its drift (Fig 15.3.b) and is strengthened in his final position similarly to the 4th.

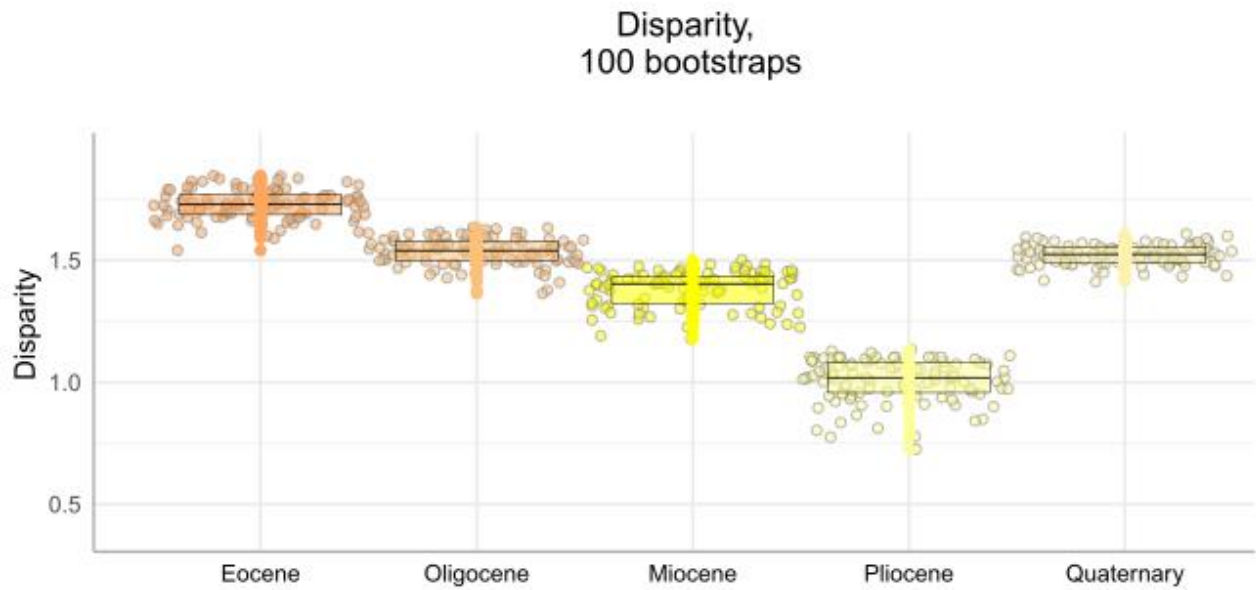


Figure 16. Disparity by Epoch among the medium to large size carnivorous guild. Bootstrap of $n=100$

Figure 16 shows the evolution of medium to large size carnivores throughout Cenozoic. The recorded disparity among studied guild is at its highest during the Eocene. A notable drop is recorded after the Eocene-Oligocene boundary that continues through Miocene. Pliocene appears remarkably low while the Quaternary is observed as remarkably higher, reaching disparity comparable to that of the Oligocene.

Variation of medium to large-sized carnivorous families through Cenozoic

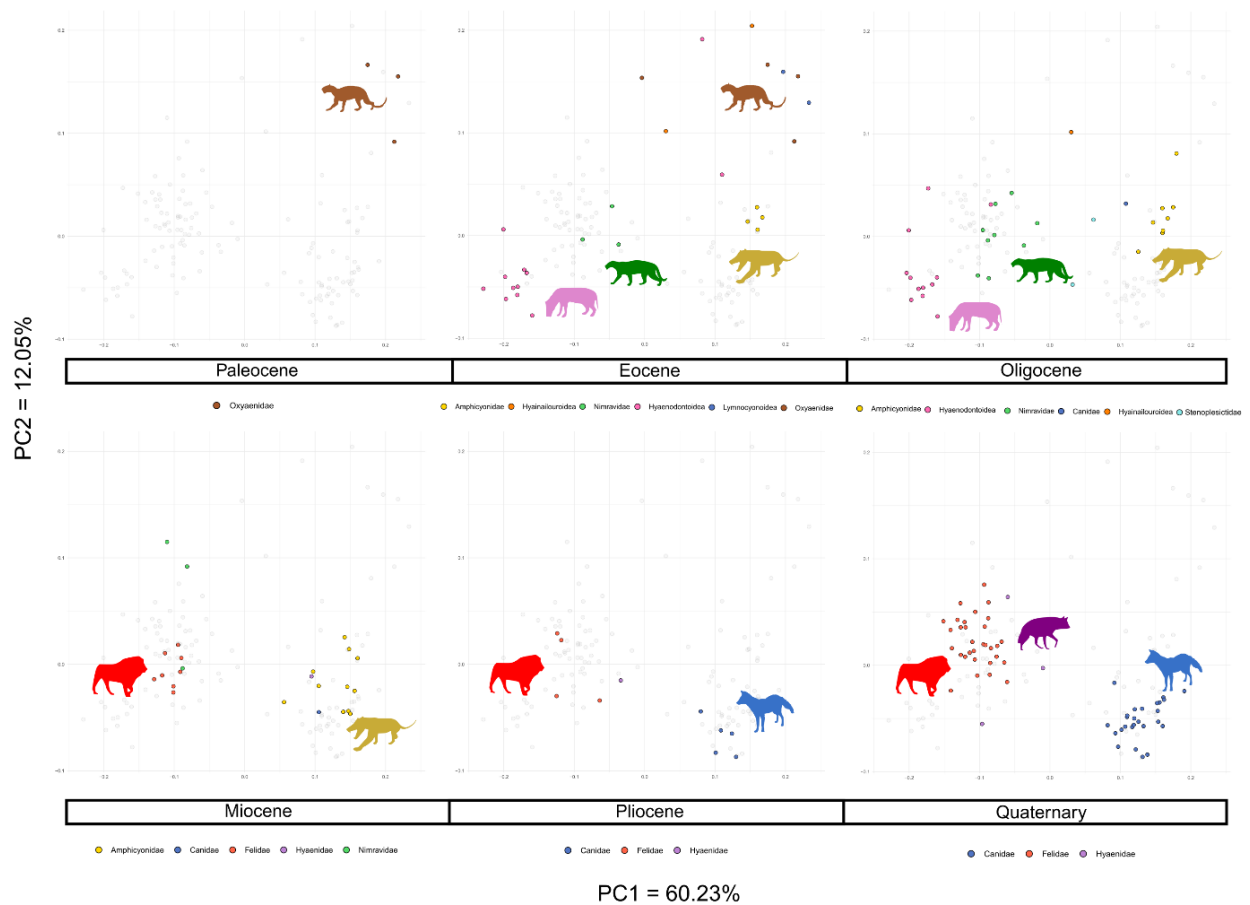


Figure 17. Cenozoic sequence of carnassial shape and predator family

The 17th figure represents the taxonomical variation of the morphological landscape in the teeth of medium to large sized carnivorous through Cenozoic.

The unique morphotype observed in the Paleocene contains 3 species of a single family of early creodont: Oxyaenidae.

The Eocene is more diverse with 6 clades: amphicyonids, hyainailouroids, nimravids, hyaenodontids, lynxocyonoids and oxyaenids, the last occupying the same zone of the morphospace as Paleocene's oxyaenids surrounded by lynxocyonoids and hyainailouroids. Hyaenodontoids form the observations described as type 2 morphologies (Elongated bicuspid carnassial) while amphicyonids form the type 3 (Canimorph carnassial). A few nimravids are already located between amphicyonids and hyaenodontoids.

The Oligocene sees the downfall of oxyaenids and lynxocyonoids with no morphological replacement observed among the selected taxa. Nimravids strengthen their position in the 'Felimorph bicuspid morphology' (type 4) zone as do amphicyonids in the type

3 zone. Hyaenodontoids occupy the same region as during the Eocene. A group of basal feliforms named stenoplesictids are observed between nimravids and amphicyonids while canids make their apparition.

The Miocene concludes a serious transition with the disappearance of many clades: no more 'creodonts' nor stenoplesictids are recorded. Nimravids experience a serious reduction of diversity and are morphologically replaced by upcoming felids. Amphicyonids stand strong on their zone and a few other clades are recorded such as hyaenids while canids diversify.

The final stage of the dynamic takes place during the Pliocene-Quaternary where the nimravids and amphicyonids are no more recorded. Their morphology is not lost as felids and canids overtake their place in the morphospace. Hyaenids, although less predominant, are located next to felids.

4. Discussion

4.1 Crown shape - diet relationships among carnivoramorphs

The extent of attained morphological diversity in carnivoramorphs is remarkable considering the small extent of the morphospace occupation of basal carnivoramorphs such as miacids and viverravids. Their lower carnassial teeth morphology is intermediate between the one exhibited by modern unspecialized carnivorans and the tribosphenic molar of late Mesozoic mammals (Cifelli, 1999; Rich et al., 2020) as it shows no large secondary modification such as elongated and sharp paracristid or cuspid reduction (Solé et al., 2014; Tomiya, 2011). This partially plesiomorphic morphology with a well-developed trigonid and a large talonid basin is also similar to the morphology of some extant herpestids (Van Standen, 1994), though it is not true for all of them since they exhibit a large morphological disparity on both two first PCs. Miacids are situated around taxa which are classified as omni-, meso- or insectivorous which support previous studies classifying them into a insectivorous – mesocarnivorous diet (Flynn et al., 2010; Wisniewski et al., 2023). Diets are generally very flexible within the animal kingdom with severe contextual, regional and temporal variation. Dietary choices are a result of many constraints regarding the ability to encounter, detect, catch, digest and be competitive in this dietary niche. In this regard, associating a precise diet to species might be illusory and, if not, generally represents a serious challenge as most species are not extremely specialised and often poorly studied (Hopkins et al., 2022; Pineda-Munoz et al., 2017; Van Valkenburgh, 1988b, 2007). However, the attribution of global dietary trends might help to better understand ecological dynamics within ecosystems and constitute therefore an imperfect but precious tool. With this in regard, groups that colonised diverse dietary niches are expected to be the ones with the largest crown shape disparity and vice versa but the results are more tempered. In the following sections, I will discuss these links between diet diversity and crown shape disparity for all important clades of carnivoramorphs.

Felids and nimravids partially overlap in all important PCs, which compels with many previous studies pointing the numerous morphological convergences of these two families (Barrett et al., 2021; Chatar et al., 2022, 2024; Van Valkenburgh, 1989, 1999, 2007). As every felid with a sufficient dietary record has been classified as ‘hypercarnivorous’, the inference of “hypercarnivory” as the main dietary niche for Nimravidae seems evident. Another dietary niche would be difficult to realise with such a specialised lower first molar, even more

considering the absence of molars posteriors to the first one (Lang et al., 2022; Van Valkenburgh, 1989). Felids and nimravids consistently have a similar low to medium disparity. The morphology of their first lower molar seems the most secondarily modified for hypercarnivory among carnivoramorphans. Despite other clades, such as canids and mustelids having also evolved hypercarnivorous diets, the extent to which felids and nimravids specialized in the development of sectorial "carnassial" teeth is unmatched. This feature, though potentially risky due to the limited ability to shift diets, could also represent a significant strength in terms of the efficiency of meat processing enabled by such sharp paracristid. The position of the m1 in the jaw, being the last tooth, implies a reduced lever arm and therefore a great strength advantage (Greaves, 1983; Lucas, 2004). These combination with other locomotory, and general morphological features has probably allowed them to be among the most competitive hypercarnivorous carnivoramorphan clades (Van Valkenburgh, 1991, 1999).

A similar degree of resemblance can be pointed for amphicyonids and canids, sharing a largely common mandibular molar morphology, at least partly due to retention of plesiomorphic features (Morales et al., 2010; Morlo et al., 2019; Tomiya, 2011). Canids are mostly described as hypercarnivorous, mesocarnivorous, and omnivorous. This wide range of dietary niches is associated with a versatile dentition: they generally possess a complete dental formula (4-1-4-3 for the mandible) and the first lower molar, the main food processing tooth, is complete and composed of a large talonid behind a well-developed trigonid with a sharp paracristid (De Muizon & Lange-Badré, 1997; Van Valkenburgh, 1989). South American canids have a particular evolutionary trajectory that is interesting to discuss in regard to their carnassial teeth morphology. Canids developed in SA from a single ancestor arriving relatively recently, 3.9-3.5 Mya, and radiated into 10 extant species (Chavez et al., 2022). This radiation led to drastic dietary partitioning with species ranging from Hypercarnivorous to frugivorous with many mesocarnivorous and omnivorous also existing (Santos et al., 2003; Varela et al., 2008). This extend of dietary diversity could have been accompanied by major morphological variation, however, the reality is more tempered. Even though hypercarnivorous species like *Speothos venaticus* and the frugivorous *Lycalopex gymnocercus* exhibit some discernible differences (reduction of the metaconid, and exacerbation of the paracristid in the first (Van Valkenburgh, 1991)), the general morphology of the carnassial teeth stays somewhat similar. This notable phylogenetic signal strengthens the hypothesis underlying the key role played by the versatility of the canid m1 morphology which enables both sectorial and masticatory treatment. Overall, their relatively low morphological diversity might just not have been a

strong brake to their global evolutionary success. The notable physiological modification observed in some species such as *Chrisocyon brachyurus* could have played a major role in their remarkable dietary and geographical journey (Chavez et al., 2022) similarly to the role of the increase in copy numbers of the gene coding for pancreatic amylase in domestic dog which, among other mutations, enabled them to rapidly transition from the hypercarnivorous diet of wolf to the more generalist of dogs (Arendt et al., 2014). These considerations are plausibly applicable to other canids. Moreover, the complex social life adopted by many hypercarnivorous canids and their ability to form and hunt in pack could have also been a strong tool to maintain a certain degree of competitiveness regarding other predators (Geffen et al., 1996; Kleiman & Eisenberg, 1973). However, it is notable that hypercarnivorous canids taxa have reached peak diversity in spatio-temporal context where few or no other hypercarnivorous placentals (amphicyonids, nimravids, felids, creodonts...) were present and were largely replaced when they encountered them. This suggest that the dietary plasticity of canids enabled by their less derived morphology does still come with a cost regarding their competitiveness in hypercarnivorous guilds (Van Valkenburgh, 1991).

On the opposite, another family which experienced a notable radiative evolution exhibit a strong disparity: Eupleridae. Euplerids are the only carnivoran lineage in Madagascar and share a common ancestor dating from 24 to 18mya (Yoder et al., 2003). Restrained to this island, euplerids seems to also have partitioned their feeding niche in a notable way even though the extend is harder to determine considering the few knowledge collected on the diet of those peculiar animals. If *Mungotictis decemlineata* and *Fossa fossana* are described as insectivorous, other species are thought to have different levels of carnivory (Goodman et al., 2003; Rasolofoniaina, 2017). One, *Cryptoprocta ferox*, is a well-known hypercarnivorous species (Dollar, 2007). This species exhibits a largely derived morphology compared to other members of the family. If other euplerids tend to keep a developed talonid and a complete trigonid, the metaconid of *C. ferox* is absent and its talonid is extremely reduced, resulting in a felid-like morphology. The extend of the resemblance appears quite clear as it is situated just next to felids and inside the nimravid convex hull. However, information about the euplerid evolutionary pattern is scarce (Barycka, 2007; Goodman, 2003). It is unclear if the primitive morphology of feliforms is closer to the one of *Cryptoprocta ferox* than to the one of other euplerids. Indeed, basal feliforms such as nimravids or *Proailurus* spp. already show this bicuspid blade-like aspect but other basal feliforms like *Protictitherium gaillardi*, the oldest

known hyaena, show a more neutral morphology (Mayda et al., 2015). This hyaena possess a complete trigonid and a developed talonid which further questions the ancestral anatomy of feliforms. Other hyaenas tend to show a felid-like morphology with secondary modification such as a buccal inclination of the protoconid-paraconid segment and rounded carnassial notch which could be a key feature to dissipate the mechanical stress induced by osteophagous diets (Hartstone-Rose, 2011; Hartstone-Rose & Stynder, 2013).

Procyonids (racoons and kin) are another exceptional clade regarding carnassial morphology, ranking first in both our disparity metrics. If they always exhibit a proportionally large talonid, its thickness as well as the height of the trigonid (shown by the PC3) is extremely variable. The antero-dextral rotation of the protoconid-paraconid is also variable as well as the sharpness of the trigonid. It is very difficult to associate this morphological diversity with diet as they often possess an extensive dietary spectrum (Bartoszewicz et al., 2008; Gatti et al., 2006; Kays, 2000; Quintela et al., 2014). Nevertheless, procyonids show a tendency for hypocarnivorous diet, with most species being omnivorous. Some species are even classified as frugivorous (such as *Potos flavus*) but other species mainly feeding on fruits are still classified as omnivorous due to the addition of a sensible proportion of insect to their diet. It is very common for frugivorous species to add invertebrates to their diet as they can provide nitrogen, which is a difficult nutrient resource to acquire from a frugivorous diet (Bryer et al., 2015; Carlos & Pacheco, 2000; Donati et al., 2017; Herrera M. et al., 2001). These frugivorous/frugi-insectivorous diet corroborates with the lack of developed trigonid and a generalised flattened tooth morphology of procyonids in this study. It is plausible that frugivorous diets do not require strong shearing or crushing mechanics but that a larger masticatory area could be advantageous, even without cuspids, to crush berries and other fleshy fruits (Anapol & Lee, 1994; Berthaume, 2016; Peters, 1987; A. B. Taylor, 2006). An hypothesis would be that flat molar teeth would allow the consumption of fruits and berries containing poisonous seed without crushing them (Crofts et al., 2020; Janzen, 1969) and releasing toxic chemicals, although this is speculative. Considering that the primary evolutionary constraint lays in frugivory, these teeth are not morphologically optimised for piercing through insect cuticula but may be sufficient to consume the amount of invertebrates necessary to compensate lacking nutrients.

Ursids show a medium disparity when compared to other carnivoramorphans. This disparity may be essentially built by the inclusion of basal ursids such as *Amphicynodon* spp. that, although commonly placed among bears, may represent a separate lineage of more basal arctoids according to some authors (Ciroto & De Bonis, 1992; Finarelli, 2008). While amphicynodonts possess a typical basal-caniform morphology with a complete trigonid and talonid (Solé et al., 2020), modern bears exhibit a less pronounced trigonid and a long talonid with many well individualised cusps. Most bears are hypocarnivorous animals with a large proportion of their diet directly consisting of vegetal matter though most of them stay opportunistic carnivores (Basnett et al., 2021; Bojarska & Selva, 2012; Clevenger et al., 1992; Panthi et al., 2019). While brown bears are regionally seasonally strongly carnivorous and/or piscivorous, polar bears are the most carnivorous one as they live inside the polar circle where vegetal matters is rare, scarce and even seasonally inexistent (Dyck & Kebreab, 2009; Florko et al., 2021; Galicia et al., 2015; Iversen et al., 2013; Petherick et al., 2021). Despite this high degree of hypercarnivory, polar bears do not show a strongly derived morphology similar to the one exhibited by other hypercarnivorous carnivorans. This may be addressed by different hypothesis ; one could be the relative late separation of brown and polar bears estimated at 1.2ma (Cronin et al., 2014) with probable multiple hybridation events during the glacial cycles which tempered morphological changes. Another hypothesis is that the relatively large size of bears would allow them to bypass the need of mechanical efficiency in their teeth to process meat. The size of their molar and the power of their bite may be sufficient for meat processing. Meat is also relatively easy to digest and has a high nutrient content, requiring mainly cutting or shredding into swallowable pieces. While these hypotheses are not mutually exclusive, they should be considered alongside the fact that, besides the first lower molar, other morphological features evolved quite rapidly during this time period (Slater et al., 2010). Besides polar bears, pandas are another ursid species that exhibit a particular first molar with its bulbous morphology that could be linked to their particular diet. Panda are famous for eating bamboo, a polyphyletic group of Poaceae with morphological and structural specificities (Pattanaik & Hall, 2011; Sungkaew et al., 2009). The bamboo they eat is made of hard, fibrous culm containing silicium phytoliths (Liu et al., 2012; Vallittu et al., 2021). This often leads to consider animals eating these as durophagous, like bone- and shell-crusher species. This particular ‘bunodont-like’ morphology, somewhat similar to the one of suids and primates (Berkovitz & Shellis, 2018), is a probable adaptation to the mechanical stress that they undergo while masticating bamboo’s culm.

Viverrids exhibit a large morphological diversity ranking as 3rd greatest Procrustes variances and 5th regarding hypervolume measurement. These animals exhibit a large repartition area and show diverse dietary patterns though they are largely hypocarnivorous with many omnivorous and frugivorous species. Some show severely derived morphology with extended and large talonid which bears notable cusps like *Paradoxurus hermaphroditus*, *Arctogalida trivirgata* and *Macrogalidia musscherbrockii*. Other like *Poiana richardsoni*, *Genetta* spp. or *Viverra* spp. exhibit a more ‘felid-like’ morphology with reduced talonid and enhanced protoconid-metaconid. Nevertheless, all its species maintained a complete trigonid. Unsurprisingly, faunivory seems more developed in the second morphological group (Colon & Sugau, 2012; Hart & Robert, 1978; M. E. Taylor & Hannam, 1987; Wemmer & Watling, 1986). However, considering that most of their species stay relatively understudied, it is challenging to sufficiently assess the link between their morphology and diet.

Mustelids also show extreme diversity in morphology and in dietary niches. They rank 3rd in hypervolume and 5th in Procrustes variances. If mustelids are known to be ecologically diverse, most are carnivorous (Kollias & Fernandez-Moran, 2015; Selig, 2023). Yet, they adapted to a wide range of prey and behaviours, with vertebrate hunters and scavengers such as ermines and wolverines (McDonald et al., 2000; Myhre & Myrberget, 1975), piscivores and malacophages otters (Carss & Parkinson, 1996; Hostos-Olivera & Valqui, 2024; Taastrøm & Jacobsen, 1999), and also omnivores such as *Meles meles* (Cleary et al., 2009; Goszczyński et al., 2000). The dietary signal in mustelid’s carnassial teeth seems very pronounced; while the omnivorous badger exhibit large and long talonid with reduced trigonid height, hypercarnivorous species such as *Mustela nivalis* bear a very sharp and elongated first molar (Lang et al., 2022; Selig, 2023). Its morphology combines a reduced metaconid with a sharp-edged talonid with a unique but well pronounced cusp in its center (Van Valkenburgh, 1991). This hyperspecialised carnassial dentition might be the result of the small size of *Mustela nivalis* which would not allow him to bypass its efficiency using strength. Equally unique is the morphology of the mandibular first molar of the sea otter: *Enhydra lutris*. Flattened, with very large, rounded cusps, and of circular shape in occlusal view, this tooth has completely lost any traces of carnassial function. Their extreme morphology is closely associated with their durophagous, mainly molluscivorous diet. Sea otters eat a wide range of shell-protected prey that must be broken before consumption (Doroff et al., 2012; LaRoche et al., 2023). While other mustelids eat crustaceans, their prey type are usually crabs and crayfish which may be

less mechanically demanding than molluscs and echinoderms (Hostos-Olivera & Valqui, 2024; Kruuk et al., 1994).

Macroevolutionary patterns in crown shape-diet relationships:

Although constructing a phylogenetic tree was not feasible within the timeframe of this master's thesis, it became evident that incorporating evolutionary information to temper the impact of diet on morphology was essential (Hopkins et al., 2022). The use of Procrustes linear models to quantify the impact of diet and family on the obtained Procrustes coordinates indicate a significant and strong impact of diet and phylogeny on the 3D configuration of teeth (table 4). The even stronger impact of diet compared to family on the shape of teeth can also be explained by ecological inertia. Species that formed the divergence base of each separate family already had a preferential ecological and dietary niche and, in absence of external or internal pressures (or significant pressure diminution as ecological pressure should be considered as an absolute value), the descending species tend to maintain similar niche. Indeed, whether it is caused by increasing or decreasing competition, change in ecological structure is expected to act as a pressure towards directional evolution.

In this study, hypercarnivorous diet seems to be represented by two relatively precise but distant morphological density peaks and rank 2nd and 3rd on disparity measures (Procrustes variance and hypervolume). Although this may seem surprising given that the mechanics of meat shearing is particular, this diet is also the most common among carnivorans as well as probably the most ancestral, increasing the likelihood that various forms have developed. One peak is formed within feliforms, which could be called the ‘feliform way’ or ‘Felimorph carnassial’; another is formed within caniforms, the “caniform way” or “Canimorph carnassial” (Fig.18). If both share some characteristics like enlarged cutting edge with trenchant paracristid and reduction of the metaconid; a notable difference lies in the morphology of the talonid. In the ‘feliform way’, the talonid regress to eventually entirely disappear in most derived taxa, leaving only a bicuspid, ‘blade-like’ protoconid. Contrarily, in the ‘caniform way’ the talonid stays always present and, in the most derived taxa, forms a supplementary longitudinal blade (Van Valkenburgh, 1991). This might be an example of “many-to-one function” as both seems evolutionary successful. However, as discussed previously, other biological, ecological or ethological factors may be needed to explain such success. From a broader point of view, if

hypercarnivory seems to bear a clear morphological signal in feliforms, this signal remains less clear for caniforms. A relative clear cut is indeed observed in the morphology of hypo- and hypercarnivorous feliforms through the development of talonid and metaconid but the difference is not always as clear regarding hyper- and mesocarnivorous, or even omnivorous caniforms. It is plausible that the presence of a notable metaconid and talonid does not negatively affect the carnassial function as much as their absence affect the ability to treat other alimentary resources. In this regard, caniforms may present a greater versatility at the evolutionary scale because of their complete m1 morphology and dental formula. Furthermore we observe that, when competition is low, some extend of “evolutionary lag” (Hopkins et al., 2022) exist between dietary niche change and its morphological impact in caniforms. This could indicate that, even if the dietary signal is known to be significative in the m1 (Holliday & Steppan, 2004; Lang et al., 2022; Van Valkenburgh, 1989, 2007), it could be lower in caniforms (and especially in canids) than in feliforms.

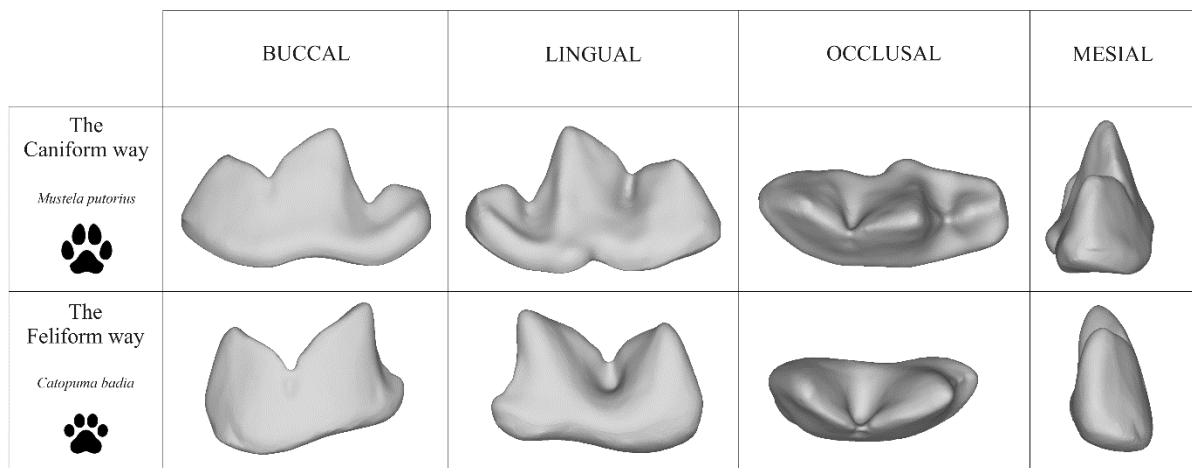


Figure 18. Type example of highly derived carnassial morphology in hypercarnivorous caniforms and feliforms.

Regarding mesocarnivorous carnivoramorphans, even if they appear to be intermediate on the PC1 between hypercarnivorous and omnivorous, their differences with the last are not significative (see supplementary material S.2). Mesocarnivorous diet is nearly entirely represented by canids (7/8 species) which makes further inferences complicated due to the strong phylogenetic signal.

The same applies to herbivorous species with 75% of sampled species being extant ursids. An interesting point is the strong morphological resemblance of *Ailuropoda melanoleuca* and *Ailurus fulgens*. While numerous morphological convergences have been extensively discussed

(Figueirido et al., 2012; Hu et al., 2017; Tamagnini et al., 2021). Their names reflect the phylogenetic classification struggle they have posed for biologists over centuries (Mayr, 1986). It is interesting to note that their bamboo durophagous diet has led to similar secondary modification on their first mandibular molar, resulting in particularly tuberous teeth. The selective pressure for this kind of diet seems notably severe among carnivorans, whose digestive tracts are not particularly efficient at processing plant matter (Guo et al., 2020; Xue et al., 2015).

Molluscivorous species are also scarce in our dataset but their morphological extend remains noteworthy. As discussed earlier, the strong difference in mechanical difference for small crustacean and molluscs might explain this plasticity. Three out of four molluscivorous species in our dataset are mustelids and, besides *Enhydra lutris*, the remaining tree molluscivorous stay opportunistic predators and are known to predate on land fauna and fish (Hostos-Olivera & Valqui, 2024; Whitfield & Blaber, 1980). Thus, if the strong overlap of molluscivorous and omnivorous species is not surprising, no conclusion can be inferred.

The omnivorous species being, by definition, a large and dietary diverse group encompassing different realities (Insecti-frugivorous, carni-vegetarian...), it is interesting to consider the medium disparity that they exhibit. It seems like excess in the trigonid cuspids development and talonid reduction both are detrimental for a large dietary niche. While talonid reduction fragilized crushing and chewing capability which are essential for nutrient extraction from vegetal resource (Berthaume, 2016; Crofts et al., 2020), an overdevelopment of cuspid height might become counterproductive. One possible explanation is that it would lead to more cuspids fractures as well as uncomfortable chewing mechanics (Van Valkenburgh, 1988a).

We could have expected a large morphological diversity for piscivorous diet since fish are easy to process and digest (Christiansen & Wroe, 2007; Hartstone-Rose et al., 2019), but opposite results were obtained. However, the limited number of observations biased by the strong phylogenetic signal (6/7 piscivorous species recorded being otters) could explain this result. This dietary niche is quite rare in carnivorans which are primarily terrestrial and the exclusion of pinnipeds, the only primarily aquatic carnivoran clade, due to methodological limitations leads to another bias. A separate study on these particular carnivorans is underway.

Frugivorous species exhibit the largest disparity ranked by both our methods. It is tempting to assume that a frugivorous diet would be associated with a lower mechanical constraint proportionally to the amount of calories and nutrients obtained (Gallagher, 2014).

Most fruits are soft and substantially nutritious besides for amino acids that can be obtained by the addition of small prey, often invertebrates. This particular diet is encountered in various families and numerous mesocarnivorous, omnivorous and insectivorous species are also known to consume fruits. Fruits consumption is also occasionally reported in hypercarnivorous species which further testify the ease source of energy that it represents (Draper et al., 2022).

Comments on disparity methods:

The hypervolume determination and the Procrustes variance analysis are two different ways of quantifying the extend of disparity achieved by defined groups. If both bear a related signal, their algorithm is significantly different and gives a disproportional weight to distinct arguments. If hypervolumes can be interesting for their resistance to small-sized dataset, they remain strongly impacted by outliers. Above this, the obtained results are often from different magnitude which hardens interpretation. The extraction of the natural logarithm of results can partially relieve this problem but the remaining results stay mostly qualitative. On the other hand, Procrustes variances are statistically robust and are less impacted by outliers. A notable example of this would be mustelids ranking 3rd in hypervolume but 5th in procrustes variance. Though this clade exhibits some extreme forms in all axes, it maintains a relatively centralised core. Extreme forms such as *Mustela nivalis* and *Enhydra lutris* may have strongly stretched hypervolumes.

4.2 Cenozoic carnassial morphology evolution

Although our sampling is limited for the Paleocene, the dominance of oxyaenids in this time bin is not coincidental. They were among the first Pan-carnivorans to develop a functioning carnassial complex with scissor-like mechanics (De Muizon & Lange-Badré, 1997; Gingerich, 1980a; Heather, 2017). This morphological feature allowed them to occupy the top of the food chain in early Cenozoic ecosystems with few mammalian competitors (Van Valkenburgh, 1999). Even if they lack a derived dentition, the absence of strong competitors might have been sufficient to allow them to thrive at higher level of the trophic chain. They will stay ecologically relevant till the late early-Eocene before their extinction around the Eocene-Oligocene border (Solé et al., 2011).

However, this dominance of oxyaenids will not last long, as the Eocene witnesses the diversification of several carnivorous groups (Christison et al., 2022; Friscia & Valkenburgh, 2010). Indeed, if some basal hyaenodonts still exhibit a dental shape similar to those of oxyaenids an early carnivoraforms (Smith & Smith, 2001), other hyaenodont lineages (e.g. Hyaenodontoid) acquired the most derived, bicuspid “blade-like teeth” ever recorded in placentals, most probably to thrive in hypercarnivorous niches (Lang et al., 2022; Van Valkenburgh, 1999). In parallel to these hyaenodonts, early nimravids colonised an adjacent morphology (i.e. bicuspid but less arched) by the middle Eocene before peaking in their diversity during the Oligocene. It seems clear that ‘felimorph’ predators (felids and nimravids) and hyaenodontoids exhibit notable convergences. Their morphological differences are largely attributable to the position of their carnassial teeth in the jaw, with hyaenodonts having them formed by the third molar rather than the first (De Muizon & Lange-Badré, 1997). Amphicyonids also colonised a new area in the morphospace (i.e. teeth with a trenchant but complete trigonid and notable talonid) that resulted in a very large general disparity during the Eocene. The Eocene thus represents the epoch where all great Pan-Carnivorans lineage coexists with a large spectrum of creodonts and carnivoramorphans (caniforms and feliforms) (Van Valkenburgh, 1999, 2007; Wesley-Hunt, 2005). This phylogenetic diversity of (likely) hypercarnivorous lineage during the Eocene is associated with a larger morphological spread of dental phenotypes. If this could be the sign of a greater dietary niche partitioning eventually due to a higher species diversity, the addition of spatial information and greater temporal discernment would be necessary to address this hypothesis. All these morphologies were not always sympatric and, in absence of direct competition with other hypercarnivorous morphologies, some could have been sufficient to colonise the top of the trophic chain even

without mechanical optimisation for ‘hypercarnivory’. The Eocene situation could therefore also be interpreted as a series of hypercarnivorous niche realisations through incomplete convergences.

The Eocene-Oligocene boundary is a dynamic event which sees the restructuration of many continental ecosystems; the event has been termed the “Grande coupure” (Solé et al., 2022; Stehlin H-G, 1909). This severe cooling event caused an important sea level regression, resulting in the connection of previously isolated regions and the onset of drier climatic conditions (Berggren & Prothero, 1992; Li et al., 2018). These multiple migration events spreading from late Eocene to early Miocene, notably between Asia, Europe and Balkan-Anatoly, homogenised faunas via direct competition dynamics as never seen before in the Cenozoic (Licht et al., 2022). During this transition period, modern faunas became established in Europe, marked by extinctions and diversification events. (Solé et al., 2022). The relatively good sampling acquired for this period in European fauna through the fossil record of Quercy draws a good picture of the morphology encountered. The peak of nimravids and amphicyonids diversity is well documented as well as the continued ecological importance of the possibly waste-basket genus *Hyaenodon*. A notable change is the total disappearance of oxyaenids, which contained a diverse array of small to (very-) large sized species (Gingerich, 1980b; Sorkin, 2008). For the smaller species, the apparent lack of morphological replacement could partially be attributed to the fact that their ecological role and morphology was overtaken by small-sized carnivoramorphans that were excluded from our analysis, which could lead to erroneous conclusions. For the larger species, the greater diversity acquired by Hyaenodonta and Carnivoramorpha may have pulled the rug out from under them. The more specialised Hyaenodonta and Carnivoramorpha may have outcompeted or at least replaced them after their eventual decline (Van Valkenburgh, 1999, 2007). The result from these dynamics eventually ushered in the dominance of two major carnassial morphologies among medium- to large-sized placental predators.

During the Miocene, creodonts disappear entirely, letting felids and the last nimravids as the last bearer of the bicuspid ‘hypercarnassial’ morphology. Canids diversify and share their position with the last Amphicyonids. Similarly as for nimravids, the reason behind the decline of Amphicyonids remains misunderstood. While locomotory arguments and changes in prey guilds have sometimes been considered (Viranta, 1996), another hypothesis suggests that an unusual tooth erupting sequence, where juvenile experience a period without functional

carnassial teeth, potentially affected their competitive ability against emerging canids (Morlo et al., 2019).

The Pliocene-Quaternary periods mark the consolidation of modern carnivoran morphology and taxonomy, coinciding with the disappearance of nimravids and amphicyonids. Felids and canids emerge as the dominant main medium-to-large predatory taxa, characterized by distinct morphologies.

If the presence of hyperspecialised carnassial morphologies appears stable since the Eocene, indicating notable functional effectiveness, the phylogenetic status of these adaptations is remarkably variable. Examining the dynamics observed in hyaenodontoids, nimravids and felids, this study aligns with the long-standing hypothesis that “hypercarnassialised” predators are less resistant to ecological crisis, potentially explaining their regular extinction and replacement dynamics during Cenozoic (Lang et al., 2022; Van Valkenburgh, 1999, 2007). Overall, this work shed light on the temporal context in which modern morphological landscape of carnassial teeth took place. If premises can be observed in the Eocene diversification, the “Grande coupure” and the associated migration events through Oligocene set the base of morphologies and phylogenetics that characterise modern medium to large carnivorous guild composed of ‘canimorphs’ and ‘felimorph’ predators.

Comment on evolutionary meaning behind long lasting morphologies:

Although it can be moderated by the role of random mutations and genetic drift, evolutionary processes operate as inertial systems. If structures tend to change in response to external absolute pressures, the maintenance of precise structures also reflects selective pressures, since the expected Brownian motion cannot explain long-term stasis in the dynamic context of ecosystems and genetics. The study of these long-lasting morphologies (such as depicted earlier) across geological time thus represent a valuable tool for understanding macro-evolution patterns and for the reconstitution of ecological networks, as they provide proxies for the structuring of trophic relationships.

5. Conclusion

The aim of this Master thesis was to contribute to the study of Cenozoic's ecosystems by clarifying the evolutionary dynamics in the shape of Pan-Carnivoran's carnassial teeth and its link with diet.

Through an extensive examination of the carnassial teeth shapes across 250 Pan-Carnivora species, we conclude that:

- 1) The carnassial teeth of carnivoramorphans bear a meaningful dietary signal and can therefore be used to infer dietary information in extinct species. However, the precision of obtained information remain to be moderated by the phylogenetic position of their bearer as all clades do not exhibit equal dietary signal.
- 2) The 'Grande coupure' and the associated Oligocene migration events correlate with significant perturbations in the disparity and range of dental phenotypes in predators. A clear signature of this event can still be seen in nowadays ecosystems through the domination of canids and felids as hypercarnivores.
- 3) Hypercarnassialised teeth are a staple of mammalian diversity since the Eocene, having been iteratively evolved by multiple lineages with no discernible temporal gap.

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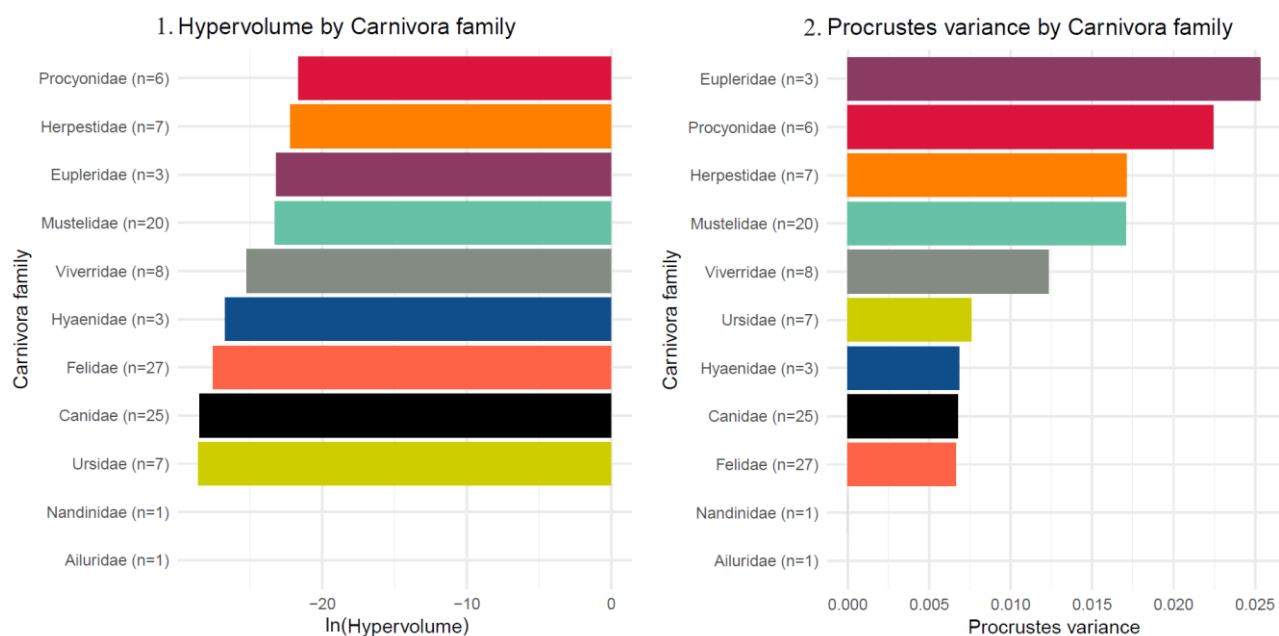
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Supplementary material

S.1) Hypervolume and procrustes variance of the carnivoran subset



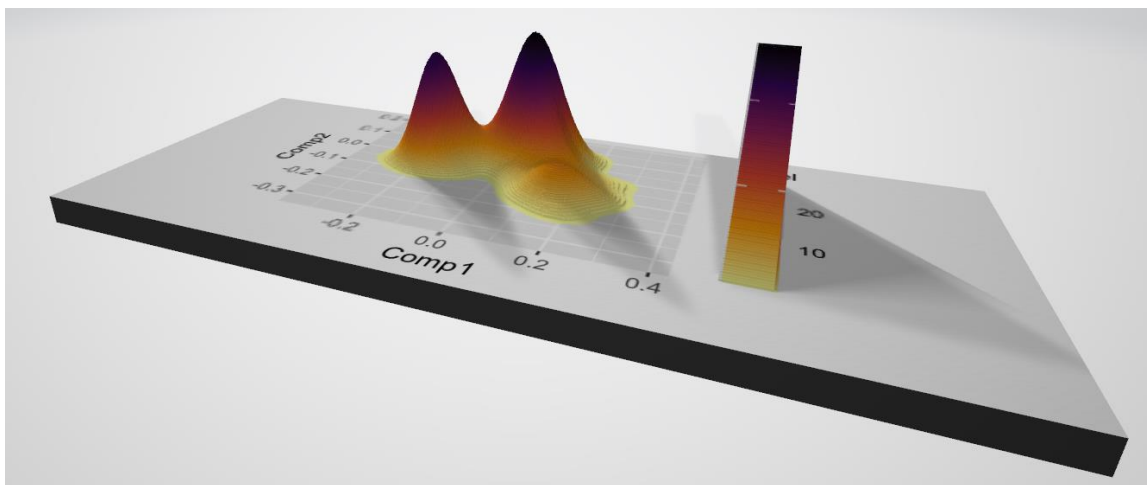
S.2) p-value of diet Procrustes coordinates comparison:

	Hypercar nivorous	Mesocar nivorous	Omniv orous	Mollusc ivorous	Insecti vorous	Pisciv orous	Herbiv orous	Frugiv orous
Hypercar nivorous	1	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Mesocarn ivorous		1	0.066	0.005	0.001	0.001	0.028	0.008
Omnivor ous			1	0.01	0.003	0.001	0.256	0.007
Mollusci vorous				1	0.109	0.033	0.061	0.606
Insectivor ous					1	0.003	0.005	0.018
Piscivoro us						1	0.004	0.009
Herbivor ous							1	0.114
Frugivoro us								1

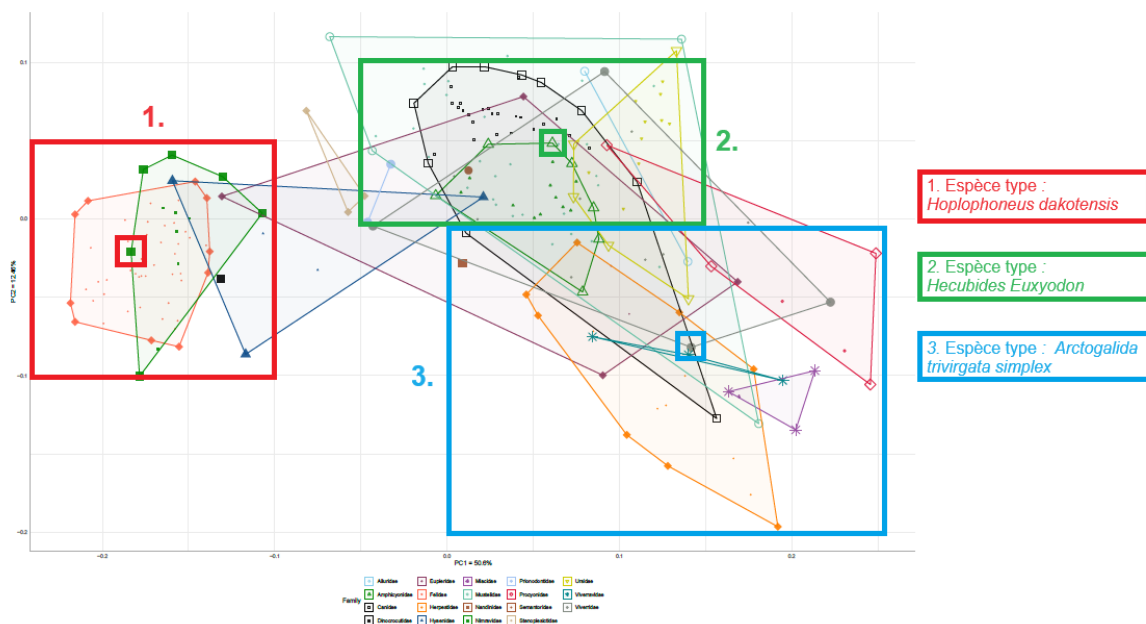
S.3) p-value of epoch pairs comparison with bootstrap of n=100

Epoch pair	p-value
Paleocene – Eocene	$< 2 \cdot 10^{-16}$
Eocene - Oligocene	$< 2 \cdot 10^{-16}$
Oligocene – Miocene	$< 2 \cdot 10^{-16}$
Miocene – Pliocene	$< 2 \cdot 10^{-16}$
Pliocene - Quaternary	$< 2 \cdot 10^{-16}$

S.4) 3D density morphospace (PC1 vs PC2) for carnivoramorphans



S.5) Visual of the 3 main morphospace regions defined for Carnivoramorphans



S.6) Carnivoramorphan intra-family disparity

Carnivoromorpha family	Procrustes variance
Ailuridae (n=2)	0.010590267
Amphicyonidae (n=19)	0.007810038
Canidae (n=36)	0.006537793
Dinocrocutidae (n=1)	0.000000000
Eupleridae (n=6)	0.021730596
Felidae (n=49)	0.007106781
Herpestidae (n=14)	0.015544046
Hyaenidae (n=5)	0.011198644
Miacidae (n=4)	0.005721387
Mustelidae (n=32)	0.014859094
Nandinidae (n=1)	0.000000000
Nimravidae (n=12)	0.010133055
Prionodontidae (n=2)	0.002504613
Procyonidae (n=6)	0.022420605
Semantoridae (n=1)	0.000000000
Stenoplesictidae (n=3)	0.003179946
Ursidae (n=15)	0.009845542
Viverravidae (n=3)	0.006994989
Viverridae (n=13)	0.017408561

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S.7) Subset carnivoramorphan intra-family disparity

Carnivoran Family (number of observations)	Procrustes variance
Ailuridae (n=1)	0.000000000
Canidae (n=25)	0.006764222
Eupleridae (n=3)	0.02533890
Felidae (n=27)	0.006636439
Herpestidae (n=7)	0.01711231
Hyaenidae (n=3)	0.006835511
Mustelidae (n=20)	0.01707991
Nandinidae (n=1)	0.000000000
Procyonidae (n=6)	0.02242060
Ursidae (n=7)	0.007569677
Viverridae (n=8)	0.01232866

S.8) Carnivoromorpha subset diet disparity

Diet (number of observations)	Procrustes variance
Hypercarnivorous (n=52)	0.018316831
Mesocarnivorous (n=8)	0.009727746
Omnivorous (n=19)	0.016801051
Piscivorous (n=7)	0.007223106
Insectivorous (n=7)	0.015773581
Molluscivorous (n=4)	0.015685270

Herbivorous (n=4)	0.010816062
Frugivorous (n=7)	0.025690615

S.9) QR code for complete dataset

