Carnivoran Dietary Adaptations
A Multiproxy Study on the Feeding Ecology of the Fossil Carnivorans of Greece

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Master's Thesis

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Contents

Introduction

The order Carnivora includes the majority of carnivoran mammals, fossil and extant. Although the name of the order means “carnivorans”, there are not only obligate carnivorans in this order. There are also many omnivores (e.g. bears, badgers) and even some herbivores (the pandas). Also, the carnivorans occupy a wide range of different ecological niches and frequently have distinct diets as insectivores (meerkats), ant-eaters (aardwolf), piscivores (pinnipeds), rodent-eaters (small felids) and hunters of large prey (large felids, sea leopards, polar bears). Another parameter of variability is that “strict” carnivory is a very unusual thing. The common meat-eaters usually complete their diet with other material such as insects, fruits, seeds or leaves. It seems that the strictest flesh-eaters are the felids.

This stunning variability requires different dietary strategies and, therefore, a wide range of adaptations. These adaptations are reflected in the skeletons of the animals and, especially, in their craniomandibular region.

The skull is the most complex skeletal element, because it is a multi-tasking tool. It protects the brain, it is the site where many of the sense organs are located and it is the beginning of the digestive system. The whole cranial system is adjusted to the dietary needs of the species. A horse uses wide and powerful molars and strong masseter muscles to chew plant material, whereas a lion uses long canines, cutting premolars and strong temporal muscles for a powerful killing-bite. The form of a skull is a reliable indicator on the analysis of diet, age, sex and life history of an individual.

This study deals with the dietary adaptations of the skull and the mandible of the fossil carnivorans of Greece. The fossil material studied belongs 47 species assigned to 8 families. The stratigraphical range of these species is between Late Miocene and Middle-Late Pleistocene. The analysis was accomplished with the use of digital and non-digital methods in comparison with many extant carnivorans.

The variety of the Greek fossil carnivorans is significant for many reasons. At first, Greece was in some occasions connected with the rest of Europe and Anatolia simultaneously, offering available space for species from both origins. This is probably the reason that the Samos fauna preserves some species that can be seen only in the northern part of the country, indicating that the migrating paths were very different from the ones we can see today. Another reason is the south to north direction of the country. The latitude (combined with altitude) is a very important ecological parameter, correlated with temperature, moisture and flora type. This fact leads to an eco-cline from the north of the country to the tip of the Balkan Peninsula, resulting in gradually different ecosystems. These results can be seen in the different faunas encountered in the northern and the southern part of the country at the same period.

The fossil record of Greece includes a lot of carnivoran species. The oldest fossil carnivorans of Greece are *Pseudailurus quadridentatus*, *Proputorius* cf. *sansaniensis*, *Pseudailurus* cf. *lorteti* and *Percrocuta* sp. from MN4-MN5 of Antonios, Chalkidiki (Koufos, 2008, 2011). *Lophocyon paraskevaidisi* is also mentioned from the MN5 locality of Thymiana B, Chios (Koufos et al., 1995).

The majority of the carnivoran species are dated in the Vallesian and Turolian in the Late Miocene. This age includes the most plentiful localities of Greece including

Pikermi, Samos Quarries and Axios Valley. The most successful taxa in this period in Greece were crocutoid hyenas, ictitheres, mustelids, bears and sabertoothed cats.

Another age rich in relevant remains is the Villafranchian, when carnivorans can be found in Sesklon, Apollonia, Dafnero, Gerakarou etc. In this age the canids are expanded to the Balkans (replacing the ictitheres) and the sabertoothed cats are gradually replaced by pantherines.

Finally, carnivorans can be found in the Middle and Late Pleistocene of Greece, including species such as *Ursus deningeri* and *Panthera pardus*. The existence of *Isolalutra cretensis*, the endemic otter of Crete is also an interesting case.

The fossil carnivorans of Greece provide a very interesting taxon for continuous studies, because of their variability. There are species, such as *Promephitis lartetii*, in the size of an extant skunk, and large sabertoothed cats, such as *Amphimachairodus giganteus*, larger than modern lions. Some groups are represented by a high number of ecologically comparable taxa. The coexistence of ecologically similar species reveals that there must be some kind of competitive exclusion, leading the different species to adapt in different ecological niches.

Many of the fossil carnivorans of Greece seem to have modern analogues, but others don’t. For example, *Simocyon primigenius* is a very strange, bear-like carnivoran found in Halmyropotamos and Pikermi with no modern analogue. Of course, the sabertooths (*Amphimachairodus giganteus*, *Paramachairodus orientalis*, *Metailurus major*, *Metailurus parvulus*, *Homotherium latidens* and *Megantereon cultridens*) are very different from any of the extant felids, because of their saber-shaped upper canines and their robust physique. The sabertoothed cats of Greece preserve high variability, from the primitive *Paramachairodus orientalis* and *Metailurus* spp. to the scimitar-toothed *Homotherium latidens* and the dirk-toothed *Megantereon cultridens*. Finally, ictitheres, the wolf-like hyenas, may be similar to canids, but their completely separate phylogeny is an indicator of their possibly different ecology.

There are some species, which are known only from small fragments, such as *Enhydriodon latipes*, the fossil otter from Pikermi (Pilgrim, 1931). Because of the absence of material on these species, it is very difficult to make accurate suggestions about their ecology.

The fossil record of Greece also includes a high variety of bovids, cervids, equids, suids, rodents and birds. This wide range of possible prey allows us to construct specific lists with the hunting target group of every carnivoran.

The basic task of this study is to uncover some cranial and dental adaptations of the fossil carnivorans associated to their diet. The analysis of these parameters is a valuable step to the knowledge of these fossil predators’ lives.

This MSc study is the first part of a more complete project on the ecology of Greek fossil carnivorans. I hope that this project will be completed by the end of a PhD, providing a useful and more reliable source for the life of the fossil predators found into Greek fossiliferous horizons.

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Figure 1: *Megantereon cultridens*. Source: Antón (2013)

Material and Methods

Material

The material used in this study is stored in many different collections. The abbreviations of the visited institutes are as follows: **AMPG** (Athens Museum of Palaeontology and Geology), **LGPUT** (Laboratory of Geology and Palaeontology, University of Thessaloniki), **NHMA** (Natural History Museum of the Aegean, Samos), **HMCEPS** (Hellenic Ministry of Culture, Ephorate of Palaeoanthropology-Speleology), **MNHN** (Museum Nationale d'Histoire Naturelle, Paris), **NHMUK** (National History Museum, United Kingdom), **SMNS** (Staatliches Museum für Naturkunde, Stuttgart), **NMNHS** (National Museum of Natural History, Sofia), **NHCV** (Natural History Collection, Vrissa), **NHMUC** (Natural History Museum, University of Crete), **ZMUA** (Zoological Museum of University of Athens), **GMNH** (Goulandris Museum of Natural History), **ZMUP** (Museum of Zoology, University of Patras).

The complete specimen list of extant species is on the appendix. The extant species used in this study are summarized in Table 1:

Table 1: Extant species used in this study.

Family	**Species**	**Family**	**Species**
Ailuridae	*Ailurus fulgens*	Felidae	*Lynx lynx*
Canidae	*Lycalopex culpaeus*	Felidae	*Neofelis nebulosa*
Canidae	*Urocyon cinereoargenteus*	Felidae	*Panthera leo*
Canidae	*Nyctereutes procyonoides*	Felidae	*Panthera onca*
Canidae	*Otocyon megalotis*	Felidae	*Panthera pardus*
Canidae	*Vulpes vulpes*	Felidae	*Panthera tigris*
Canidae	*Canis aureus*	Felidae	*Puma concolor*
Canidae	*Canis adustus*	Felidae	*Acinonyx jubatus*
Canidae	*Canis familiaris*	Felidae	*Prionailurus viverrinus*
Canidae	*Canis latrans*	Herpestidae	*Mungos mungo*
Canidae	*Canis mesomelas*	Herpestidae	*Suricata suricatta*
Canidae	*Canis lupus*	Herpestidae	*Herpestes edwardsi*
Canidae	*Lycaon pictus*	Herpestidae	*Herpestes ichneumon*
Canidae	*Cuon alpinus*	Herpestidae	*Ichneumia albicauda*
Canidae	*Speothos venaticus*	Hyaenidae	*Crocuta crocuta*
Eupleridae	*Galidia elegans*	Hyaenidae	*Parahyaena brunnea*
Felidae	*Felis catus*	Hyaenidae	*Hyaena hyaena*
Felidae	*Felis silvestris*	Hyaenidae	*Proteles cristatus*
Felidae	*Leopardus wiedii*	Mephitidae	*Mephitis mephitis*
Felidae	*Leopardus tigrinus*	Mephitidae	*Conepatus humboldti*
Felidae	*Leopardus pardalis*	Mephitidae	*Conepatus chinga*
Felidae	*Profelis aurata*	Mustelidae	*Mustela nivalis*
Felidae	*Caracal caracal*	Mustelidae	*Mustela putorius*
Felidae	*Leptailurus serval*	Mustelidae	*Gulo gulo*

Table 1 (continued)

Family	Species	Family	Species
Mustelidae	*Lutra lutra*	Procyonidae	*Potos flavus*
Mustelidae	*Amblonyx cinereus*	Ursidae	*Ursus maritimus*
Mustelidae	*Enhydra lutris*	Ursidae	*Ursus thibetanus*
Mustelidae	*Pteronura brasiliensis*	Ursidae	*Ursus arctos*
Mustelidae	*Eira barbara*	Ursidae	*Ursus americanus*
Mustelidae	*Martes foina*	Ursidae	*Tremarctos ornatus*
Mustelidae	*Martes martes*	Ursidae	*Helarctos malayanus*
Mustelidae	*Meles meles*	Ursidae	*Ailuropoda melanoleuca*
Mustelidae	*Vormela peregusna*	Viverridae	*Civettictis civetta*
Nandiniidae	*Nandinia binotata*	Viverridae	*Genetta genetta*
Phocidae	*Monachus monachus*	Viverridae	*Genetta tigrina*
Procyonidae	*Nasua narica*	Viverridae	*Poiana richardsonii*
Procyonidae	*Nasua nasua*	Viverridae	*Arctictis binturong*
Procyonidae	*Procyon lotor*	Viverridae	*Paradoxurus hermaphroditus*

The complete specimen list of the fossil species is in the appendix. The fossil species catalog is the following:

Table 2: Fossil species studied, dividing the species in Miocene and Villafranchian.

Late Miocene		**Villafranchian**	
Family	**Species**	**Family**	**Species**
Felidae	*Metailurus major*	Felidae	*Lynx issiodorensis*
Felidae	*Metailurus parvulus*	Felidae	*Panthera gombaszoegensis*
Felidae	*Amphimachairodus giganteus*	Felidae	*Homotherium latidens*
Felidae	*Pristifelis attica*	Felidae	*Megantereon cultridens*
Felidae	*Paramachairodus orientalis*	Hyaenidae	*Pliohyaena perrieri*
Hyaenidae	*Plioviverrops orbignyi*	Hyaenidae	*Pachycrocuta brevirostris*
Hyaenidae	*Protictitherium gaillardi*	Hyaenidae	*Chasmaporthetes lunensis*
Hyaenidae	*Protictitherium crassum*	Canidae	*Canis arnensis*
Hyaenidae	*Hyaenotherium wongii*	Canidae	*Canis apolloniensis*
Hyaenidae	*Ictitherium viverrinum*	Canidae	*Canis etruscus*
Hyaenidae	*Lycyaena chaeretis*	Canidae	*Vulpes praeglacialis*
Hyaenidae	*Adcrocuta eximia*	Canidae	*Vulpes alopecoides*
Hyaenidae	*Belbus beaumonti*	Canidae	*Nyctereutes megamastoides*
Percrocutidae	*Dinocrocuta gigantea*	Canidae	*Lycaon lycaonoides*
Percrocutidae	*Dinocrocuta salonicae*	Mustelidae	*Meles dimitrius*
Mustelidae	*Martes woodwardi*	Mustelidae	*Baranogale aff. helbingi*
Mustelidae	*Promeles palaeattica*	Ursidae	*Ursus etruscus*
Mustelidae	*Plesiogulo crassa*		
Mustelidae	*Parataxidea maraghana*		
Mustelidae	*Sinictis pentelici*		
Mephitidae	*Promephitis lartetii*		
Ursidae	*Indarctos atticus*		
Ursidae	*Ursavus depereti*		
Ursidae	*Ursavus ehrenbergi*		
Ailuridae	*Simocyon primigenius*		

It is obvious in Table 2 and Fig. 2 that the majority of the studied fossil species comes from the Late Miocene of Greece.

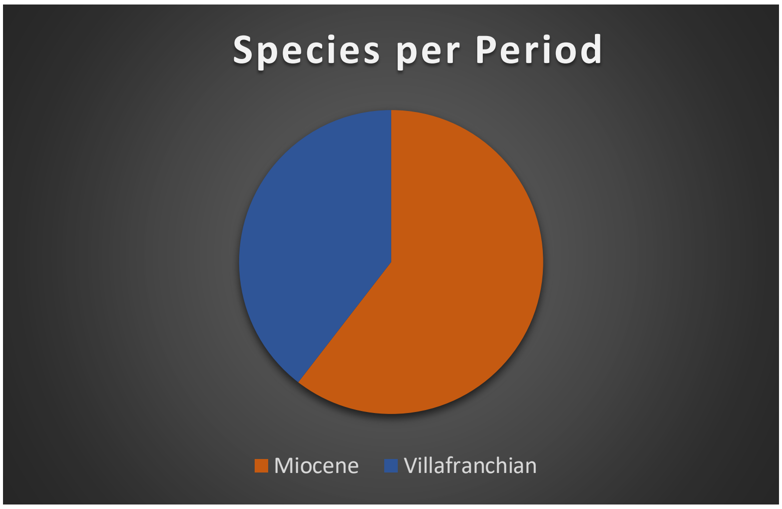


Figure 2: Division of the fossil species in the two studied ages.

In Fig. 3 it is obvious that the most abundant families in terms of species number are Hyaenidae, Felidae, Mustelidae and Canidae, followed by Ursidae, while Percrocutidae, Mephitidae and Ailuridae are represented by 1 or 2 species.

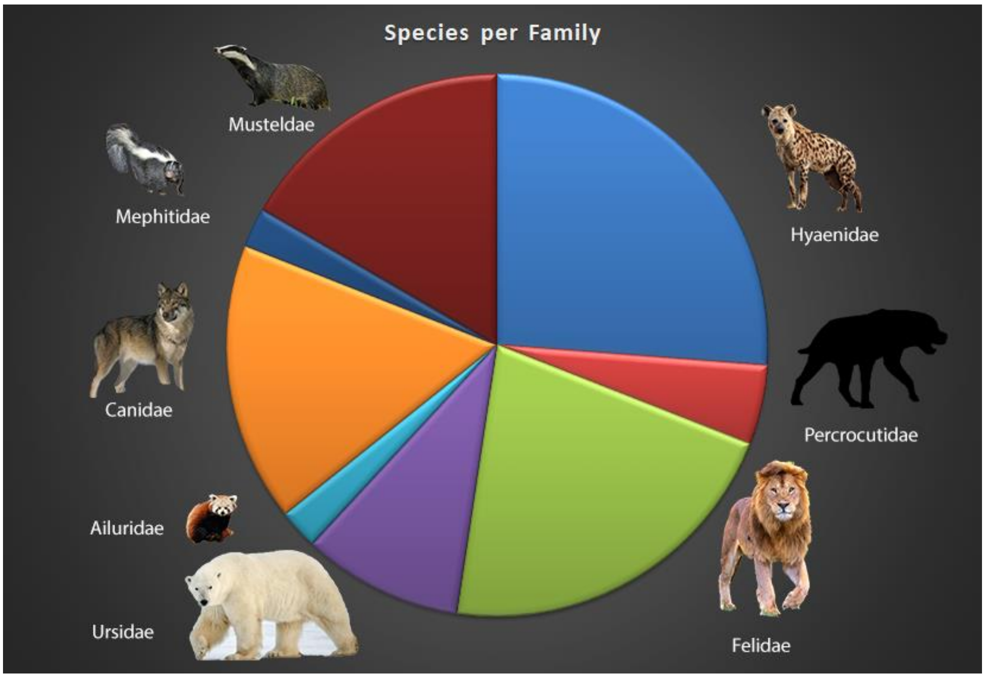


Figure 3: Division of the fossil species in the seven studied families.

Methods

The main purpose of this study is to separate the distinct dietary categories of the Carnivora using a multiproxy analysis based on cranial parameters. These categories are here defined as follows:

1. Predators hunting prey smaller than their own size
2. Predators hunting prey approximately equal to their size
3. Predators hunting prey larger than their own size
4. Piscivores
5. Bone-eaters
6. Shell-eaters
7. Ant-eaters
8. Insectivores
9. Omnivores preferring plant material
10. Omnivores equally preferring plants and meat/invertebrates
11. Omnivores preferring animal material
12. Herbivores

The results for the extant species are presented in Table 3. The categorization is based on the study of Christiansen & Wroe (2007), with some additions and alternations based on the records of the species on encyclopaedias (Stubbe & Krapp, 1993a, 1993b; Hurchins et al., 2003) and their records in Mammalian Species (Taylor, 1972; Mech, 1974; Bekoff, 1977; Chorn & Hoffmann, 1978; Lotze & Anderson, 1979; Mazák, 1981; Rieger, 1981; Mills, 1982; Currier, 1983; Roberts & Gittleman, 1984; Tumlison, 1987; Ford & Hoffman, 1988; Seymour, 1989; Pasitschniak-Arts, 1993, 1995; van Staaden, 1994; Ray, 1995; Larivière & Pasitschniak-Arts, 1996; Grompper & Decker, 1998; Presley, 2000; Larivière, 2001, 2003; Larivière & Calzoda, 2001; Walton & Joly, 2003; Clark Jr, 2005; Gorsuch & Larivière, 2005; Haas et al., 2005; Krausman, 2005; de Mello Beisigel & Zuercher, 2005; Stein & Hayssen, 2013) or other sources (Kruuk, 1972; Kruuk & Sands, 1972; Bowland & Perrin, 1993; Fitzgerald, 2002; Wang, 2002; Amstrup, 2003; Clavero et al., 2003; Loveridge & Macdonald, 2003; García-Rangel, 2012; Lambert et al., 2014; Sunquist & Sunquist, 2014). The omnivores were divided into three categories, reflecting the different preferences of the species. The ant-eaters were separated from insectivores, because they tend to have different “hunting” strategies, due to the colonial nature and the small size of their prey. The shell-eaters were seperated from the piscivores, because they tend to preserve broad, powerful teeth, able to crush shells, while the piscivores usually have slender, pointed teeth, able to hook on the prey. The bone-eaters (the hyenas and the wolverine) preserve very specific adaptations for the consuming of very hard animal material, but they are also active predators belonging to category 3.

Table 3: Dietary categories of the studied extant species

Species	**DC**	**Species**	**DC**
Ailurus fulgens	**11**	*Herpestes edwardsi*	**9**
Canis adustus	**9**	*Herpestes ichneumon*	**9**
Canis aureus	**10**	*Ichneumia albicauda*	**9**
Canis familiaris	**9**	*Mungos mungo*	**1**
Canis latrans	**9**	*Suricata suricatta*	**8**
Canis lupus	**3**	*Amblonyx cinereus*	**6**
Canis mesomelas	**9**	*Eira barbara*	**9**
Cuon alpinus	**3**	*Enhydra lutris*	**6**
Lycaon pictus	**3**	*Gulo gulo*	**5**
Nyctereutes procyonoides	**10**	*Lutra lutra*	**6**
Otocyon megalotis	**7**	*Martes foina*	**9**
Speothos venaticus	**3**	*Martes martes*	**9**
Urocyon cinereoargenteus	**10**	*Meles meles*	**9**
Vulpes vulpes	**9**	*Mustela nivalis*	**3**
Galidia elegans	**1**	*Mustela putorius*	**3**
Acinonyx jubatus	**2**	*Pteronura brasiliensis*	**6**
Caracal caracal	**3**	*Vormela peregusna*	**9**
Felis catus	**1**	*Nandinia binotata*	**11**
Felis silvestris	**2**	*Monachus monachus*	**6**
Leopardus pardalis	**3**	*Nasua narica*	**9**
Leopardus tigrinus	**1**	*Nasua nasua*	**10**
Leopardus wiedii	**1**	*Potos flavus*	**11**
Leptailurus serval	**1**	*Procyon lotor*	**10**
Lynx canadensis	**3**	*Ailuropoda melanolecua*	**12**
Lynx lynx	**3**	*Helarctos malayanus*	**10**
Neofelis nebulosa	**3**	*Tremarctos ornatus*	**11**
Panthera leo	**3**	*Ursus americanus*	**11**
Panthera onca	**3**	*Ursus arctos*	**10**
Panthera pardus	**3**	*Ursus maritimus*	**3**
Panthera tigris	**3**	*Ursus thibetanus*	**11**
Prionailurus viverrinus	**4**	*Arctictis binturong*	**11**
Puma concolor	**3**	*Civettictis civetta*	**9**
Crocuta crocuta	**5**	*Genetta genetta*	**9**
Hyaena brunnea	**5**	*Genetta tigrina*	**9**
Hyaena hyaena	**5**	*Paradoxurus hermaphroditus*	**11**
Proteles cristatus	**7**	*Poiana richardsonii*	**10**
Conepatus chinga	**10**		
Conepatus humboldti	**9**		
Mephitis mephitis	**9**		

It is obvious that some categories overlap. Omnivores preferring animal material are, of course, predators, falling in one of the first three categories. Bone-eaters can either be scavengers or predators. The selection of the dietary category was based mainly on the ability of the species to act in this particular way and not only on its usual diet. Caracal is basically a bird-eater, but it can take down small antelopes, if necessary. This fact leads to its characterization as a predator hunting prey larger than its own size, because it is built to act in such a way.

The percentages of species per dietary category per family are presented in Table 4:

Table 4: Number and percentage of species per family per dietary category in the sample of extant carnivorans.

Families/DC	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**Sum**
Ailuridae											1 100%		1
Canidae			4 29%				1 7%		6 43%	3 21%			14
Eupleridae	1 100%												1
Felidae	4 24%	2 12%	10 59%	1 6%									17
Herpestidae	1 20%							1 20%	3 60%				5
Hyaenidae					3 75%		1 25%						4
Mephitidae									2 66%	1 33%			3
Mustelidae			2 17%		1 8%	4 33%			5 42%				12
Nandiniidae										1 100%			1
Phocidae						1 100%							1
Procyonidae									1 25%	2 50%	1 25%		4
Ursidae			1 14%							3 43%	2 29%	1 14%	7
Viverridae									3 50%	1 23%	2 9%		6
Sum	6 8%	2 3%	17 22%	1 1%	4 5%	5 7%	2 3%	1 1%	20 26%	11 13%	6 14%	1 1%	76

The most common DC is 9, the omnivores that feed mostly on meat. This fact is reasonable, since it probably represents the plesiomorfic state of Carnivora. Some families preserve high percentages in certain DCs or groups of DC, indicating that most likely their fossil members that do not differ significantly from their extant cousins will probably fall in these DCs. For example all the felids are carnivorans. Viverrids, herpestids, ursids, procyonids and mustelids are mostly omnivores.

The prey size and form affect the cranial morphology of the predator, in order to catch, kill, dismember and digest it successfully. This fact shows that the skulls, the mandibles and the teeth of the species that belong to the aforementioned dietary categories will probably exhibit some indistinguishable differences. These differences can be uncovered with the use of many proxies or parameters. In this study the following proxies are used:

1. Bite Force
2. Bending Strength Canines
3. Bending Strength Incisors
4. Endocranial Volume
5. Mastoid Musculature
6. Relative Rostrum Width
7. Dental Mesowear
8. Dental Morphology

These proxies are the most handy and inexpensive. There are other methods, which will be only mentioned in this study, that require specific tools (micro CT scanning) or software, while they can be very expensive (e.g. isotopes). Results from the literature using such methods will act as supplementary data in this study.

Bite Force

The most important task of the carnivoran jaws is to crush/slice the food material. They also usually need to kill their prey. Therefore, the jaws must be powerful and robust to fulfil such a task. This power comes from the muscles of the jaws, which form the masticatory apparatus. There are four main groups of jaw muscles: the masseter (*m. masseter* and *m. zygomandibularis*), the temporalis (*m. temporalis*), the medial pterygoid (*m. pterygoideus*) and the digastric group (*m. digastricus*). The first three of them close the jaws (adductive muscles), while the fourth opens the jaws (abductive muscle) (Turnbull, 1970). The most powerful are the masseter and the temporalis groups. The masseter acts to the posterior part of the jaws, while the temporalis acts to the anterior part of the jaws (Elbroch, 2006).

Each muscle is formed by many filaments of actin (thin filaments) and myosin (thick filaments). These two types of filaments form parallel connected lines. During the contraction of the muscle, the actin filaments slide across the myosin filaments. The energy for this process is given by Adenosine Triphosphate (ATP). The whole system is controlled by Ca^{2+}, Troponin and Tropomyosin.

As mentioned by Kiltie (1984): “Since the maximum force that a muscle can exert is proportional to the number of fibres composing it, the cross-sectional area of the muscle may be taken as an index of its strength”.

The Bite Force (BF) is a very important cranial parameter for carnivorans, because it determines the range of their possible prey (Meers, 2002). Predators need powerful jaws to catch, kill, dismember and chew their food.

The power of the jaws is not the same in every part of the skull. The posterior part of the jaws is more powerful and the anterior part is less powerful. That happens because the posterior part of the jaws is more closely located to the glenoid cavity (or temporo-mandibular joint), which is the contact point of the upper and the lower jaw and, thus, it is the mechanical centre of the whole process.

Researchers started to study the aspect of bite force in the early 20th century. Shufeldt (1924) wrote for the skull of wolverine (*Gulo gulo*): “The animal possessed a wonderful set of teeth, and those of this mandible are most elegantly arranged in their sockets; the entire armature, during life, must have been quite equal to inflicting a bite of unusual severity”. During the 80s some scientists managed to construct some methods to calculate bite forces. Two of them are Kiltie (1982, 1984) and Greaves (1978, 1983, 1985), which used mainly geometrical parameters for their calculation.

The most effective study on bite force, due to its major impact in many following studies, was the study of Thomasson (1991). He introduced the “dry skull method”. In this method the cross-sectional areas of temporalis and masseter muscles are measured using photographs, as in Figure X. Both areas are multiplied with 300 KPa (misspelled as 300 MPa in Thomasson, 1991), the maximum tension per unit area that mammalian muscle can generate. The centroids of both areas were calculated and their distances from the temporomandibular joint (TMJ) was measured (in-levers m for masseter and t for temporalis). The bite force in every point of the palate depends on the distance of this point to TMJ (out-lever o). This point is usually the tip of the canine or the paracone of the carnassial. The final equation is **Bs = 2*(M*m*300 KPa + T*t*300 KPa)/o**. When all the measurements are in the S.I., the Bite Force is in N. The duplication is due to the two sides of the toothrow. The “t” was calculated as proposed by Sakamoto et al. (2010) by taking the half of the average of the distances of the two postorbital tips from TMJ.

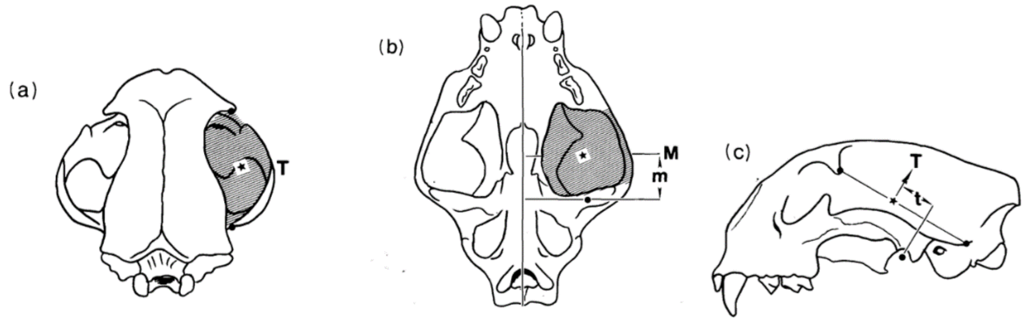


Figure 4: The view for the calculation of the areas and the in-levers of the muscles. Source: Thomasson (1991).

Many other studies followed this method, but all of them made some changes. A first usual change is that the maximum tension per unit area is set in 370 KPa and not in 300 KPa (Christiansen 2005, Christiansen & Wroe 2007, Christiansen 2007a). Some of them do not include the duplication in the equation (Christiansen 2005, Christiansen & Wroe 2007, Christiansen 2007a). The most important source of error is the view that leads to the calculation of the masseter area. In the majority of studies this view is caudal-dorsal (Thomasson 1991, Wroe 2005, Christiansen & Wroe 2007, Christiansen 2007a), while in Christiansen (2005) is lateral-caudal-dorsal and in Damasceno et al. (2013) it is completely dorsal (Figure 5).

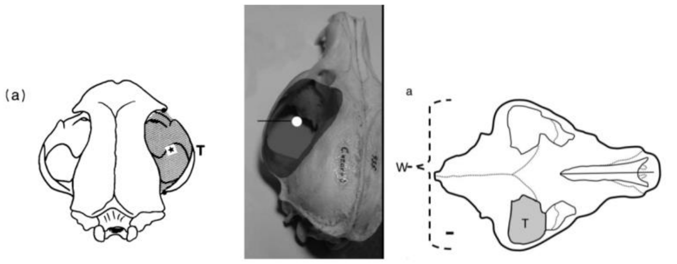


Figure 5: Variation in the view leading to the masseter area. From left to right: Thomasson (1991), Christiansen (2005) and Damasceno et al. (2013).

To test if this variation leads to different results, the area of temporalis was calculated in these three views for *Crocuta crocuta*, *Felis catus*, and *Canis lupus familiaris*. These species were selected because of their differences is skull proportions. Each measurement was taken 10 times to co-calculate random variance. For every species these three groups of values were compared using t-test. Every comparative pair resulted to $p=0.001$. Therefore, these three measurements provide different values. Sakamoto et al. (2010) solved this problem by taking the average of a range of views. In this study the average of the postero-dorsal and the latero-postero-dorsal views was taken.

The bite force from Thomasson’s (1991) equation leads to slightly low values. Therefore, he constructed a corrective equation as follows: $\mathbf{F_{corr} = 10^{(0.859*logF+0.559)}}$. This correction may be caused by the difference between 300 and 370 KPa for the maximum tension per unit area.

There is an allometry between BF and Body Mass (BM) (Meers, 2002 & Christiansen, 2007a). This means that large animals tend to have relatively larger BFs, only due to their size, and not due to their ecology. To study Bite Force, independently from body size, Bite Force Quotient was introduced. This value is calculated through BF and BM as follows: $\mathbf{BFQcan} = [\mathbf{BFcan}/10^{(0.663\pm0.028*\log\{BM\}+1.561\pm0.027)}]*100$ and $\mathbf{BFQcarn} = [\mathbf{BFcarn}/10^{(0.650\pm0.028*\log\{BM\}+1.762\pm0.028)}]*100$ for the canine and the carnassial respectively (Christiansen & Wroe, 2007). BFQ values approximately equal to 100 are intermediate. Values lower than 100 are low, while higher than 100 are high.

Damasceno et al. (2013) calculated BFQ using a different method. They calculated $\mathbf{F_L=10^{(1.95*\log SL-1.12)}}$, while SL is the total skull length. Then they calculated $\mathbf{BFQ = F_{corr}/F_L}$. This equation is useful because often the weight of fossil species is not known, or it requires to be calculated based on equations (e.g. Van Valkenburgh, 1990) that include a bias.

Figure 6: The jaguar (*Panthera onca*) can kill its prey (including even alligators) by breaking their skull in the occipital region staving keratin protection, skin and bone with its powerful bite. Afterwards, it can carry its heavy prey through the river and bring it in a silence spot to eat it peacefully. Source: youtube.com

Bending Strength of Canines

The canines are directly connected with the diet and the hunting method of the animal. Depending on their size and shape, they can withstand different stresses and to complete different functions. Their dimensions can be calculated through three measurements: the height from the base of the tooth to the tip (h), the anteroposterior (a) and the mediolateral (b) diameter of the tooth in its base (Figure 7).

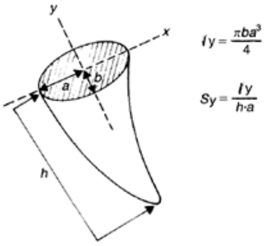


Figure 7: canine measurements according to Van Valkenburgh & Ruff (1987).

Van Valkenburgh & Ruff (1987) introduced the term maximum stress $\sigma_{max}=My/I$, considering the canine as a beam. M is the bending moment (equal to the force applied to the tip of the canine multiplied by the height of the tooth), y is the distance from the neutral axis of the cross-section to the outermost fibre, while “I” is the second moment of area about the neural axis. Because of the symmetry of the canine, “y” is equal with the half of the diameter in the cross-section. The second moment area for the anteroposterior diameter is **$Ix=(\pi*a*b^3)/4$**, while for the mediolateral diameter is **$I_y=(\pi*b*a^3)/4$**. Finally, stress in these two directions can be calculated as **$S_x=I_x/F*h*b$** and **$S_y=I_y/F*h*a$** respectively.

In that study the authors used the same F for all the species, because their task was to compare only the mechanical properties of the canine, independently from the other parameters of the skull and dentition. However, Christiansen (2007b) used different BFs, to calculate the absolute S.

Additionally, Christiansen (2007b) did not use only the base diameters, but also the diameters at 15%, 30%, 45%, 60%, 75% and 90% of the height of the canine. This method led to a more integrated study of the canine shape.

In this study the method by Van Valkenburgh & Ruff (1988) will be applied, because the complexity of Christiansen’s (2007b) method does not easily allow for combined results with other proxies.

Figure 8: The least weasel (*Mustela nivalis*) needs high canine bending strength to kill a struggling prey much larger than itself. Source: arkive.org

Bending Strength of Incisors

In the same aspect as in *Bending Strength of Canines*, Biknevicius et al. (1996) applied the same method for the upper incisors, and particularly for I1 and I2. They introduced the section modulus for mediolateral and anteroposterior axis as $\mathbf{Z_x=\pi(ML)(AP)^2/32}$ and $\mathbf{Z_y=\pi(AP)(ML)^2/32}$ respectively. This modulus led to the calculation of the stress as: $\mathbf{S_x=Z_x/h}$ and $\mathbf{S_y=Z_y/h}$.

They also calculated the dental cross-sectional area (CA) as $\mathbf{CA=\pi(ML)(AP)/4}$.

They studied the shape of the incisor arch, placing landmarks in the cusps or in the centres of the teeth.

Correlations were made with the distance from the occiput to the infraorbital foramen, because this distance is relatively constant to body mass, independently of phylogeny, to study the effect of allometry.

Figure 9: A lioness (*Panthera leo*) feeding on a wildebeest (*Connochaetes gnou*) using her incisors.
Source: aboutanimals.com

Endocranial Volume

Hunting is a powerful, but also a delicate process that requires intelligence, effective senses and excellent harmony in the body parts. These characteristics are connected to the brain, the organ that controls the whole body. The endocranial volume in a skull reflects the size of the brain. The size of the skull is one considerable proxy about the intelligence of the animal, but the whole analysis is very complex and requires the examination of many more parameters. This fact does not reduce the value of the endocranial volume as an important part of skull analysis.

Endocranial volume can be accurately measured with the use of CT tomography (e.g. Swanson et al. 2012). This method requires a CT scanner and specialized software. Therefore, it is handier to use another method, based on external skull measurements.

The method of Finarelli (2006) is very simple. There are just three cranial measurements to be taken as in Figure 10. The Length (L) is measured from the midline of the nasal-frontal suture to the furthest point of the occipital bone. The Width (W) is measured as the widest point of the parietal and the squamosal bones. The Height (H) is measured as the greatest diameter of the cranium perpendicular to the plane of the basioccipital and basisphenoid bones, excluding the sagittal crest. All three measurements are in mm.

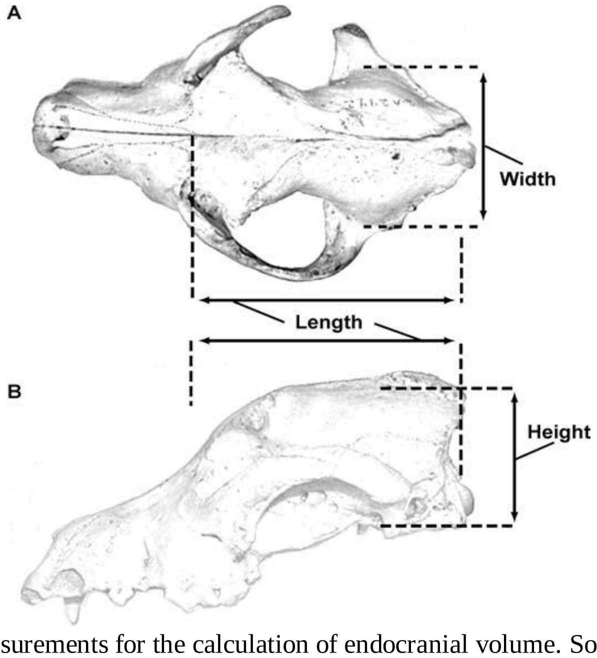


Figure 10: External measurements for the calculation of endocranial volume. Source: Finarelli (2006)

These three measurements are combined in an equation as follows:

$$\ln(\text{Brain Volume}) = -6.23 + 1.06 * \ln(H) + 0.28 * \ln(L) + 1.27 * \ln(W)$$

Logan & Clutton-Brock (2012) tested the correlation between the value of endocranial volume measured by the methods of Finarelli, CT, glass beads and the simple linear measurements L*W*H in red deer skulls (*Cervus elaphus*). It seems that the best method is the glass beads method, following by L*W*H and Finarelli’s method. Nevertheless, the correlation was found strong for all three methods (r = 0.9552, r = 0.8361 & r = 0.8085 respectively). They suggest that Finarelli's method must be used in interspecific (and not intraspecific) comparisons only.

We have to mention that the endocranial volume is not the same with the brain volume. Firstly, the brain cavity includes many bony areas that do not contain soft tissue. Secondly, the endocranial volume includes the frontal sinus, a structure relatively large in some taxa, e.g. *Crocuta crocuta* (Joeckel, 2010). Wroe et al. (2003) mention that the brain mass is 0.96 * Endocranial Volume. This transformation is very useful, allowing for the calculation of the ratio Brain Mass / Body Mass, an important indicator of the level on intelligence.

Damasceno et al. (2013) made a regression function between brain volume and skull length as follows:

$$\log(BV) = 1.7501*\log(SL) - 2.0889$$

They also created a brain volume quotient (BVQ) for the same reasons as BFQ in bite force. BVQ is calculated using the brain volume measured through Finarelli (2006) (BV_1) and brain volume measured through skull length (BV_2) as follows:

$$BVQ = BV_1 / BV_2$$

The measurements taken by the authors for Finarelli's (2006) method are surprisingly inaccurate, because they calculated the whole skull dimensions (including the rostrum and the zygomatic arches) and not the dimensions of the braincase, as seen in Figure 11. This mistake may be just graphical. Nevertheless, their allometrical approach about the BVQ seems useful.

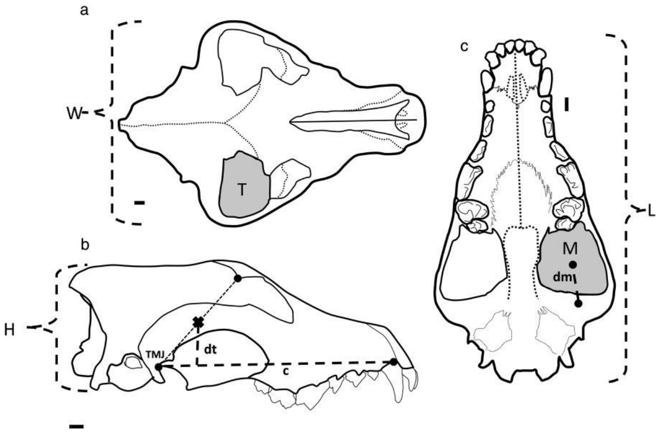


Figure 11: Application of Finarelli (2006) and Thomason (1991) methods by Damasceno et al. (2013). Source: Damasceno (2013)

Mastoid Musculature

This chapters refers only to the saber-toothed cats. These cats were mainly large and robust species, with elongated saber-like upper canines. These characteristics fit with predators that hunt relatively large prey. However, these cats had relatively low Bite Force (and Bite Force Quotient) values (Wroe et al., 2005) and very thin and fragile canines improper for a powerful killing bite (Christiansen, 2007b). Several studies on the cervical anatomy of the more derived forms of saber-toothed cats (e.g. *Smilodon*), showed that the neck length was relatively large, whereas the first cervical vertebrae (atlas and axis) are very robust with elongated processes, formed to nest powerful neck muscles. This fact was combined with the special characteristics of the mastoid region of their skulls: relative to the felines, the paraoccipital process is reduced with large ventral projection, while the mastoid process is very broad, robust and antero-ventrally projected. These differences indicate a completely different muscular system in two lineages, probably correlated with their different killing methods.

Based on Antón et al. (2004), the cervical muscles that play a significant role for the felids are the following:

- *M. brachiocephalicus*: In the very dorsal portion of the neck, starting from the humerus and ending to an aponeuroticus insertion until the end of mastoid process to the mastoid crest and the middle of nuchal crest.
- *M. rhomboideus* & *M. splenius*: They start in the anterior thoracic spinous processes and end ventrally relative to *M. brachiocephalicus*.
- *M. sternomastoideus*: It starts from the sternum and ends in the tip of mastoid process, while some fibers tend to lead to the mastoid crest.
- *M. biventer cervicis*, *M. smispinossus capitis*, *M. complexus capitis* & *M. longissimus capitis*: These are the neck extensors muscles, ventral to *M. splenius*, which end in the occipital region, above the mastoid.
- *M. obliquus capitis caudalis*: It starts from the process of the axis towards the atlas’ wings.
- *M. obliquus capitis cranialis*: It starts in the ventral portion of the atlas towards the mastoid process and the nuchal crest.
- *M. digastricus*: It starts from the paraoccipital process and it runs through the mandible towards the mandibular symphysis.
- *M. rectus capitis lateralis*: It starts from the ventral part of the atlas, medially to *M. obliquus capitis cranialis*, towards the medial portion of the paraoccipital process.

From these muscles, the most important differences are preserved in the muscles that start from the atlas, *M. obliquus capitis caudalis* and mainly *M. obliquus capitis cranialis*, as can be seen in Figure 12:

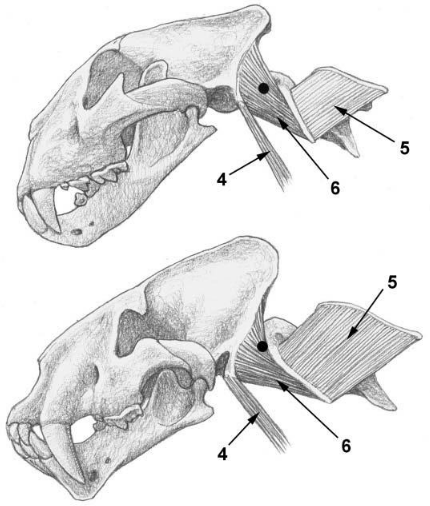


Figure 12: *M. sternomastoideus* (4), *M. obliquus capitis caudalis* (5) and *M. obliquus capitis cranialis* (6) in *Panthera tigris* (top) and *Homotherium latidens* (bottom). Source: Antón et al. 2004

It seems that during the killing bite, the sabertooths did not hold their prey with their teeth (as can be seen in modern felids), but mainly with their forepaws, while their teeth sheared towards the throat and the blood vessels combining suffocation and blood loss (Salesa et al., 2005). During this procedure, the mandible (with the incisor-shaped lower canines) was used as a stabilizer. This technique led to instantaneous death, protecting the fragile upper canines from the struggling of the prey. During this behavior the *M. obliquus capitis cranialis* was used in the flexion of the skull, forcing it postero-ventrally, while it was rotated in the occipital-atlas axis. This fact was enhanced by the vertical occiput of the evolved forms that allowed the more dorsally extended braincase, a necessary trait for a larger gape angle. The significance of these muscles has been questioned by others (Wroe et al., 2008; McHenry et al., 2007).

The aforementioned cranial traits tend to preserve evolutionary variability in the sabertooths. The more primitive *Paramachairodus ogygia* has mastoid and paraoccipital process of intermediate size, allowing for a longer *M. digastricus*, while *M. obliquus capitis cranialis* was mostly above the skull's rotation axis. In any case, it preserves the necessary traits for the canine shear-bite.

In this study the characteristics of the mastoid area of the sabertooths found in Greece will be analysed, focusing in differences that indicate different musculature systems. The material is useful for such a study, because it contains highly derived species, such as *Amphimachairodus giganteus* and more primitive ones, such as *Metailurus parvulus*.

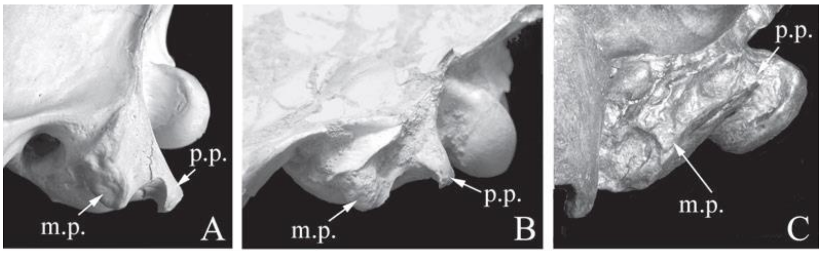


Figure 13: Mastoid region of *Panthera leo, Paramachairodus ogygia* and *Smilodon fatalis.* Source: Salesa et al. 2005

Relative Rostrum Width

The shape of the skull is very important for grasping prey and this fact is most visible in the rostrum, the main tool for this function. In general, species that hunt larger species have shorter and wider rostra, while species that hunt small species have elongated and narrow rostra. Herein the ratio of rostrum width and skull length will be used to test if this is true.

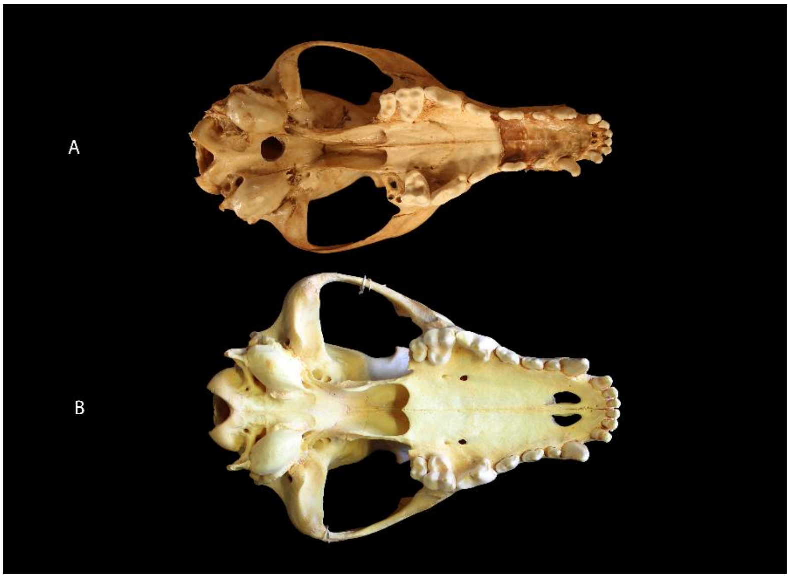


Fig. 14: *Vulpes vulpes* (A) and *Lycaon pictus* (B) preserving elongated & narrow and wide & short rostrum respectively

Dental Mesowear

The tearing of the food particles in the teeth causes their wear. There are two distinct (but connected) types of wear: mesowear and microwear. Mesowear reflects the lifetime diet of the animal, whereas microwear reflects just the last meals of the individual. Mesowear is handier because it does not have technological requirements compared to microwear. The more the tooth is used, the more worn it will be. Hard food material (such as bones) cause more wear. There are several protocols, preserving the different stages of dental mesowear, but the majority of them concerns ungulates.

The simpler categorization is the one proposed by Flower & Schreve (2014) as follows: (1) slight - no apparent wear and blunting of cusps present and (2) heavy - sever wear with strongly blunted cusps.

Van Valkenburgh (1988) divided wear stage into three categories: (1) slight, little or no apparent wear observed as shear facets or blunting of cusps; (2) moderate, shear facets apparent on carnassial teeth, cusps blunted on most teeth; and (3) heavy, carnassial teeth with strong shear facets or blunted cusps, premolars and molars with well-rounded cusps.

Relatively similar to this categorization is the method by DeSantis et al. (2017) as follows: (1) minimal - wear facets are visible but little to no dentin is exposed, <1mm (2) moderate - wear facets are moderate to large and dentin is exposed > 1 mm and (3) extreme - wear facets are well developed and significant dentin is exposed, the width of dentin exposure is greater than the wear facets.

In this study the dental mesowear will be researched using the method of DeSantis et al. (2017), because of the more precise distinction of the categories.

Figure 15: *Hyaena hyaena* upper premolars and canine mesowear.

Dental Morphology

Intercuspid Notches

Hartston-Rose (2011) based his research on intercuspid notches as follows: “Each crest on the third and fourth premolars was evaluated as either sharp (a crest whose buccal and lingual faces met at c. 451 or less) or dull (a crest whose buccal and lingual faces met at a roughly rounded edge consisting of an angle more than c. 451).” “Each intercuspid notch on each lower premolar was scored on a scale of 0–5 (Fig. 1) with ‘0’ assigned to teeth with no intercuspid notches, ‘1’ assigned to a barely-present minor accessory cuspid, ‘2’ assigned to a notch formed by the confluence of two dull crests, ‘3’ assigned to a notch formed by one dull and one sharp crest, ‘4’ assigned to a confluence of two sharp crests and ‘5’ assigned to a confluence of two sharp crests that also displays the ‘carnassiform’ notch morphology”. The carnassiform notch is any notch that displays a keyhole shape, because of the convergence of postparacristid and preprotocristid in the carnassial or any other tooth. The main notch of a tooth is between the paraconid and the first distal accessory cuspid. It has the maximum score range than any other tooth.

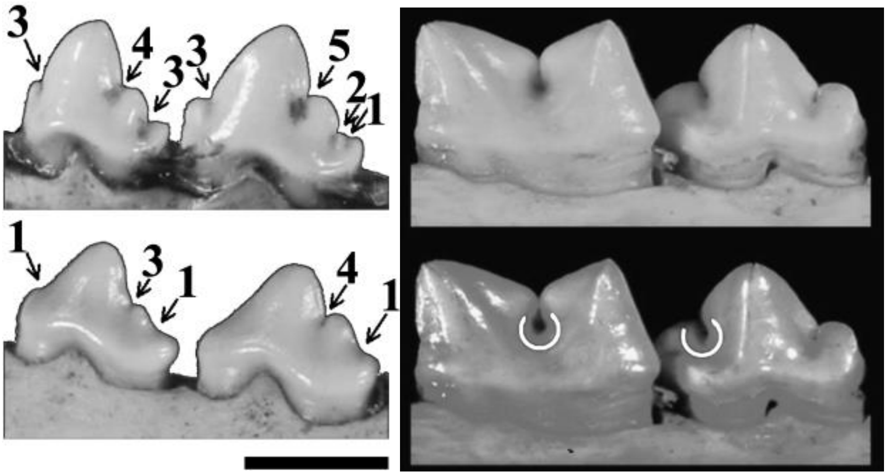


Figure 16: Examples of notch scoring (left) and carnassiform notch morphology (right). Source: Harston-Rose (2011).

He studied the following parameters:

1. Notch score of the main notch on p4.
2. The number of notches of p4.
3. The sum of notch scores of p4.
4. The sum of main notch score of p3 and main notch score of p4.
5. The sum of the number of notches of p3 and p4.
6. The sum of all the notch scores of p3 and p4.

Carnassial vs Grinding Areas

Sacco & Van Valkenburgh (2004) used the following parameters:

1. The maximum anteroposterior length of the trigonid divided by dentary length (M1BSZ). Dentary length was measured as the distance between the approximate centre of the mandibular condyle and the anterior margin of the canine tooth.
2. The square root of m2 area divided by dentary length (M2SZ).
3. The square root of the summed areas of the m1 talonid, m2 and m3 divided by dentary length (LGR).
4. The square root of the summed areas of M1 and M2 divided by dentary length (UGR).

These methods were used only in bears, where the grinding surface claims an important area of the toothrow. The same will be done in mustelids, canids, ictitheres and ailurids which also present large grinding surfaces.

Similar proxies are used in Popowics (2003) on mustelids and viverrids. The author used the following measurements:

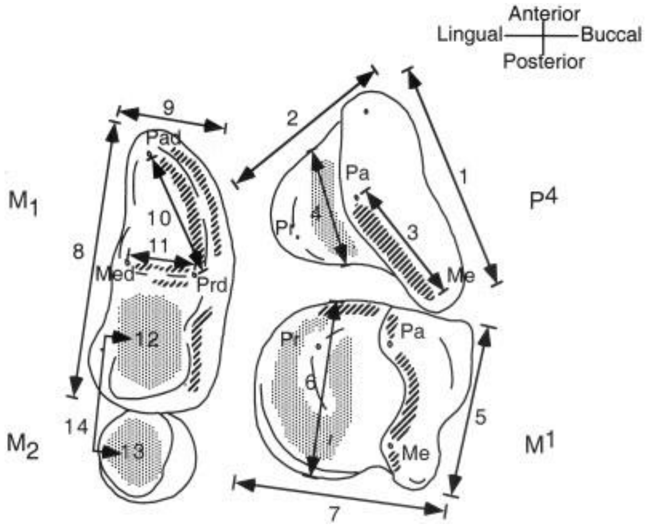
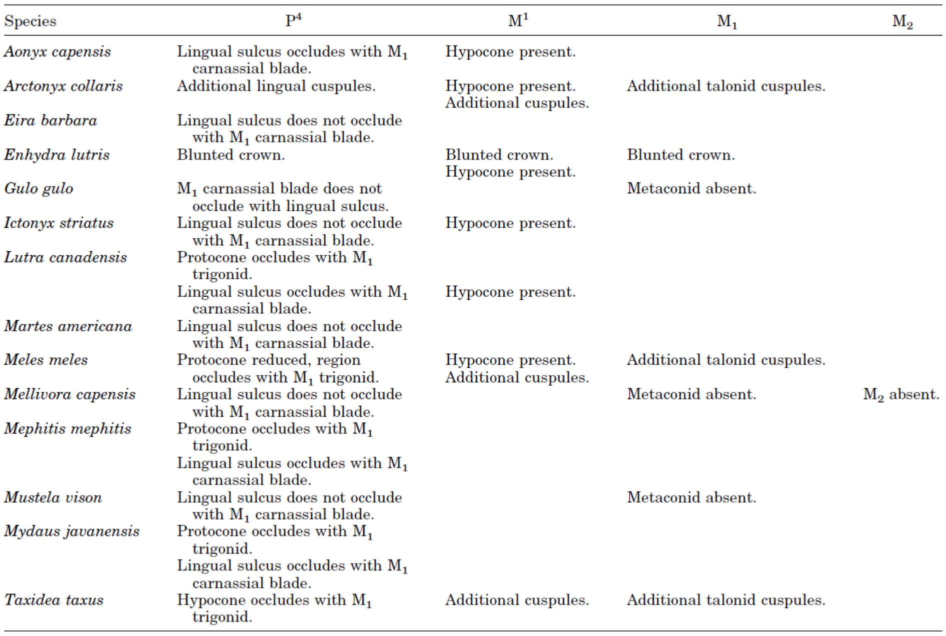


Figure 17: The measurements taken by Popowics (2003): 1, P4LB; 2, P4W; 3, P4PM; , PRBL; 5, M1BL; 6, M1LL; 7, M1W; 8, N1L; 9, N1W; 10, N1PP; 11, N1MP; 12, TALAREA; 13, M2AREA; 14, TOTAREA.

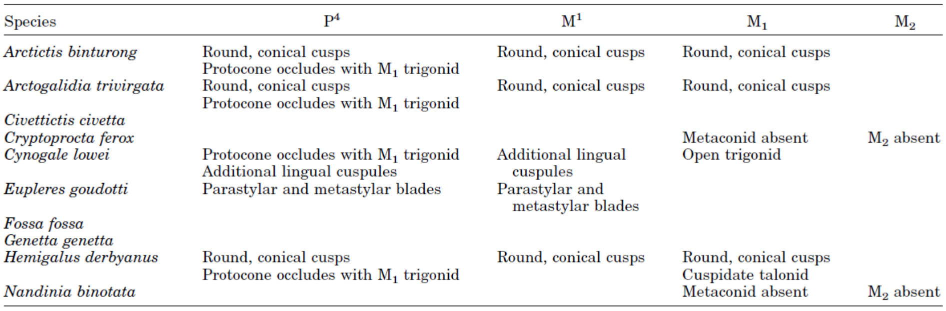
The metrical comparison was enhanced by morphological descriptions:

Table 5: Morphological comparison of mustelids’ postcanine teeth. Source: Popowics (2003).



Species	P^4	M^1	M_1	M_2
Aonyx capensis	Lingual sulcus occludes with M_1 carnassial blade.	Hypocone present.		
Arctonyx collaris	Additional lingual cuspules.	Hypocone present. Additional cuspules.	Additional talonid cuspules.	
Eira barbara	Lingual sulcus does not occlude with M_1 carnassial blade.			
Enhydra lutris	Blunted crown.	Blunted crown. Hypocone present.	Blunted crown.	
Gulo gulo	M_1 carnassial blade does not occlude with lingual sulcus.		Metaconid absent.	
Ictonyx striatus	Lingual sulcus does not occlude with M_1 carnassial blade.	Hypocone present.		
Lutra canadensis	Protocone occludes with M_1 trigonid. Lingual sulcus occludes with M_1 carnassial blade.	Hypocone present.		
Martes americana	Lingual sulcus does not occlude with M_1 carnassial blade.			
Meles meles	Protocone reduced, region occludes with M_1 trigonid.	Hypocone present. Additional cuspules.	Additional talonid cuspules.	
Mellivora capensis	Lingual sulcus does not occlude with M_1 carnassial blade.		Metaconid absent.	M_2 absent.
Mephitis mephitis	Protocone occludes with M_1 trigonid. Lingual sulcus occludes with M_1 carnassial blade.			
Mustela vison	Lingual sulcus does not occlude with M_1 carnassial blade.		Metaconid absent.	
Mydaus javanensis	Protocone occludes with M_1 trigonid. Lingual sulcus occludes with M_1 carnassial blade.			
Taxidea taxus	Hypocone occludes with M_1 trigonid.	Additional cuspules.	Additional talonid cuspules.	

Table 6: Morphological comparison of viverrids’ postcanine teeth. Source: Popowics (2003).



Species	P^4	M^1	M_1	M_2
Arctictis binturong	Round, conical cusps Protocone occludes with M_1 trigonid	Round, conical cusps	Round, conical cusps	
Arctogalidia trivirgata	Round, conical cusps Protocone occludes with M_1 trigonid	Round, conical cusps	Round, conical cusps	
Civettictis civetta				
Cryptoprocta ferox			Metaconid absent	M_2 absent
Cynogale lowei	Protocone occludes with M_1 trigonid Additional lingual cuspules	Additional lingual cuspules	Open trigonid	
Eupleres goudotti	Parastylar and metastylar blades	Parastylar and metastylar blades		
Fossa fossa				
Genetta genetta				
Hemigalus derbyanus	Round, conical cusps Protocone occludes with M_1 trigonid	Round, conical cusps	Round, conical cusps Cuspidate talonid	
Nandinia binotata			Metaconid absent	M_2 absent

Herein Studied Diets at Species Level

[1] *Indarctos atticus, Ursavus ehrenbergi, Ursavus depereti, Ursus etruscus*

Indarctos is considered by Qiu et al. (2014) as member of the Tribe Indarctini and the Subfamily Ailuropodinae, whose only extant member is the giant panda (*Ailuropoda melanoleuca*), one of the very few strictly herbivorous members of Carnivora. The teeth of *Indarctos atticus* indeed preserve interesting similarities with those of the panda, creating questions about its diet.

The genus *Ursavus* is placed by Qiu et al. (2014) in the Tribe Ursini and the Subfamily Ursinae, closely related to *Ursus* bears. The majority of the extant *Ursus* are omnivorous, with the exception of the polar bear (*Ursus maritimus*), who is almost entirely carnivorous.

Despite the fact that some species of *Ursus* are mainly herbivorous (e.g. *U. arctos*), most bears are also capable of killing live prey, sometimes even large herbivores such as caribou (e.g. Pasitschniak-Arts, 1993). This behaviour is rare, but the physique of bears enables them both to eat from carcasses and to hunt live prey.

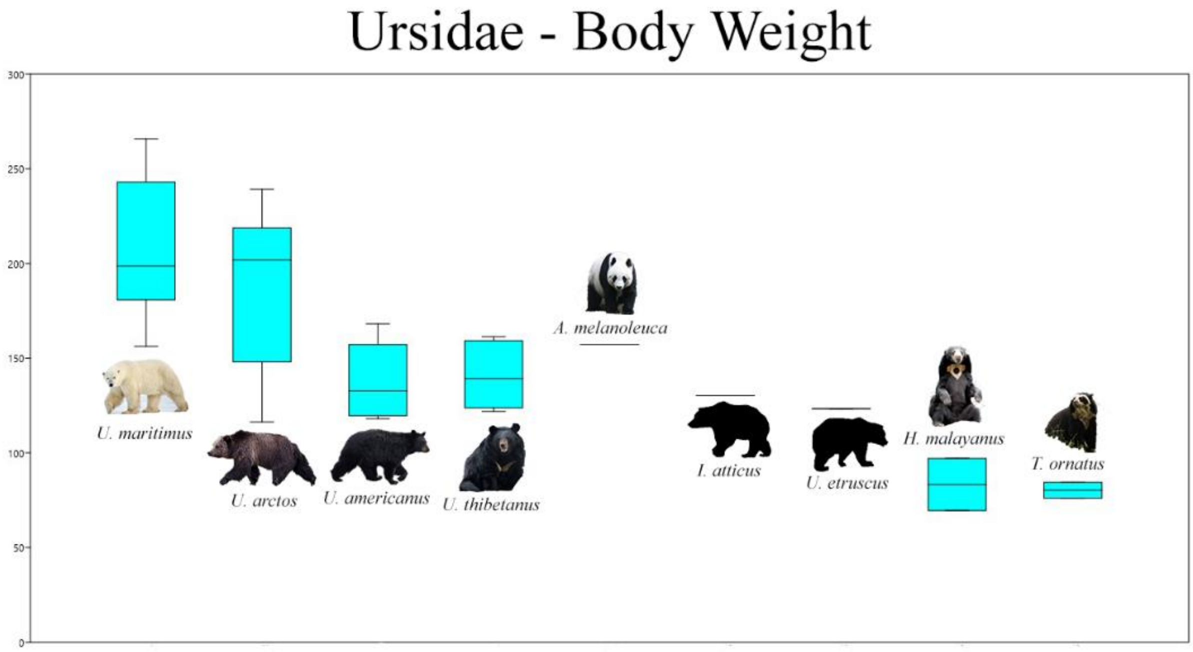


Fig. 18: Body Weight estimates of the studied ursids based on skull length

The Body Weight estimates (Fig. 18) are based on Skull Length, as this is the most reliable source of data, according to Van Valkenburgh (1990). We can see that both *Indarctos atticus* and *Ursus etruscus* seem to fit with approximately 130 kg, but (considering that they were sub-adults) slightly higher values would probably be more accurate. This difference is probably more important for *Indarctos*, since it is considered as a relatively large species (Roussiakis, 2001).

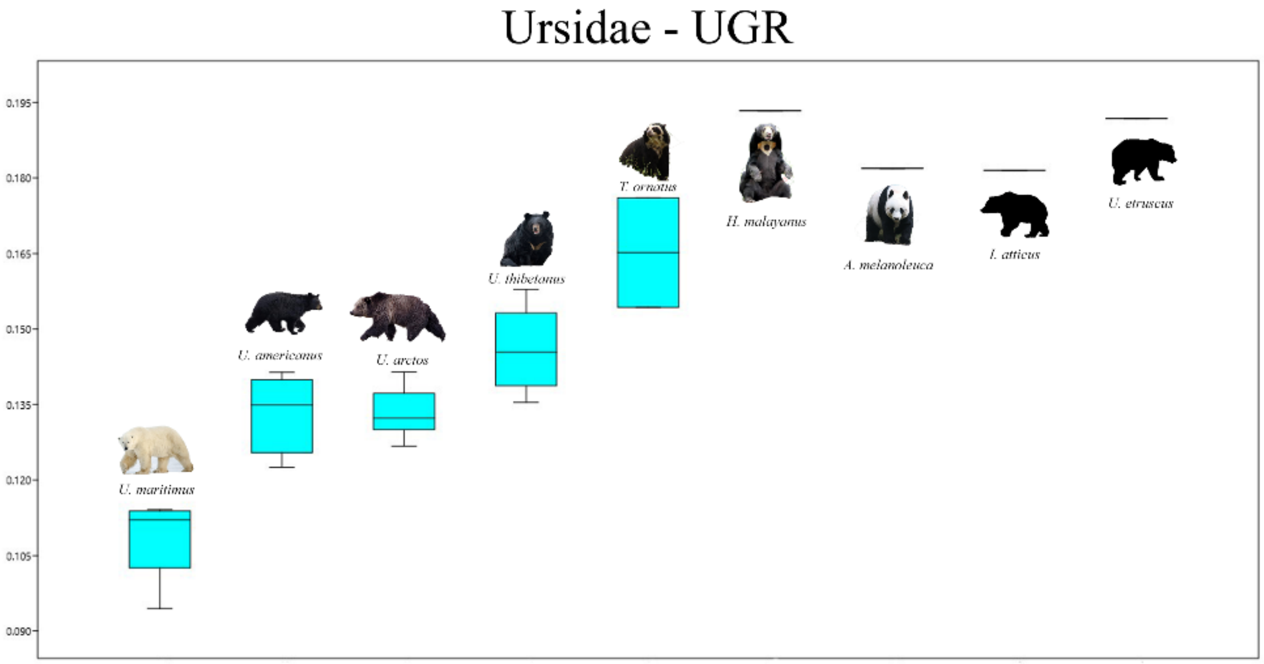


Fig. 19: The levels of UGR proxy (Sacco & Van Valkenburgh, 2000) in the studied ursids

The use of UGR proxy (Sacco & Van Valkenburgh, 2000) is discriminating among the recent bears, with the carnivorous polar bear having the lowest values and the herbivorous species having the highest values. The significantly high value of *H. malayanus* is based only on one specimen and it probably is an outlier. However, if it is true, it is caused probably because of the very short rostrum of this species, and not because of the enlarged molars. The values of *I. atticus* and *U. etruscus* are very high, with *Indarctos* preserving almost identical value with the giant panda. However, both species were represented with sub-adult specimens, and therefore their values are slightly overrated. In any case, this boxplot shows that both species were majorly herbivorous.

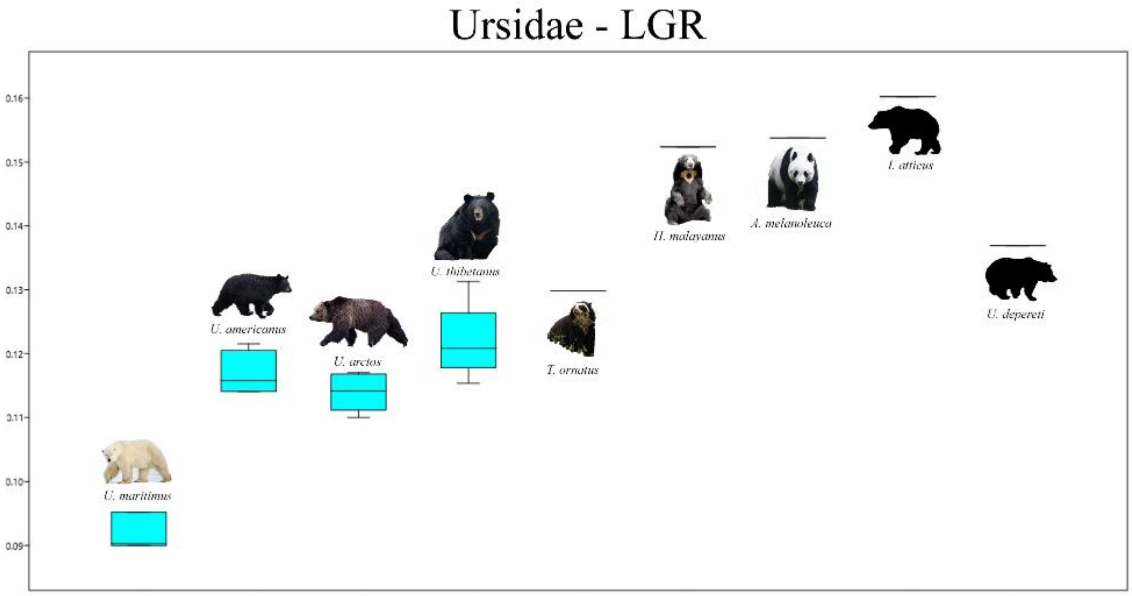


Fig. 20: The levels of LGR proxy (Sacco & Van Valkenburgh, 2000) in the studied ursids

The LGR proxy for the lower cheek teeth presents a similar pattern as UGR for the extant bears, as the most carnivorous having the lowest values and the most herbivorous the highest. Again, *Indarctos atticus* preserves a very high value, higher than that of the giant panda, indicating a plant-based diet. *Ursavus depereti* preserves a relatively high value between the omnivorous and the herbivorous extant species.

The graph on M2SZ is following a similar pattern with LGR, while the proxy M1BSZ does not provide a very clear dietary discrimination.

The graphs on the bending strength of all I1, I2 and C are not discriminating between the dietary categories of the extant bears.

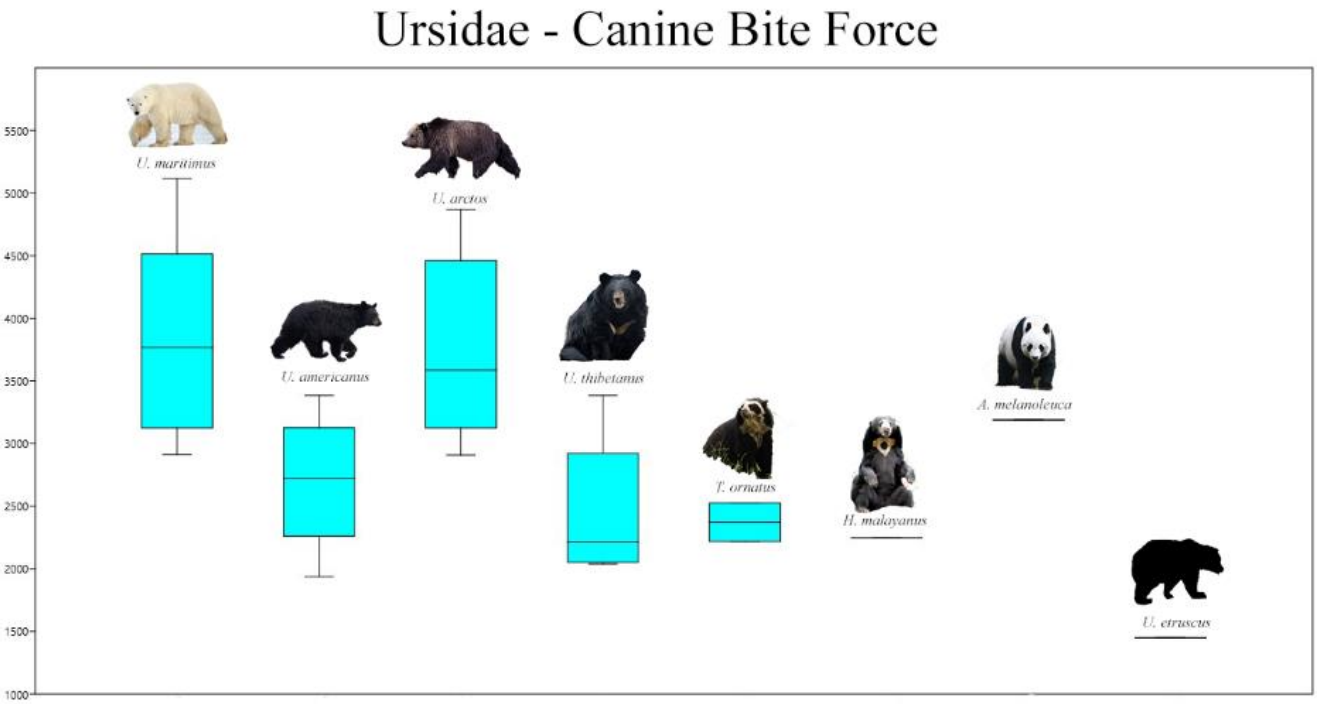


Fig. 21: The levels of Bite Force in the upper canines of the studied ursids

The graph on the Bite Force indicates the significance of phylogenetic constraint between *U. maritimus* and *U. arctos*: two very different ecologically (but closely related) species preserve almost identical bite force ranges. These constraints are more visible, when BFQ is studied, where there are no clear patterns between all the species. There is a sight tendency of decreasing BFcan in herbivorous bears, but the giant panda is preserving a higher BF, because of its diet with thick bamboo sticks that require high bite force in order to break them. The specimen of *U. etruscus* preserves a very low BFcan, probably because of the sub-adult age of the individual, a fact that is very important in the calculation of bite forces. It can be assumed that the BF of this species would be significantly higher than the one calculated here, probably reaching the levels of the more herbivorous-friendly omnivorous bears.

The values of the rostrum width divided by the skull length are also homogenous between all the fossil and extant species, with the exception of the short-faced *Helarctos* and *Tremarctos*, which had higher values. It seems that an allometric transformation took place for these two genera, retaining the rostrum width while shortening the skull length (Erbrink, 1953).

The patterns in Dental Mesowear are somewhat informative. Comparing the carnivorous *U. maritimus* with the other species, it is visible that there is a trend for higher values in Horizontal than Transverse Wear, suggesting that its toothrow is more adapted to a carnassial and not to a grinding function (Sacco & Van Valkenburgh, 2003). Unfortunately, there is not a high number of studied specimens for any of the fossil species. The exclusively low wear in *U. etruscus* is probably caused from the young age of the individuals. *Indarctos atticus* preserves one value of 3 in Transverse Width, indicating that its molars were exposed to plant grinding. The same is visible for the two *Ursavus* species. The lack of a considerable amount of specimens decreases the validity of the results of this method, but they are enough to provide some useful hints, indicating herbivorous behavior in both *Indarctos* and *Ursavus*.

Table 7: Patterns on Dental Mesowear on the studied ursids

Family	**Species**	**n**	**Transverse**			**Horizontal**			**Premolars**
			1	**2**	**3**	**1**	**2**	**3**	
Ailuridae	*Ailuropoda melanoleuca*	1	1	0	0	1	0	0	0
Ursidae	*Ursus thibetanus*	5	0.4	0.2	0.4	0.8	0.2	0	0.4
Ursidae	*Ursus maritimus*	5	0.6	0.4	0	0.4	0.6	0	0.2
Ursidae	*Ursus americanus*	4	0.5	0.5	0	0.75	0.25	0	0.25
Ursidae	*Ursus arctos*	11	0.18	0.36	0.45	0.8	0.1	0.1	0.72
Ursidae	*Helarctos malayanus*	2	0	1	0	1	0	0	0.5
Ursidae	*Tremarctos ornatus*	2	0	1	0	0.5	0.5	0	0
Ursidae	*Ursus etruscus*	3	1	0	0	1	0	0	0
Ursidae	*Ursavus depereti*	1	0	0	1	1	0	0	1
Ursidae	*Ursavus ehrenbergi*	1	0	0	1	1	0	0	1
Ursidae	*Indarctos atticus*	2	0.5	0	0.5	1	0	0	0

The Endocranial Volume of all the species was not informative on their dietary ecology, as the BVQ values were homogenous. Additionally, the only specimen with a complete braincase was TSR-E21-50 of *Ursus etruscus*, so a more detailed comparison was not possible. This skull preserved an Endocranial Volume of 263.2 ml, similar with the mean value for *Ursus thibetanus* (277.2 ml). This value is also similar with the endocast volume calculated by Koufos et al. (2018), which was 273.7 cm^3 (probably misspelled as mm^3 in the paper).

The PCA based on the measurements proposed by Popowics (2003) for the upper cheek teeth is depicted in Fig 23. PC1 and PC2 interpreted 87.4 % and 6.3 % of total variability respectively, resulting in a satisfying 93.7 %. It is clear that *U. etruscus* falls into the range of *U. arctos*. The values for *U. ehrenbergi* fit within the values of *U. maritimus*, but this may be caused by the generally smaller size of this species in comparison to the polar bears. The giant panda and *I. atticus* fall well as outliers, indicating their different adaptations. However, they are not closely depicted. This fact is caused probably because the teeth of *I. atticus* are more primitive and generalized in comparison to *A. melanoleuca*. The most important difference is the size of the P4 protocone as seen in Fig. 22. This still functional protocone may be a hint of a slightly more opportunistic diet, in comparison to the strictly herbivorous giant panda.

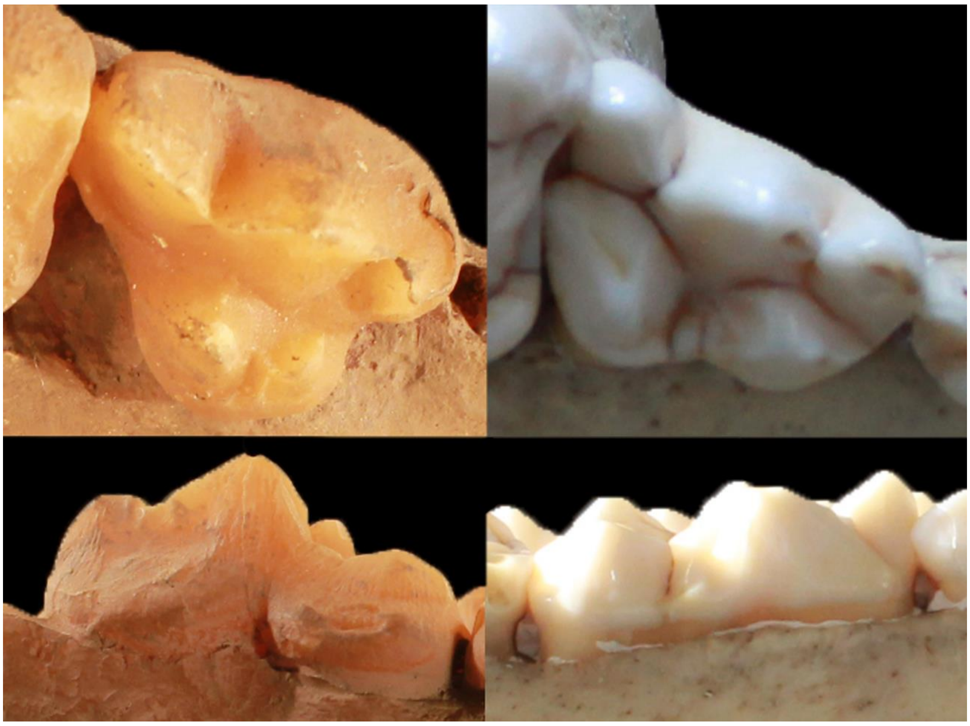


Fig. 22: Upper P4 and lower m1 of *I. atticus* (left) and *A. melanoleuca* (right)

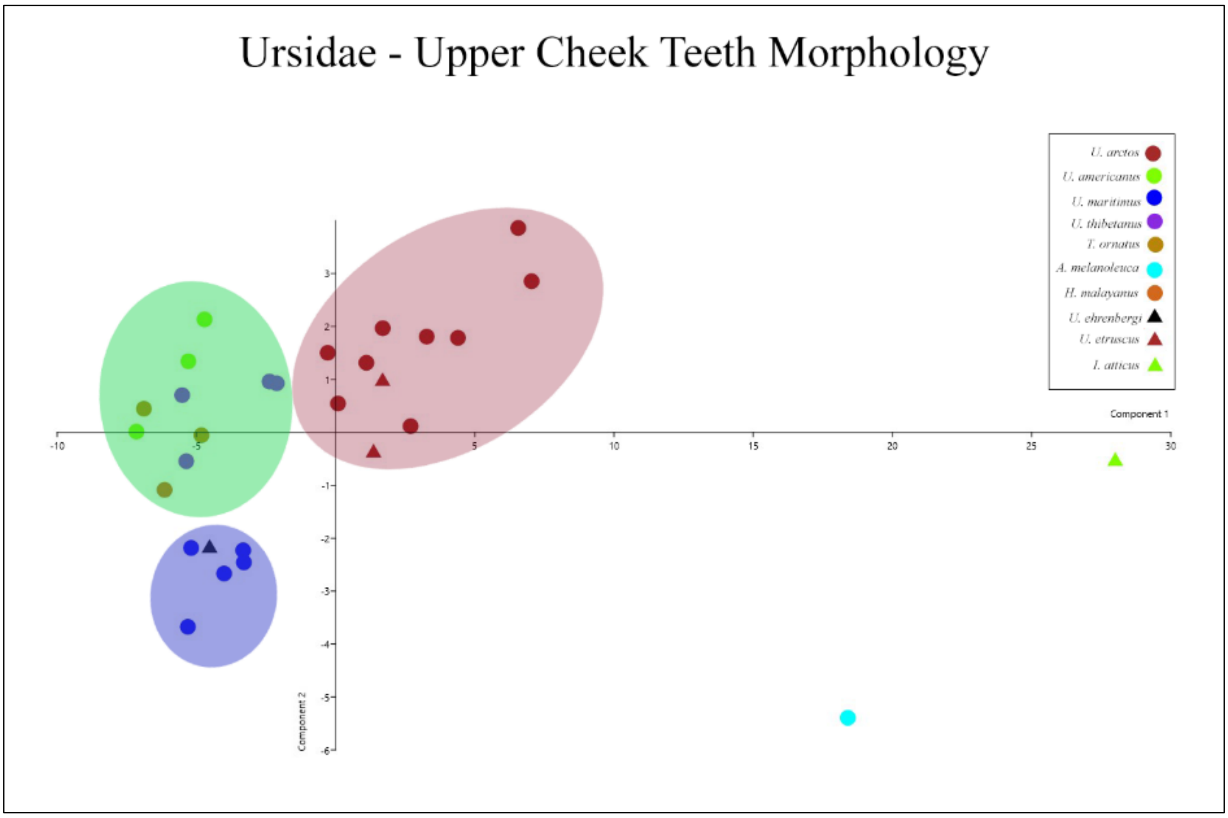


Fig. 23: PCA for the upper cheek teeth of the studied Ursidae based on Popowics (2003)

The PCA for the lower cheek based on Popowics (2003) is depicted in Fig 24. PC1 and PC2 interpreted 95.4 % and 2.0 % of total variability respectively, resulting in 97.4 %. In this diagram there is no clear discrimination inside Ursinae. However, Ailurinae again fit well far from them and *I. atticus* is not close to *A. melanoleuca*. The teeth of *Indarctos* are significantly larger than in *Ailuropoda* and that the protoconid of m1 is considerably higher and more carnassiform in *Indarctos* (Fig. 24). *Ursavus depereti* fits well with the other Ursinae, fitting more into the ranges of *Ursus arctos*.

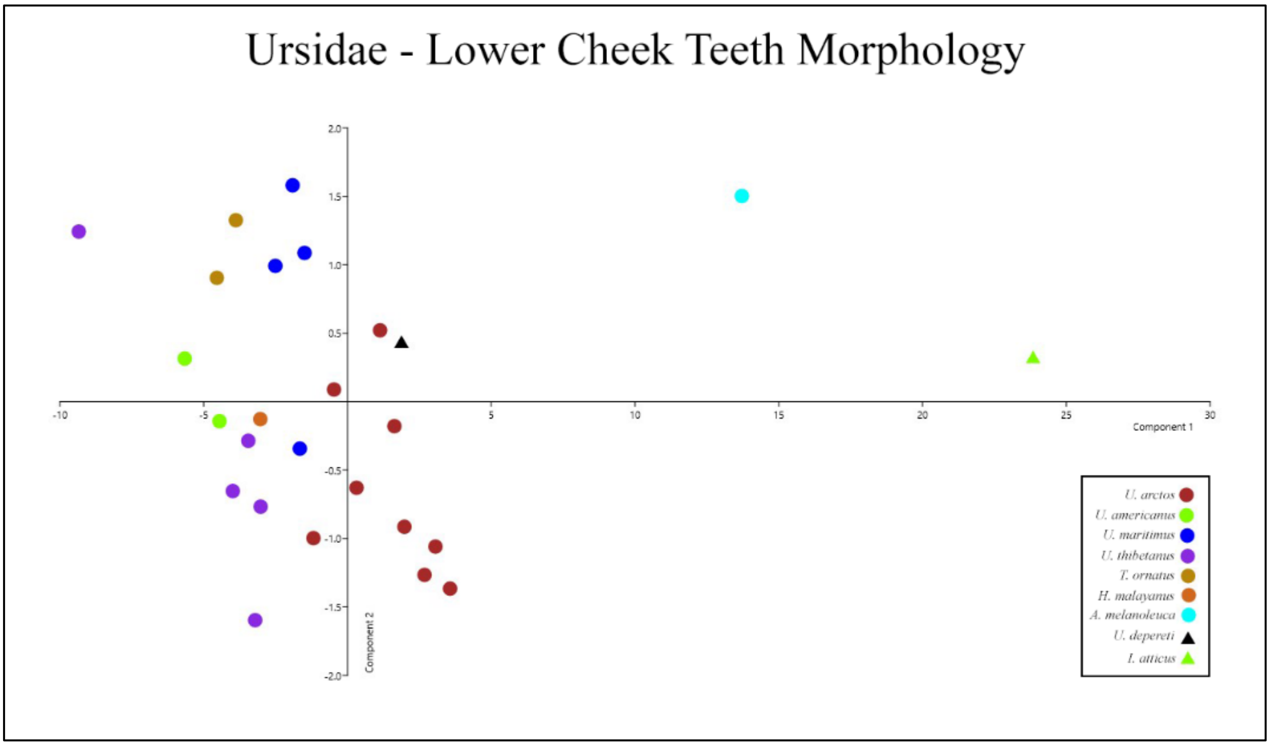


Fig. 24: PCA for the lower cheek teeth of the studied Ursidae based on Popowics (2003)

Results: ***Indarctos atticus*** seems to be indeed ecomorphologically comparable to *Ailuropoda melanoleuca*, but its more carnassiform P4 and m1 may be hints for a slightly more opportunistic diet. ***Ursavus depereti***, ***Ursavus ehrenbergi*** and ***Ursus etruscus*** were probably omnivores, with plant material being a major part of their diets, similar with modern day *Ursus arctos* or *Ursus thibetanus*. However, the scarcity of remains for the two *Ursavus* species and the inclusion of non-adult individuals of *Ursus etruscus* still retain the possibility of a different outcome in future studies.

[2] *Simocyon primigenius*

This species is controversial in many ways. At first, its taxonomy is not clear. Different approaches have considered it as amphicyonid (Pilgrim, 1931), procyonid (2002) or ailurid (Koufos, 2011). A future phylogenetic study based on both dental, cranial and auditory morphology will hopefully uncover its real taxonomy. Another problem is that postcranial material of this species is almost unknown. Therefore, there are no clear suggestions about its body plan.

The morphology of the cheek teeth of *Simocyon* resembles more the canids' pattern. However, its rostrum is significantly shorter, resulting to a very different overall skull morphology. Therefore the weight of *S. primigenius* is here calculated based on its m1 length (Van Valkenburgh, 1990). A number of 7 specimens has revealed a body weight range between 16 and 21 kg, similar to a modern coyote.

Most of the extant canids are opportunistic omnivores, based mainly on meat. Some medium-sized canids have a larger part of plant material in their diet (e.g. *Nyctereutes*, *Urocyon*), while four species are considered hypercarnivorans (*Canis lupus*, *Cuon alpinus*, *Lycaon pictus*, *Speothos venaticus*). *Otocyon* is also an opportunist, since living in the desert does not allow for many specific preferences, but it does restrict the nature of the living prey. Therefore, this genus is considered mainly as an insectivore and an ant-eater in particular. The present comparison is based on extant canids, which are divided into three groups: *Vulpes* group (*Vulpes vulpes*, *Nyctereutes procyonoides*, *Urocyon cinereoargenteus* and *Otocyon megalotis*), *Canis aureus* group (*Canis adustus*, *Canis aureus*, *Canis mesomelas* and *Canis latrans*) and *Canis lupus* group (*Canis lupus*, *Speothos venaticus*, *Cuon alpinus* and *Lycaon pictus*)

The bending strength of the upper canine of *Simocyon* is considerably higher than those of canids of the same body weight (Fig. 25). This fact is present both in S_xC and S_yC. Unfortunately only one specimen with upper canine has been included in this study.

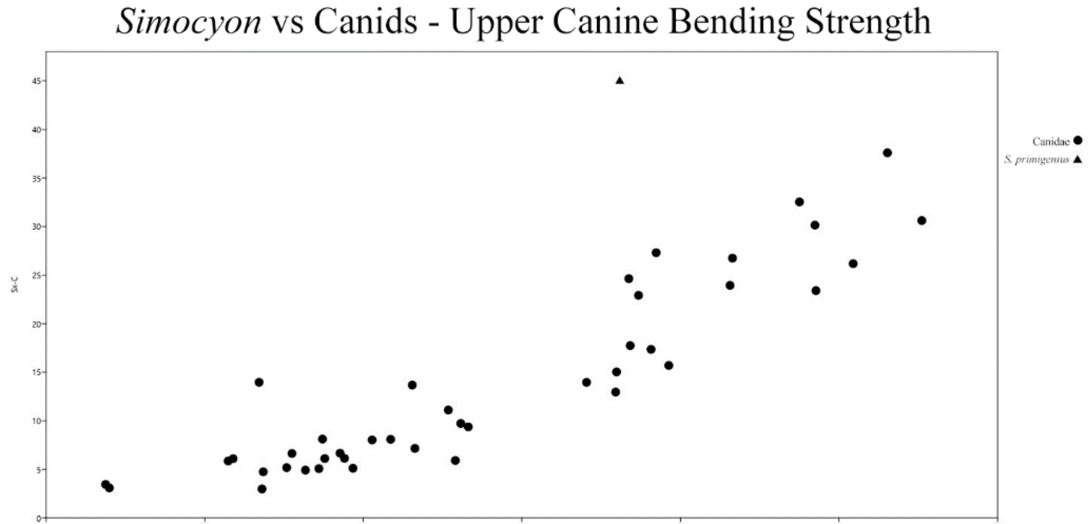


Fig. 25: Bending strength of the upper canine (S_xC) and body mass of *Simocyon primigenius* and the comparative dataset of canids.

Using the ratio M1BSZ by Sacco & Van Valkenburgh (2004) it is possible to calculate the relative m1 trigonid length. In Fig. 26 it is clear that (despite the significant overlaps) there is a trend of gradually higher values in the more carnivorous canids. As seen in the boxplot, *Simocyon* seems to fit more to the range of hypercarnivorous species. This fact is probably driven by the reduction of the mandibular length between m1 and c.

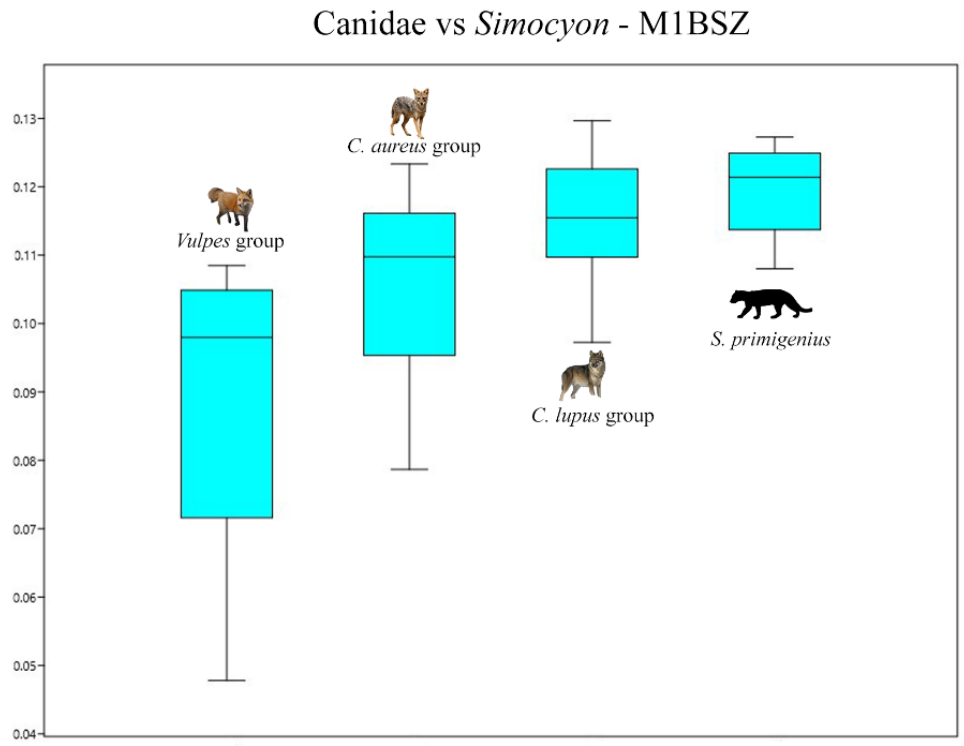


Fig. 26: M1BSZ (Sacco & Van Valkenburgh, 2004) of *Simocyon primigenius* and the comparative dataset of canids.

The proxy LGR by Sacco & Van Valkenburgh (2004) uses the summed area of m3, m2 and m1's talonid divided by the dentary length, uncovering the non-carnassial areas of the cheek teeth. Despite the fact that *S. primigenius* lacks the lower third molar, it can be seen in Fig. 27 that it preserves significantly higher values than the extant canids, which tend to be relatively homogenous in this trait. This fact can be explained, as these areas can be used both in grinding plant material (in omnivores) and in crushing bones (in hypercarnivorans). Unfortunately it is not possible only from this diagram to understand which of these two functions is enhanced.

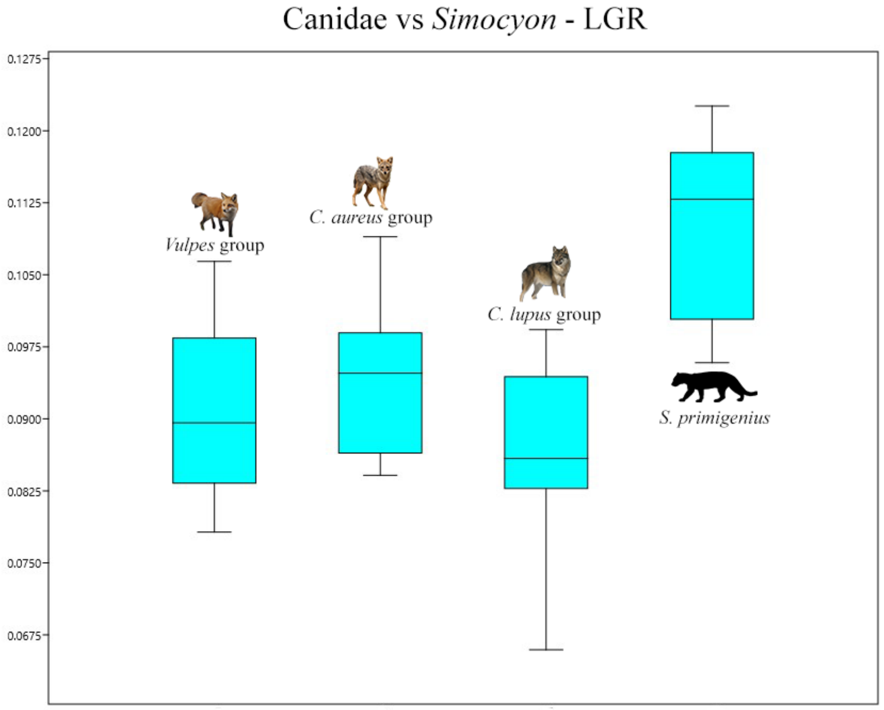


Fig. 27: LGR (Sacco & Van Valkenburgh, 2004) of *Simocyon primigenius* and the comparative dataset of canids.

Despite the short rostrum, the Bite Force of *S. primigenius* is not sufficiently stronger than in the canids of similar size, as seen in Fig. 28. It seems that it fits with the general trend of canids' ranges, plotted between the ranges of *C. aureus* and *C. lupus* groups. A similar pattern is seen in BFcarn. However, only one complete skull is known, which is slightly distorted and was found only as a cast in the visited museums (NHMUK and MNHN). An additional measurement of the less distorted skull from Karaslari (Spassov & Geraads, 2011) would be helpful.

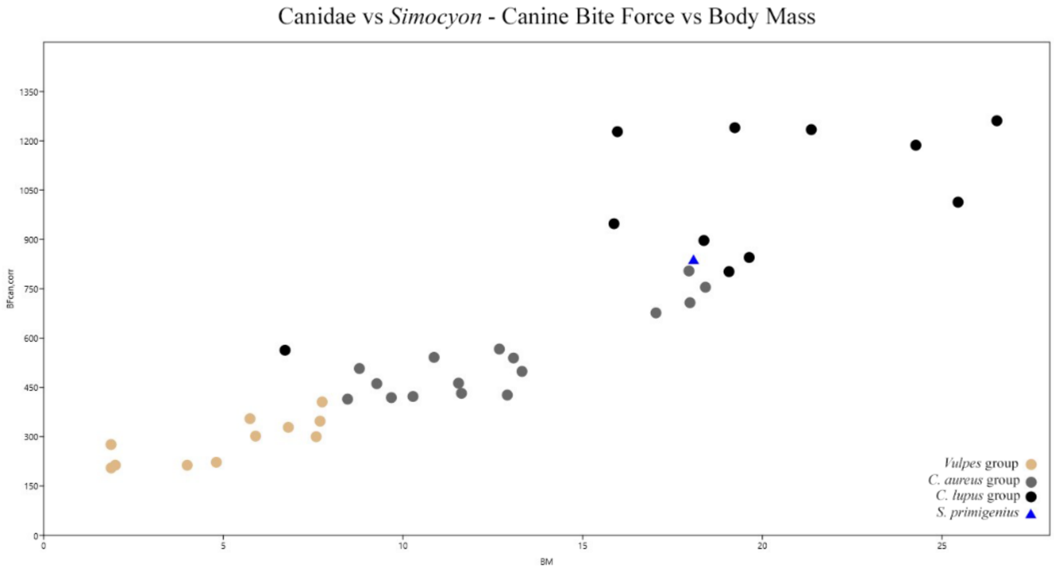


Fig. 28: Canine Bite Force of *Simocyon primigenius* and the comparative dataset of canids in relation to their Body Mass.

Table 8: Dental Mesowear pattern of *Simocyon primigenius.*

Species	**n**	**Transverse**			**Horizontal**			**Premolars**
		1	**2**	**3**	**1**	**2**	**3**	
Simocyon primigenius	6	0.66	0.12	0.12	0.6	0.4	0	0.25

The Dental Mesowear pattern of *S. primigenius* is not very informative, since the transverse and the horizontal wear stages are relatively similar. The low value of the premolars' transverse wear indicates that any possible bone-crushing function was not made in the premolars, but in the strong molars.

The Endocranial Volume of MNHUK-49675 was 83.79 ml, similar to that of a modern day coyote (*Canis latrans*), which also is of similar body mass.

By dividing the rostrum width with the total skull length is possible to discriminate the hypercarnivorous canids (Fig. 29). In this boxplot, we can see that the value of *Simocyon* is higher even from the maximum values of the hypercarnivorans, probably due to its short rostrum.

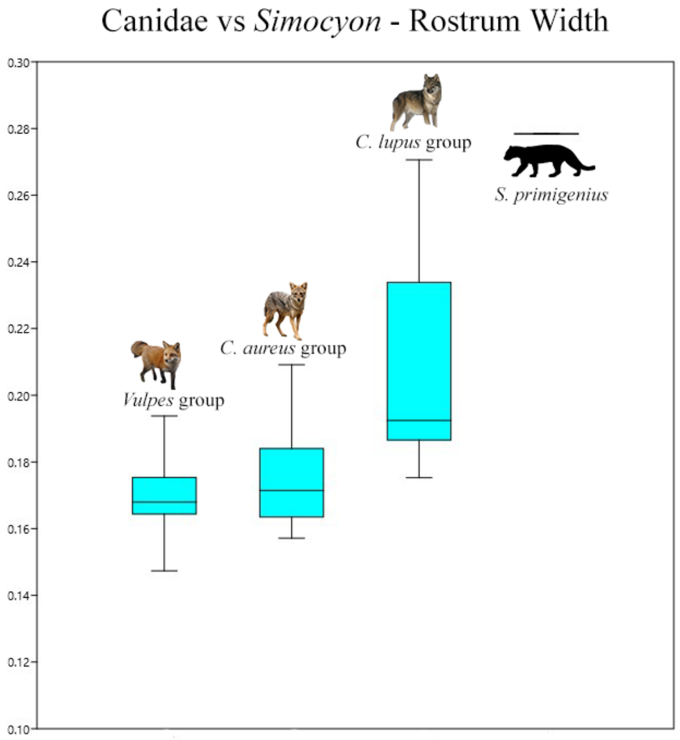


Fig. 29: Rostrum Width divided by Skull Length on *Simocyon* primigenius and the comparative canids.

When analyzing the morphology of the upper and the lower cheek teeth through the method of Popowics (2003) using PCA (Fig. 30) it can be seen that the upper teeth of *Simocyon* fit more to those of hypercarnivorous canids, but they are close to the *C. aureus* group too. On the other hand, the lower carnassial seems to be relatively different from all the extant canids, but again it seems to be closer to *C. lupus* group.

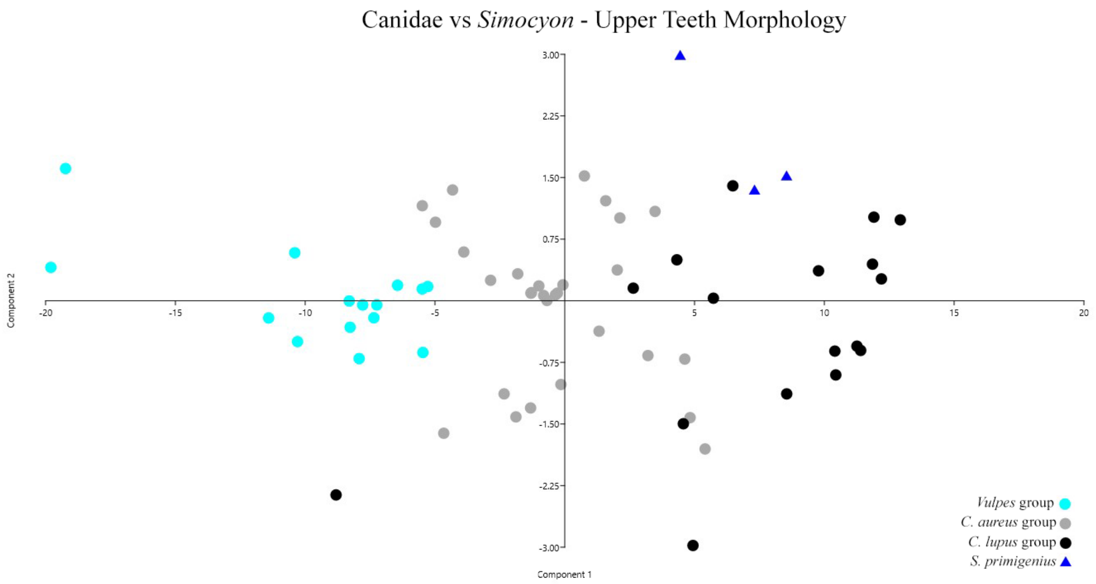


Fig. 30: Upper teeth morphology of *Simocyon* and the comparative dataset of canids using the measurements of Popowics (2003) and PCA

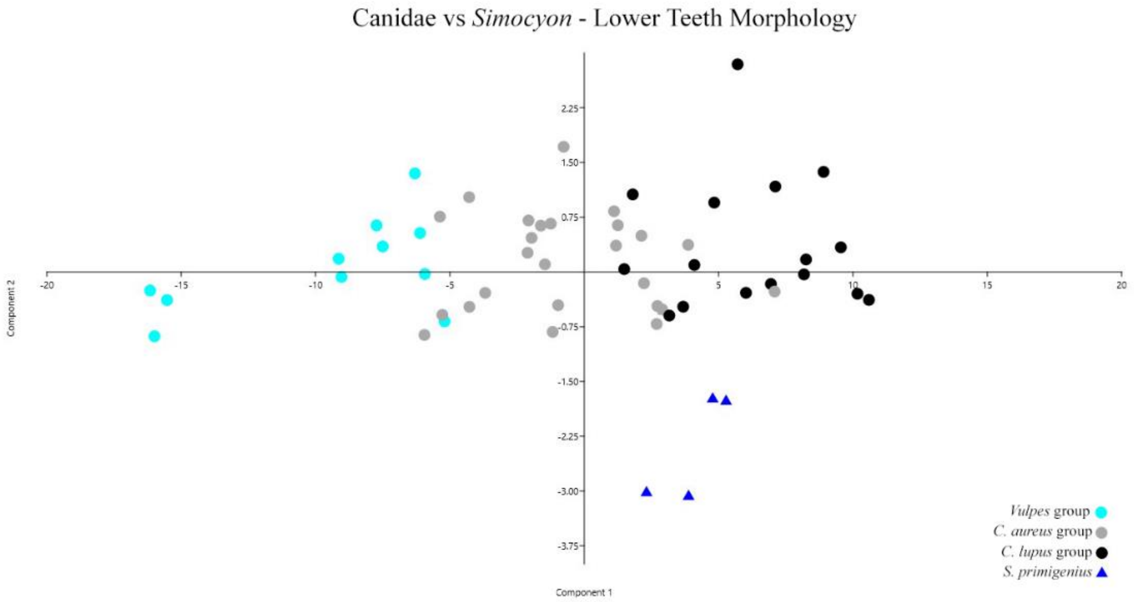


Fig. 31: Lower teeth morphology of *Simocyon* and the comparative dataset of canids using the measurements of Popowics (2003) and PCA

Results: ***Simocyon primigenius*** seems to be an opportunistic carnivoran. Its teeth (both canines and cheek teeth) seem to be designed to withstand high bite forces, despite the fact that its BF is not significantly high. This result fits with the hypothesis of Spassov & Geraads (2011), who said that the enlarged frontals cover enhanced frontal sinuses, which may correlate with the ability to bear a strong bite force, which in the posterior teeth of the carnivorans can be connected only with bone crushing. A future detailed study of these sinuses would be really helpful. Therefore, the present study has resulted that *Simocyon* probably was an opportunistic meat-eater and bone-crusher, maybe primarily a scavenger in a niche similar to extant wolverines (*Gulo gulo*).

[3] *Plesiogulo crassa*

This species is the largest mustelid found in the fossil record of Greece. With a skull length of 201.55 mm and a lower carnassial length of 26.41 mm, its body weight is estimated around 60-80 kg. Extant wolverines (*Gulo gulo*) weight up to 30 kg, but they usually weight between 5 and 25 kg. Unfortunately, there are no extant mustelids of this size, so the comparison will be probably affected by a bias. The studied specimens are an associated pair of skull and mandible from Perivolaki (LGPUT-1239).

The bite force of the mustelids seems to be slightly stabilized in relation to their skull length, with slightly higher values in the small-sized *Vormela* and *Mustela*. *Plesiogulo* does not seem to differ substantially from this patter in neither BFcarn nor BFcan.

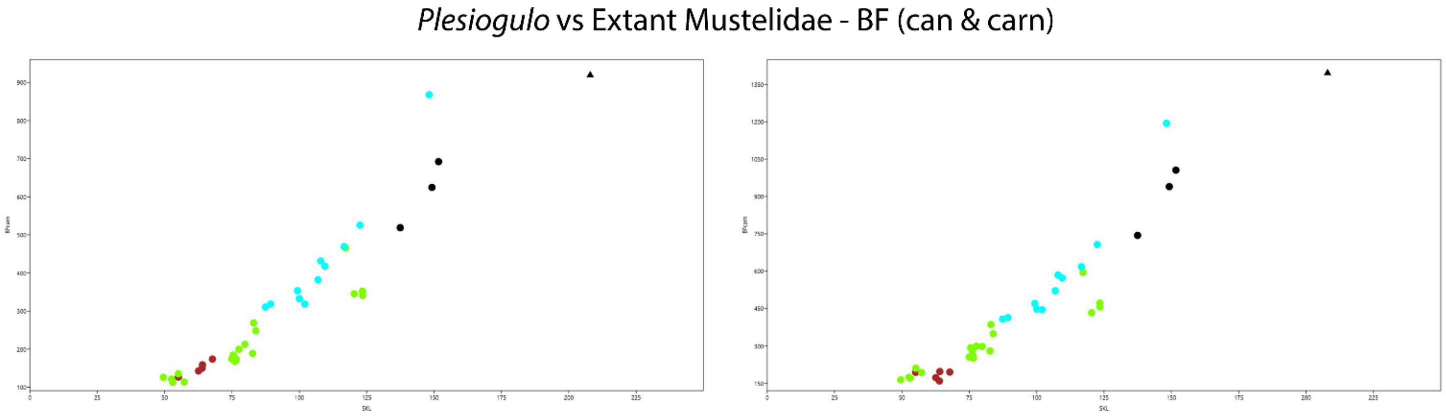


Fig. 32: Comparison of bite force (BFcan and BFcarn) of extant mustelids (*Mustela*-red, Omnivores-green, otters-aqua, *Gulo*-black) and *Plesiogulo crassa* (black triangle)

In Canine Bending Strength, all mustelids again seem to follow a common pattern with the larger species having relatively more powerful canines. *Plesiogulo* again fits with this trend, despite its size difference (Fig. 33).

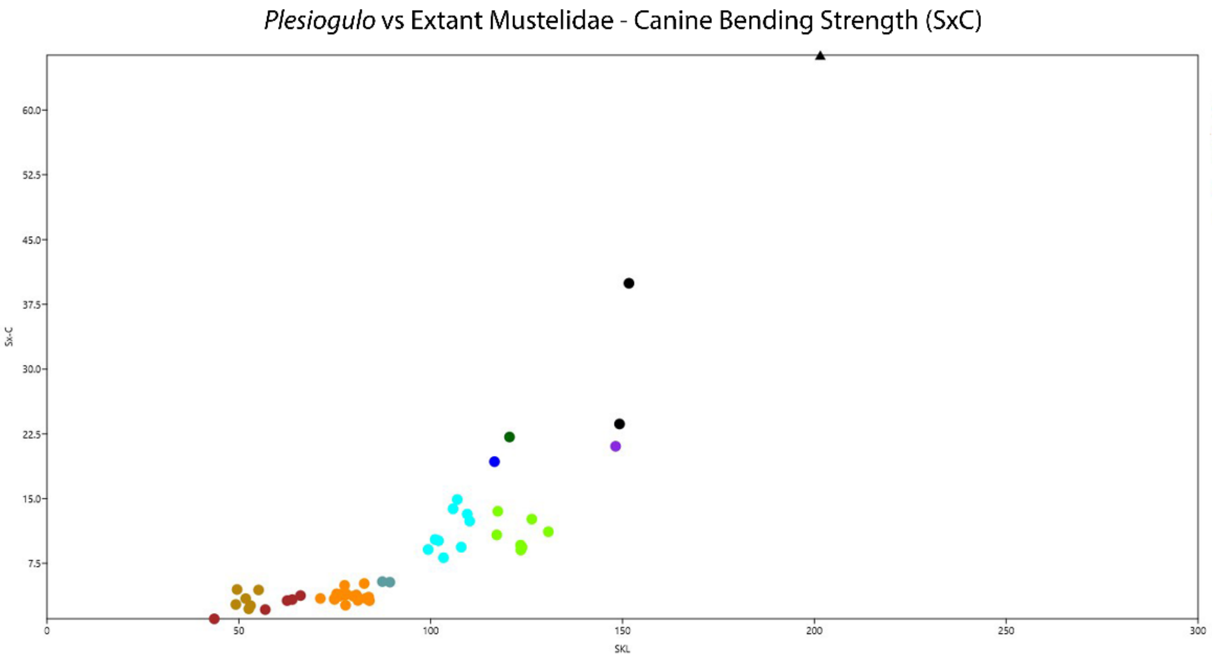


Fig. 33: Comparison of canine bending strength (SxC) between *Plesiogulo* (black triangle) and extant mustelids (*Gulo*-black, *Mustela*-red, *Vormela*-brown, *Martes*-orange, *Eira*-dark green, *Meles*-light green, *Amblonyx*-dark aqua, *Lutra*-aqua, *Enhydra*-purple, *Pteronura*-blue)

The Dental Mesowear for the Perivolaki material is in level 2 for both wears, indicating that the teeth were significantly used for both grinding and shearing functions.

Both LGR and UGR values (Sacco & Van Valkenburgh, 2003) indicate that *Plesiogulo* is different from both Lutrinae and the mostly herbivorous *Meles*, but it is situated close to the omnivorous-carnivorous species (Fig. 34 & 35).

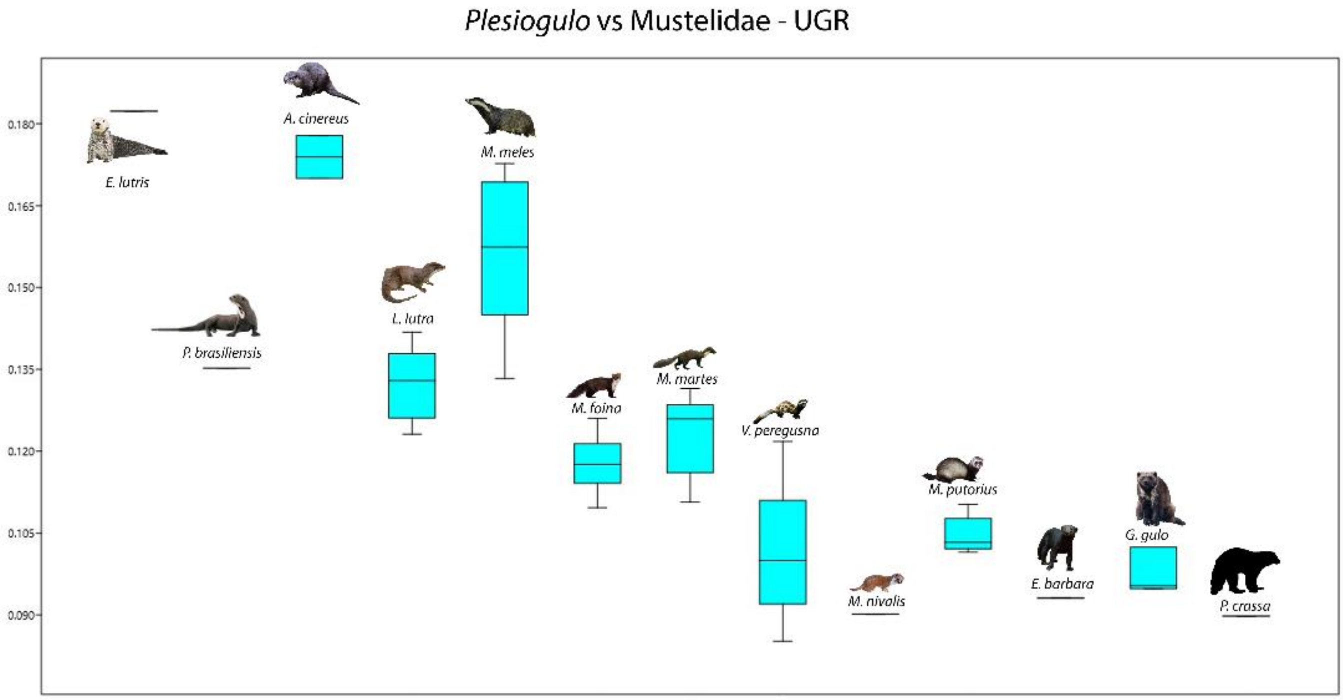


Fig. 34: Comparison of *Plesiogulo crassa* with the extant Mustelidae in UGR

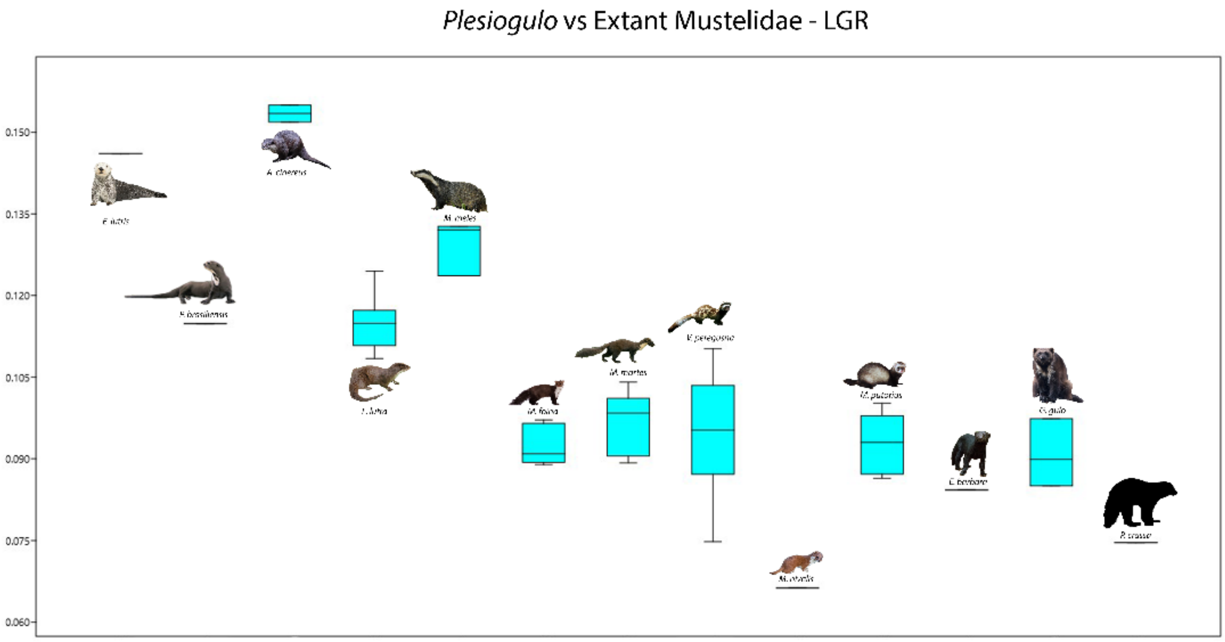


Fig. 35: Comparison of *Plesiogulo crassa* with the extant Mustelidae in LGR

The value of M1BSZ doesn’t fit with the more carnivorous species, but it is more similar to the omnivorous species, like *Martes martes* (Fig. 36).

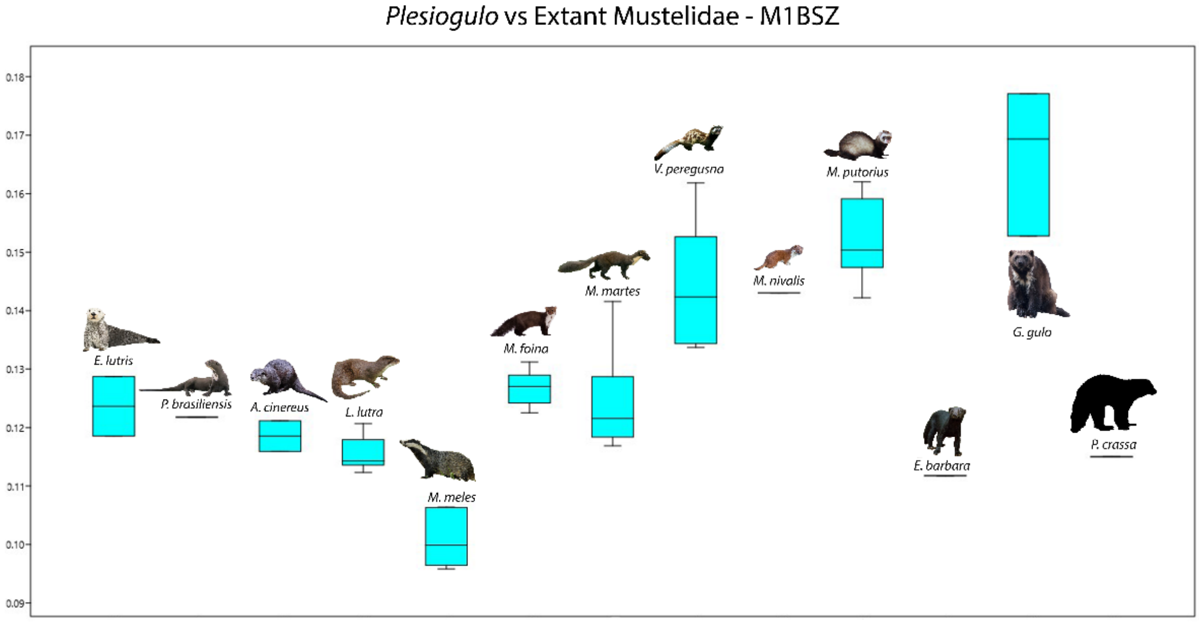


Fig. 36: Comparison of *Plesiogulo crassa* with the extant Mustelidae in M1BSZ

The ratio of the rostrum width to the skull length is not discriminating between the different dietary categories in the present dataset. Therefore, this proxy is not informative on the ecology of *Plesiogulo*.

The first two principal components of the PCA for the dimensions of upper cheek teeth based on Popowics (2003) interpreted 78.86 % and 14.11 % respectively, resulting to 93.97 %. The proximity to *Pteronura* and *Enhydra* is probably caused by the large dimensions of these otters and not because of a similar ecology. It is clear that *Plesiogulo* seems to be a separate category, not fitting to any of the known genera.

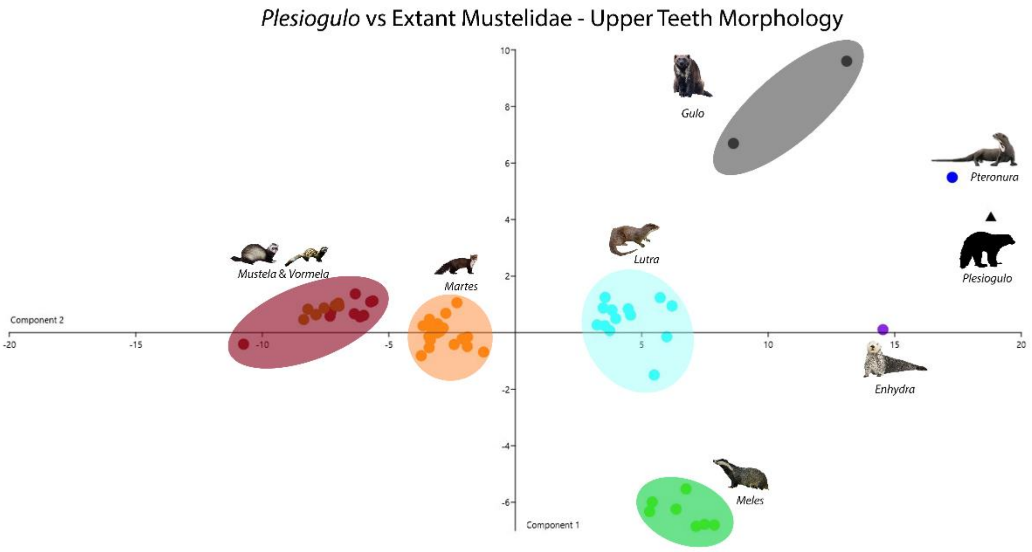


Fig. 37: PCA based on the morphology of upper teeth of *Plesiogulo* and extant Mustelidae

The first two principal components of the PCA for the dimensions of m1 based on Popowics (2003) interpreted 88.96 % and 7.25 % respectively, resulting to 96.21 %. Again *Plesiogulo* seems to be a separate category, not fitting to any of the extant taxa, except a distant proximity to *Gulo*.

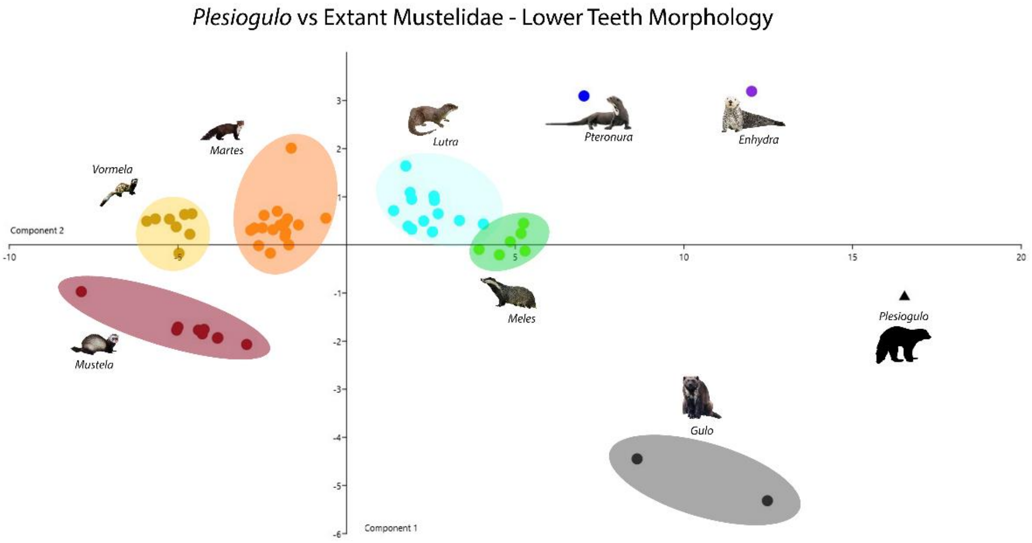


Fig. 38: PCA based on the morphology of lower teeth of *Plesiogulo* and extant Mustelidae

<u>Results</u>: ***Plesiogulo crassa*** seems to be an opportunistic carnivoran. Unfortunately the result is not clear, probably because of the large body size of this genus, unequal to any of extant comparative genera. However, the most probable scenario is that it followed the ecological niche of modern honey badgers in terms of dietary

preferences’ percentages, with plant material being about 30-40% of its diet. The size of the possible prey of this species is still unknown. Its cranial mechanics must have enabled it to kill prey about 20-30 kg and, if its physique (and temper) was similar to modern wolverines’, it would be able to easily take down even larger prey. However, a more opportunistic diet based on small vertebrates (lizards, small birds, eggs etc.) probably is the more safe hypothesis.

[4] *Baranogale* aff. *helbingi*

The only material attributed to this species is a fragmentary left hemimandible from Dafnero (LGPUT-DFN-189). This mandible is broken in the cranial border of masseteric fossa and just anteriorly of p2. This fact, along with the absence of visible wear in its teeth, doesn't enable for a wide comparison. The only proxies available are Intercuspid Notches and the measurements by Popowics (2003).

The intercuspid notches' score on mustelids seems to have many interpretations, since both piscivores and insectivores possess simple teeth. The same is true for *Gulo* and *Vormela*, despite the fact that they are mainly carnivorans. *Baranogale* seems to have an intermediate value, similar with the skunks, *Mustela* and *Meles*.

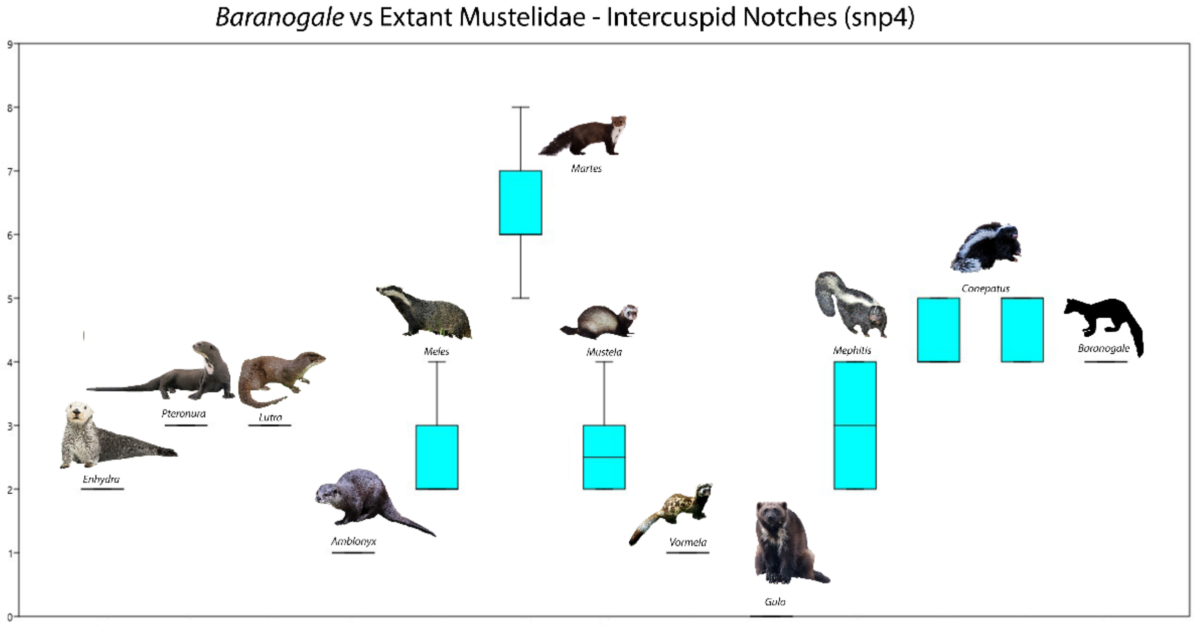


Fig. 39: Comparison of intercuspid Notches (snp4) in *Baranogale* and extant mustelids

PC1 interpreted 86.7% and PC2 8.7% of total variance, resulting to 95.4%. In this plot, *Baranogale* seems to fit into the ranges of skunks and martens.

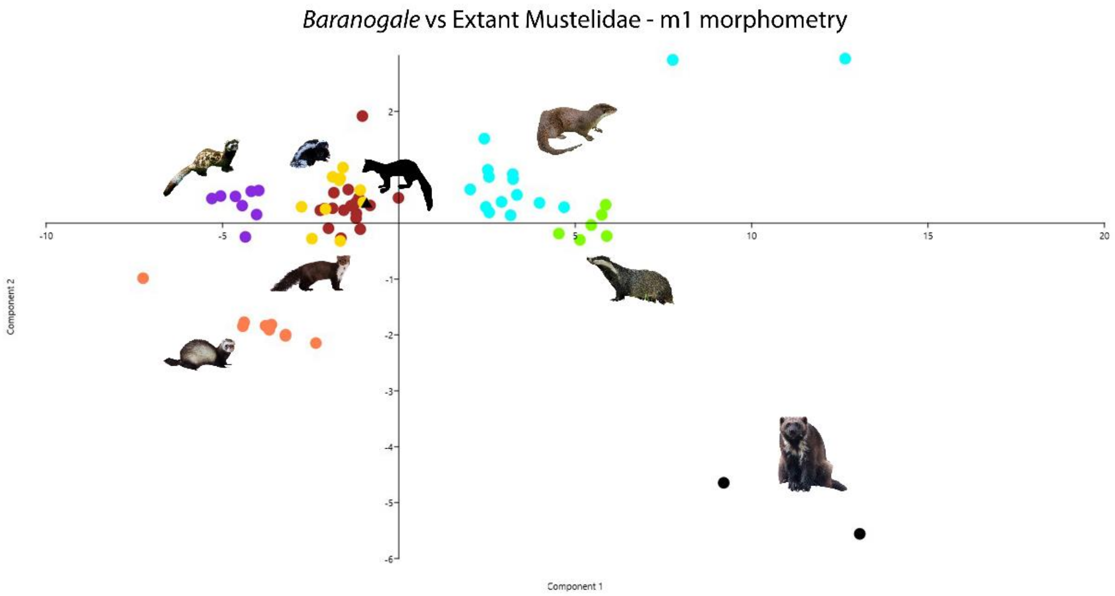


Fig. 40: PCA based on measurements of m1 by Popowics (2003) on *Baranogale* (black triangle) and extant mustelids

The morphology of *Baranogale* teeth indicate that it probably was a generalist, possibly based on carnivory. The carnassial trigonid of m1 is developed, but so is the talonid. However, both of them are not particularly enhanced or enlarged.

Fig. 41: The specimen attributed to *Baranogale* aff. *helbingi* (LGPUT-DFN-189)

Results: Probably ***Baranogale*** aff. ***helbingi*** was a generalist opportunist with a diet based on meat, while plants probably constituted approximately 30% of its diet, similar to extant martens. Unfortunately, the lack of specimens doesn't allow for a more certain result.

Contemporary and Ecologically Similar Species

[1] *Adcrocuta eximia, Lycyaena chaeretis* & *Belbus beaumonti*

The hyenas reached their maximum abundance and diversity over the Turolian (Werdelin & Solounias, 1991). During this epoch the Pikermian faunas included many ictitheres (next chapter) and the herein studied *Crocuta*-like hyenas (*Adcrocuta eximia*, *Lycyaena chaeretis*, *Hyaenictis graeca* and *Belbus beaumonti*). Unfortunately no material of *Hyaenictis graeca* was available to be studied here.

Comparing the other three species, it is obvious that *A. eximia* is a much more common hyena than the other two. In this Thesis, *A. eximia* is represented by 42 specimens (the highest of all species), *L. chaeretis* with 8 and *B. beaumonti* with 1. This extremely high abundance of *A. eximia* probably is an indicator of sociality, similar to their modern analogues, the spotted hyenas (*Crocuta crocuta*). The length of m1 was used as an indicator of body size comparison, but with no absolute values, in Table 9.

Table 9: m1 length in *A. eximia, L. chaeretis, B. beaumonti, C. spelaea* and *C. crocuta*. Data from Werdelin (1988), Beke (2010) and present study

Species	**m1 Length**	**n**
Adcrocuta eximia	28.01 (24.25-29.87)	10
Lycyaena chaeretis	22.55 (21.50-24.50)	6
Belbus beaumonti	24.89	1
Crocuta spelaea	31.6 ± 5.2	18
Crocuta crocuta	27.3 ± 3.6	29
Hyaena hyaena	20.6 (18.4-23.1)	23
Parahyaena brunnea	23.2 (21.7-25.2)	13

Therefore, the body size of *A. eximia* is assumed to be similar with the extant *C. crocuta*, while *L. chaeretis* and *B. beaumonti* were slightly smaller, probably similar to extant *H. hyaena*. In the following diagrams (Fig. 42) it is clear that most of the studied parameters of *L. chaeretis* fit with (or even below) the lowest values of *A. eximia*.

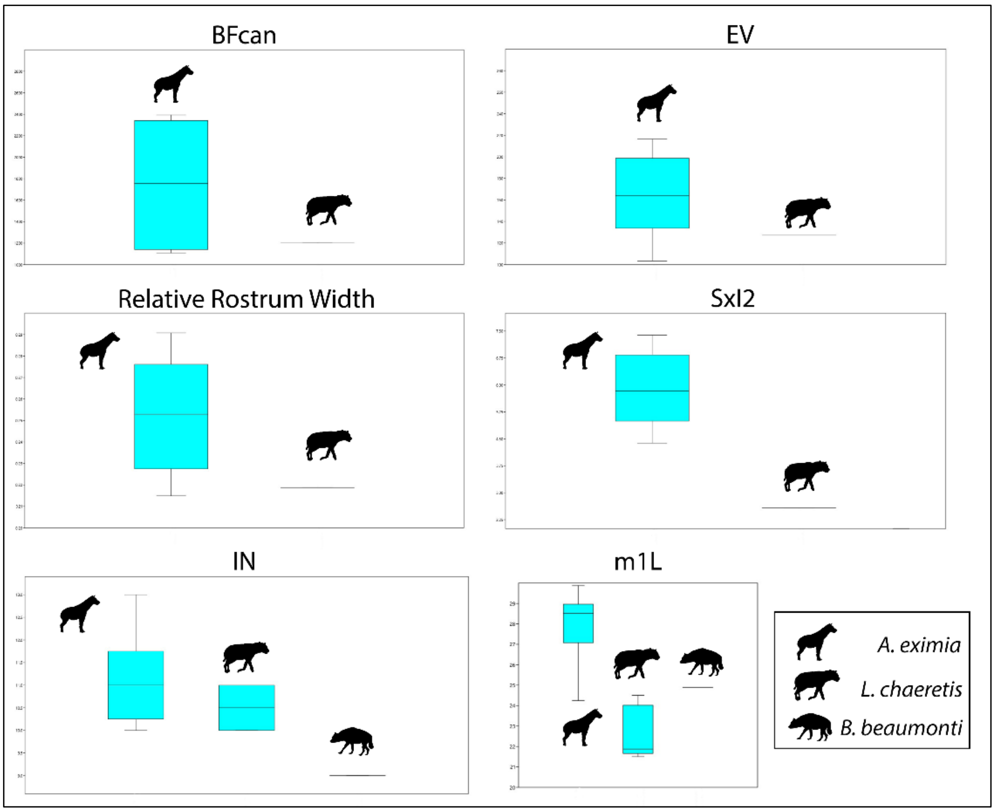


Fig. 42: Comparison of *A. eximia*, *L. chaeretis* and *B. beaumonti* in Canine Bite Force, Endocranial Volume, Relative Rostrum Width, I2 Anteroposterior Bending Strength, Intercuspid Notches and m1 Length.

These graphs show that, in general, *Lycyaena* was not as robust as *Adcrocuta* in terms of Bite Force, Bending Strength and Rostrum Width. It was also smaller (based on m1L) and not as social as *Adcrocuta* (based on the abundance of the specimens).

There are also two hints showing that it was not so capable of crushing bones. The first is the width of P3, p4 and p3 which are much more slender than in *Adcrocuta* (Fig. 43). The other fact is the wear pattern seen in the upper premolars in the only complete skull studied (MNHUK-M8978). Despite the transverse wear of these premolars, there is an interesting horizontal wear, visible in the posterior part of the teeth (Fig. 44). This pattern of wear is probably caused through a carnassial-like friction with the lower premolars, a different case with the crushing P2 and P3 of *Adcrocuta*. This result agrees with Galiano & Fraily (1977) and Werdelin & Solounias (1991).

Therefore, it can be concluded that *Adcrocuta* was more successful than *Lycyaena* and *Belbus* for three reasons: sociality, robustness and scavenging. Sociality must have enabled *Adcrocuta* to kill larger prey and to claim prey from other hunters as today’s spotted hyenas do. Its larger size was also a boost to this fact. Finally, its more wide premolars were more capable of crushing bones enabling it to exploit the nutrients of bones and marrow.

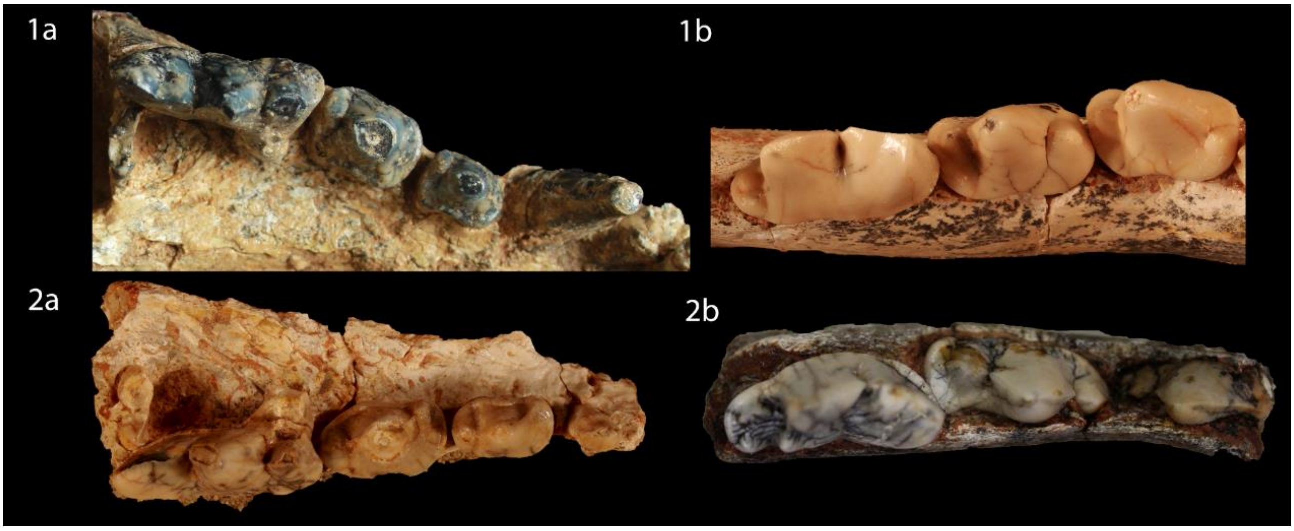


Fig. 43: Comparison of relative premolars width in *Adcrocuta* (1) and *Lycyaena* (2) skulls (a) and mandibles (b)

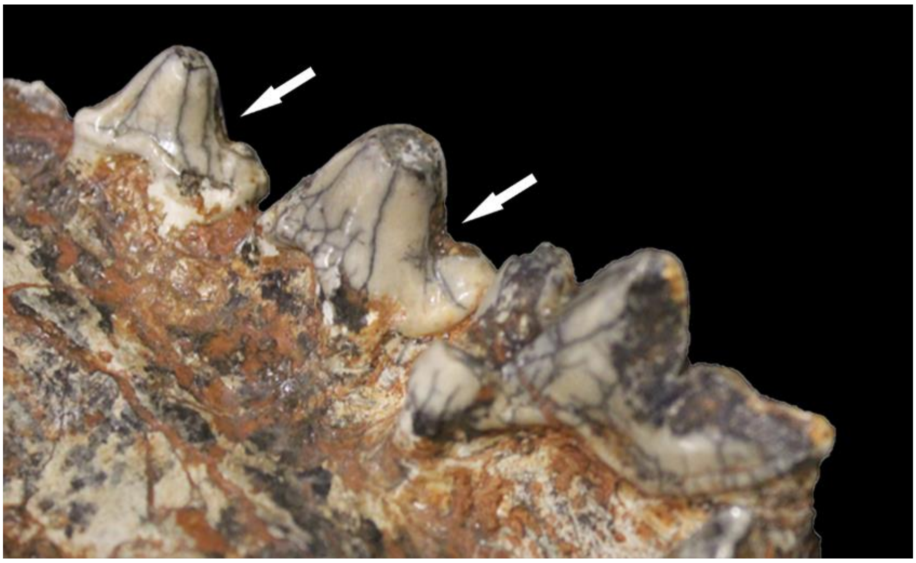


Fig. 44: Wear pattern of P3 and P2 of *Lycyaena chaeretis* (MNHUK-M8978)

[2] *Hyaenotherium wongii, Ictitherium viverrinum, Protictitherium crassum, Plioviverrops orbignyi*

During the late Miocene, the ecological niche today filled by the canids was occupied by ictitheres, compirsing in Greece four genera: *Hyaenotherium*, *Ictitherium*, *Protictitherium* and *Plioviverrops*. Some genera are represented by more than one species, but their intraspecific variability is herein considered ecomorphologically insignificant. In general these genera are of different size with *Hyaenotherium* being the largest and *Plioviverrops* being the smallest. However, Semenov (2008) states that body size is not useful in identifications above the species level. The ictitheres are herein compared with canids, because of their ecomorphological similarities. The studied canids are divided into three groups as in the chapter concerning *Simocyon*.

At first, as already aforementioned, there is a difference in size between these species. In Fig. 45 it can be seen that, based on their skull length, *Plioviverrops* weighted between 2 and 5 kg, *Ictitherium* between 9 and 20 kg and *Hyaenotherium* between 15 and 20 kg. Using the length of m1 for *Protictitherium*, the resulting body mass is approximately 5-6 kg.

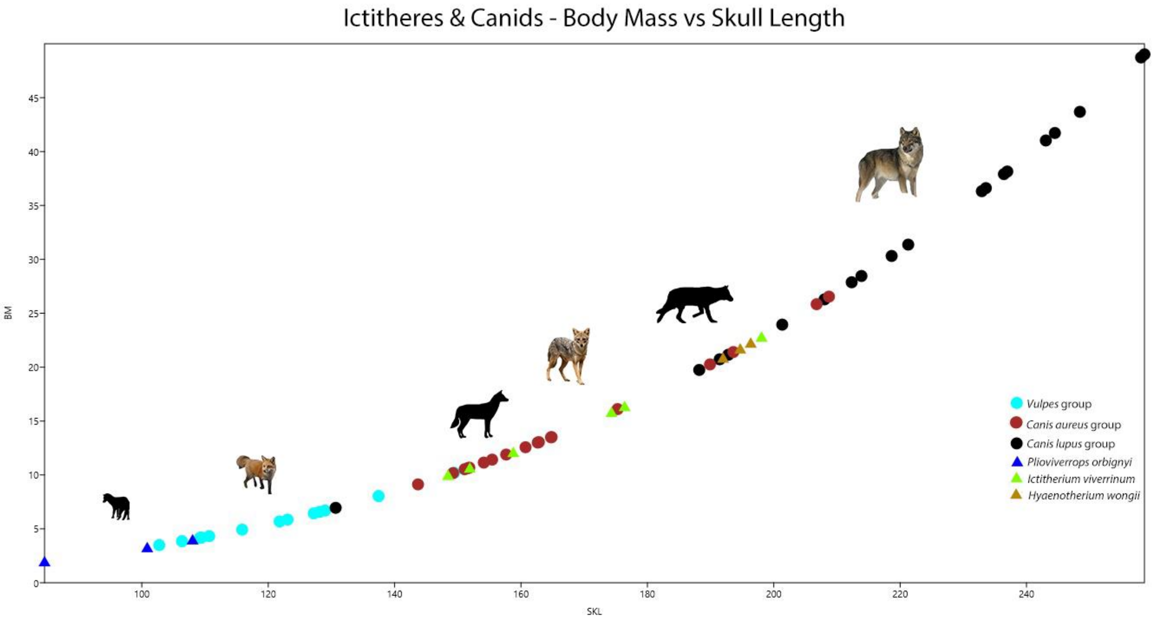


Fig. 45: Body Mass vs Skull length of ictitheres and the comparative canids

The Bite Force of the canids is increasing successively in the three groups. It is visible that *Plioviverrops* fits only into the range of *Vulpes* group, while *Ictitherium* and *Hyaenotherium* have similar values, falling within the covariance range of *Canis aureus* and *Canis lupus* groups.

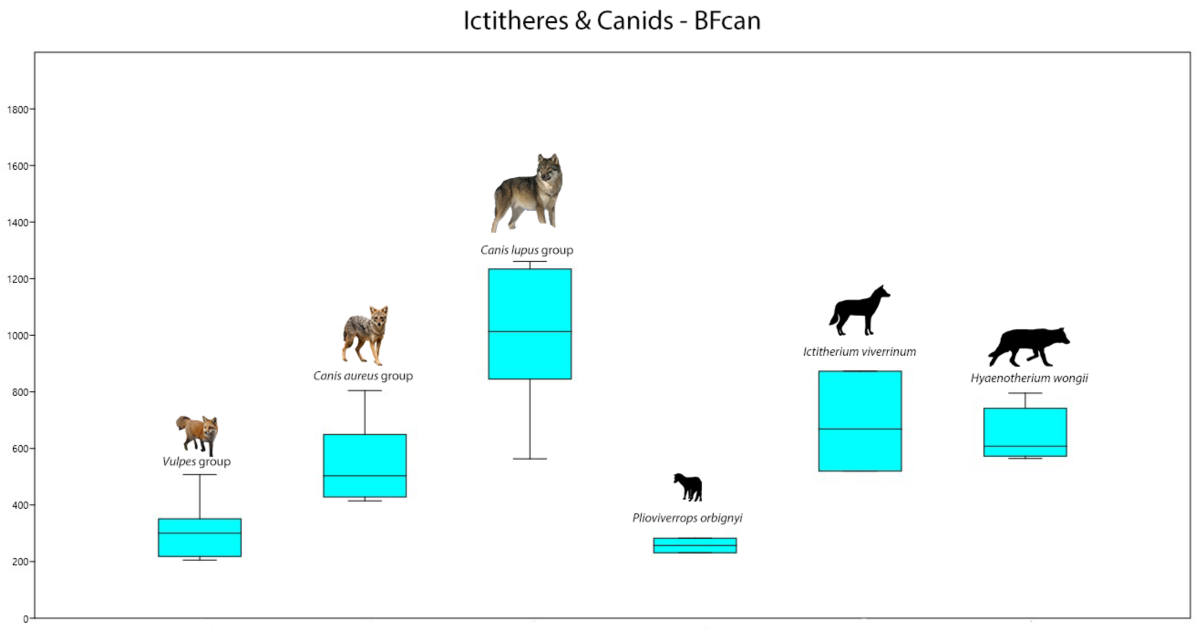


Fig. 46: Canine bite force for ictitheres and comparative canids

A similar pattern is seen in the bending strength of the upper canine. Again the canids form an increasing succession towards *Canis lupus* group and *Plioviverrops* fits in the *Vulpes* group. The value for *Protictitherium* fits into the range of *Canis aureus* group. Again the values of *Hyaenotherium* and *Ictitherium* have a very similar averages fitting in the covariance range of *Canis aureus* and *Canis lupus* groups. It is interesting that *Ictitherium viverrinum* preserves high variability. High interspecific differences in upper canine are common in primates, due to sexual dimorphism. Perhaps a similar reason may cause this variability.

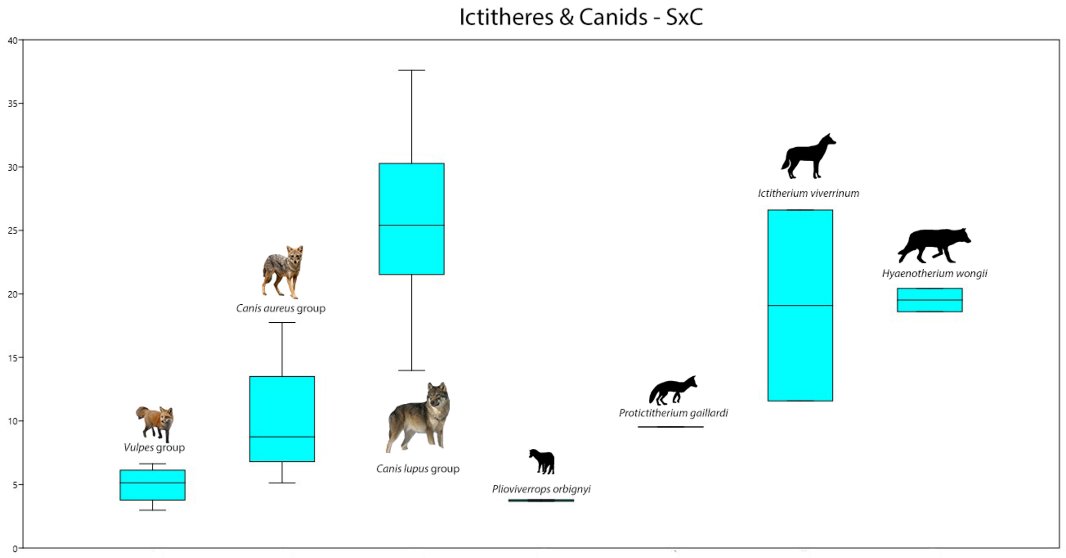


Fig. 47: Canine bending strength for ictitheres and comparative canids

The Intercuspid notches of canids show a clear stable increasing towards the hypercarnivorans. *Plioviverrops* fits in the borders between the *Vulpes* and *Canis* *aureus* groups. The two large ictitheres again have similar averages (with *Ictitherium* again having significant variability), fitting better with the group of hypercarnivorans.

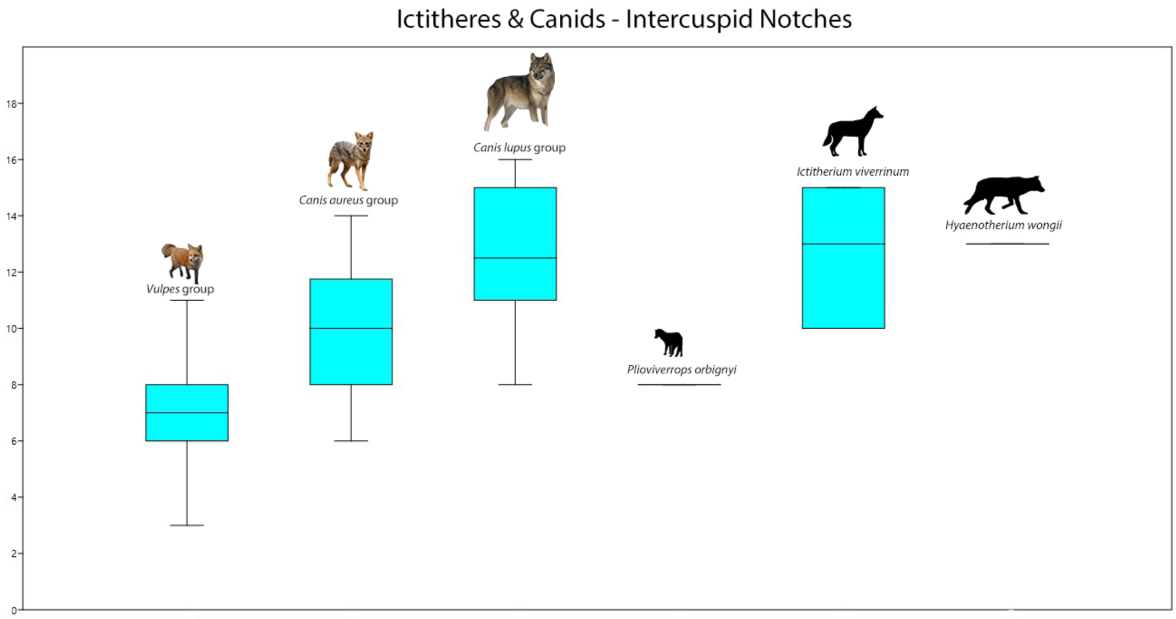


Fig. 48: Intercuspid notches for ictitheres and comparative canids

The relative area of upper cheek teeth (UGR) is not very variable in canids (Fig. 49). The ictitheres seem to have lower values than the canids, with a decreasing succession through *Plioviverrops*-*Ictitherium*-*Hyaenotherium*. This proxy is the first to discriminate the two large ictitheres.

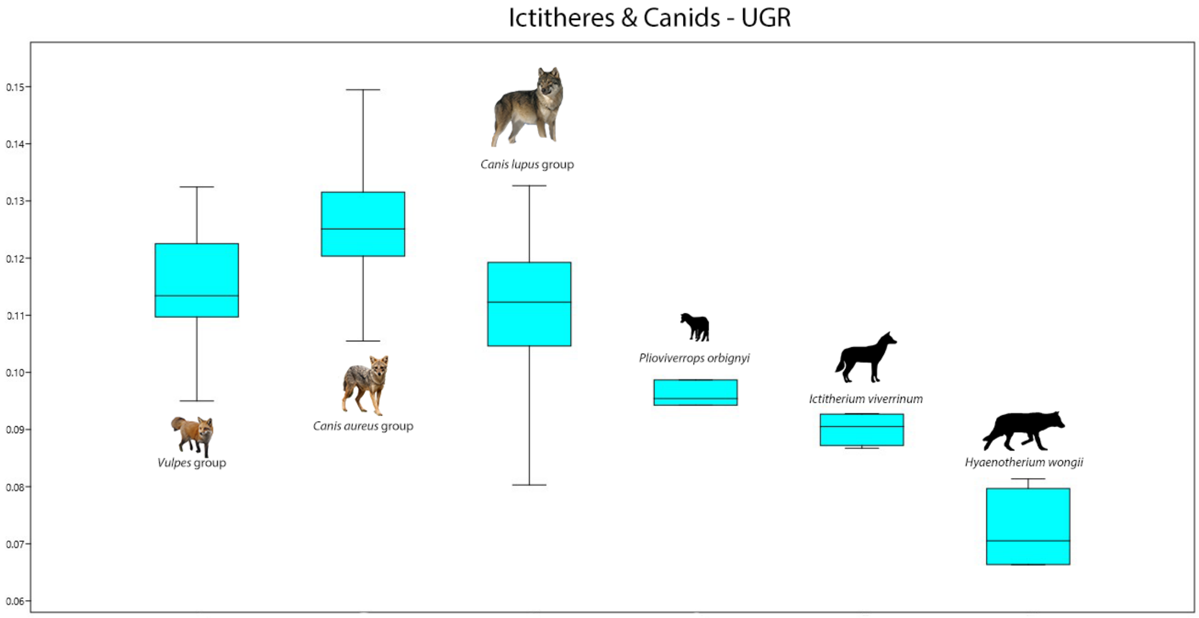


Fig. 49: UGR in ictitheres and comparative canids

A similar pattern can be seen in the relative area of lower cheek teeth (LGR) (Fig. 50). Canids again are somewhat uniform, with the hypercarnivorans preserving some low values, due to the slight reduction of grinding areas. Again, in general ictitheres preserve lower values than canids, with *Ictitherium* having higher average than *Hyaenotherium* and a wide range.

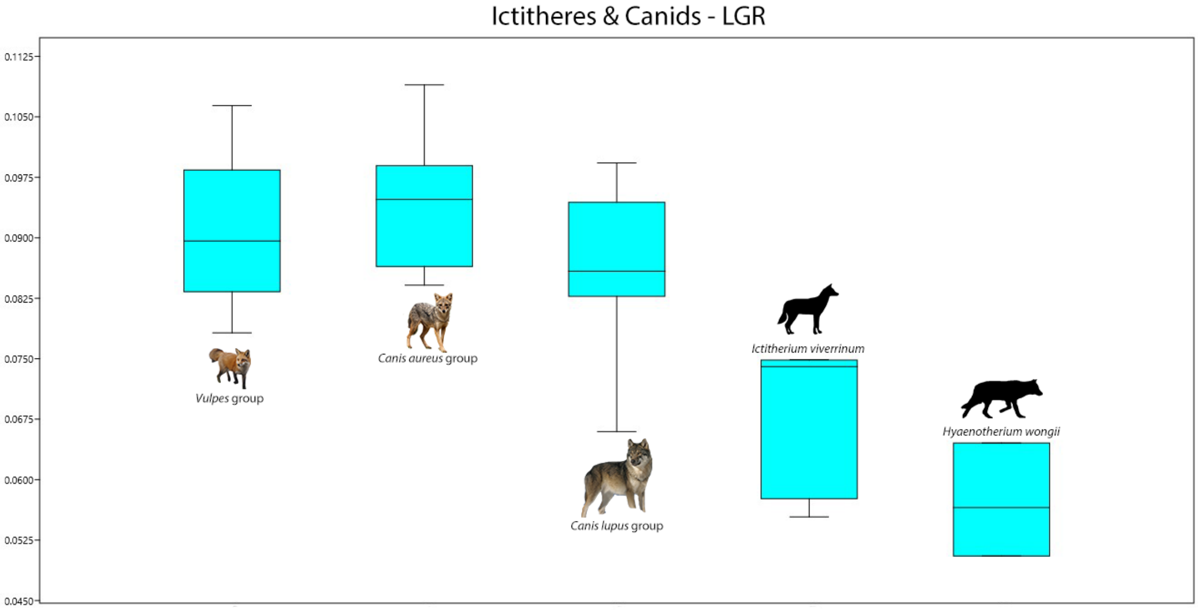


Fig. 50: LGR in ictitheres and comparative canids

The relative length of m1 talonid (M1BSZ) is increased in the canids towards the hypercarnivorans, since they require an enhanced carnassial function in their cheek teeth. The ictitheres preserve relatively high values. *Plioviverrops* is mainly in the *Vulpes* group's range again. The other three species have similar values between *Canis aureus* and *Canis lupus* group.

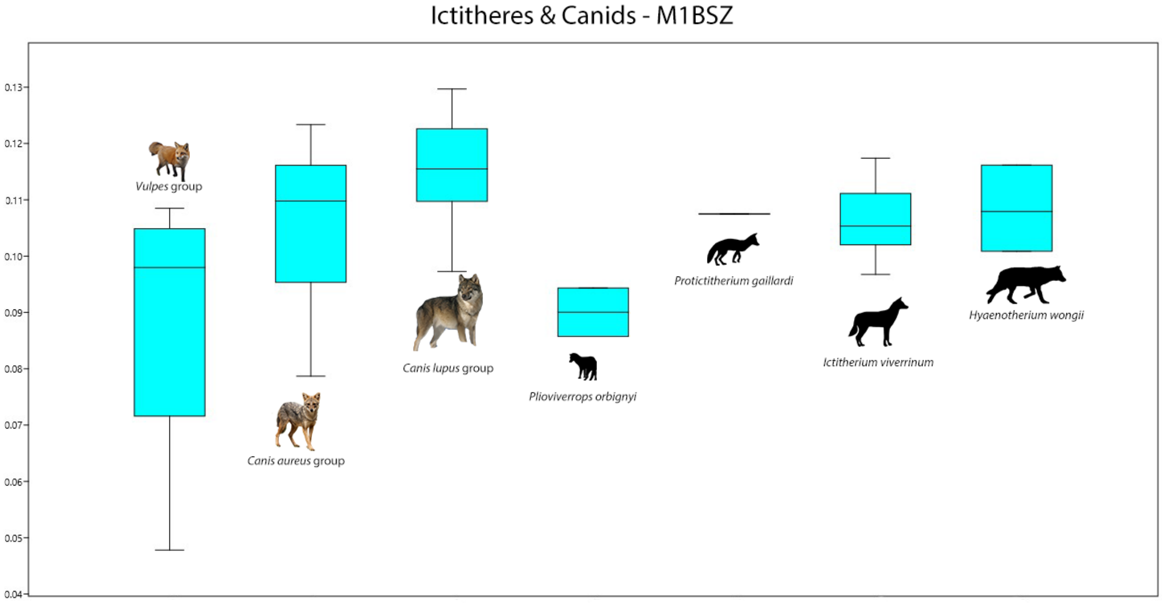


Fig. 51: M1BSZ of ictitheres and their comparative canids

The two axes of PCA based on the measurements of Popowics for the upper teeth interpreted 87.9% (PC1) and 9.1% (PC2), 97.0% of total variation. *Plioviverrops* fits into the range of *Vulpes* group. The other two ictitheres form a separate group, associated to the borders between *Canis aureus* and *Canis lupus* groups.

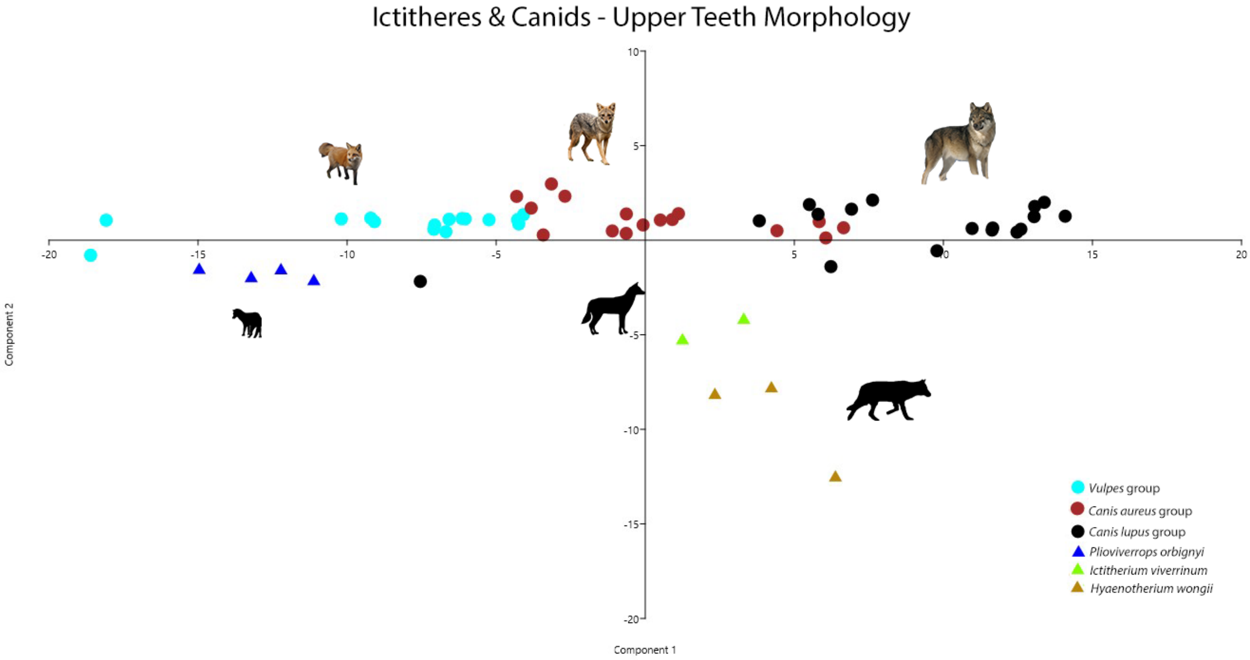


Fig. 52: PCA based on upper teeth morphology for the ictitheres and the comparative canids

The two axes of PCA based on the measurements of Popowics for the lower teeth interpreted 95.7% (PC1) and 2.0% (PC2), 97.7% in total. *Protictitherium* fits in the borders of *Vulpes* group. Again *Hyaenotherium* fits in the range between *Canis aureus* and *Canis lupus* groups, with *Ictitherium* being more similar to *Canis aureus* group.

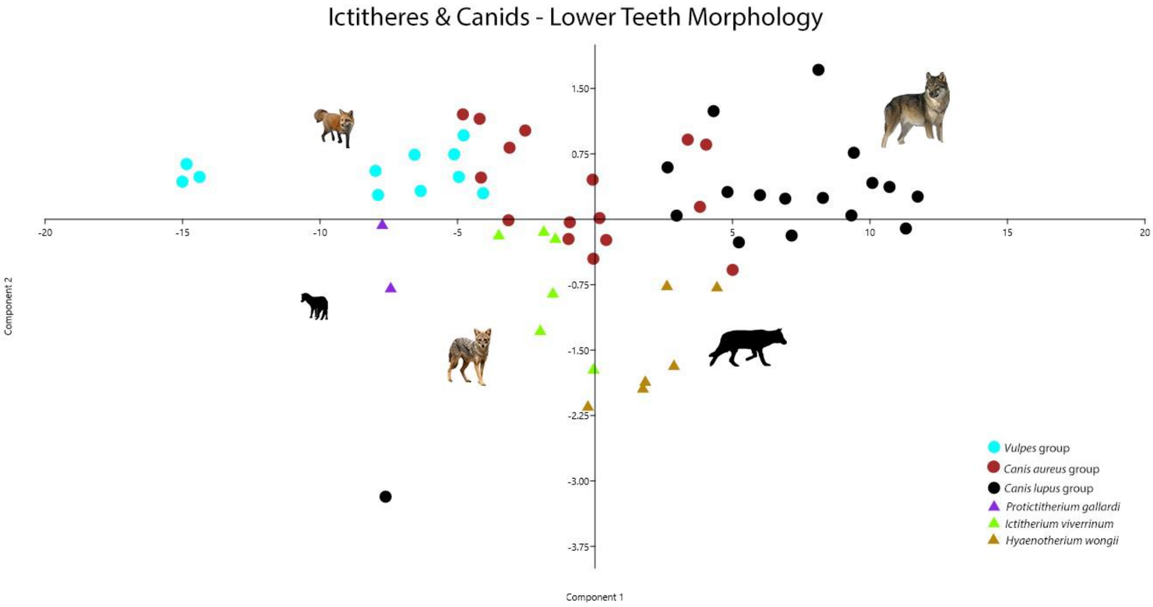


Fig. 53: PCA based on lower teeth morphology for the ictitheres and the comparative canids

The dental mesowear patterns (Table 10) of the canids' groups are not significantly different from each other. At first, it is obvious that the ictitheres (except *Protictitherium*) have higher values of wear than the studied canids in both transverse and horizontal wear. The patterns on transverse and horizontal wear are similar in all ictitheres, indicating that none of the grinding or carnassial functions was favored over the other. The high percentage of premolars' wear in *Hyaenotherium* and *Ictitherium* indicate that the transverse wear was not only a result of plant material, but probably of bones too.

Table 10: Dental Mesowear pattern of ictitheres and comparative canids.

Species	n	Transverse			Horizontal			Premolars
		1	2	3	1	2	3	
Otocyon megalotis	4	0.75	0	0.25	1	0	0	0.25
Vulpes vulpes	12	0.75	0.13	0.08	0.83	0.17	0	0.13
Urocyon cinereoargenteus	1	1	0	0	0	1	0	0
Nyctereutes procyonoides	3	0.66	0.33	0	0.66	0.33	0	0
Canis adustus	5	0.4	0.4	0.2	0.6	0.2	0.2	0.6
Canis mesomelas	4	0.75	0	0.25	1	0	0	0
Canis aureus	4	0.5	0.5	0	0.5	0.5	0	0
Canis latrans	5	0.4	0.4	0.2	0.4	0.4	0.2	0.4
Speothos venaticus	1	1	0	0	0	1	0	0
Cuon alpinus	1	1	0	0	0	1	0	0
Canis lupus	13	0.69	0.15	0.15	0.69	0.15	0.15	0.15
Lycaon pictus	4	0.25	0.75	0	0.25	0.5	0.25	0.5
Hyaenotherium wongii	16	0.25	0.44	0.31	0.31	0.31	0.38	0.75
Ictitherium viverrinum	15	0.4	0.33	0.27	0.4	0.47	0.13	0.57
Protictitherium gaillardi	2	1	0	0	1	0	0	0
Plioviverrops orbignyi	4	0.5	0	0.5	0.75	0.25	0	0

Results: Combining these results with teeth morphology (Figs. 54 and 55) it is clear that ***Hyaenotherium wongii*** was more similar to the extant coyote in most parameters (body mass, canine bending strength, endocranial volume, bite force), but had reduced upper molars, decreasing the area used for both grinding plant material and breaking bones. ***Ictitherium viverrinum*** on the contrary was slightly smaller, in the size of a black-backed jackal (also with similar bite force, endocranial volume and canine bending strength). It had larger molar area, allowing a more opportunistic diet with a possible higher percentage of plants and possibly better exploitation of scavenging. However, the structure of hyaenid enamel of both genera is not characteristic of bone-eaters (Stefen & Rensberger, 1999), while Semenov (2008) states that the members of Hyaenotherinii "do not possess morphological adaptations to bone crushing". Despite the difference on molar area, the two species seem to have relatively similar ecological niche, which is making them difficult to coexist in high numbers. Additionally, Semenov (2008) states that the size of M2/m2 and the length of m1 talonid are very variable inside the genera. This is the cause that *Ictitherium* is abundant in Pikermi and almost absent in Samos, while the opposite is true for

Hyaenotherium. *Ictitherium* preserved very high intraspecific variability, which could be related to sexual dimorphism. Both species are found in large numbers in Samos and Pikermi respectively. Extant carnivorans (including the ecologically similar canids) are not so abundant in their ecosystems with the exception of social species. Therefore, it is possible that both species possibly were social. This fact is correlated with sexual dimorphism, since the social species are most commonly sexually dimorphic, because of the struggle for hierarchy inside the clan. ***Plioviverrops orbignyi*** and ***Protictitherium crassum/gaillardi*** seem to be even more opportunistic feeders, probably feeding in a variety of plants, small vertebrates and invertebrates. The pointed premolars of *Protictitherium* indicate that it probably was mainly an insectivore, completing its diet with plant material. All these results agree with Coca-Ortega & Pérez-Claros (2019).

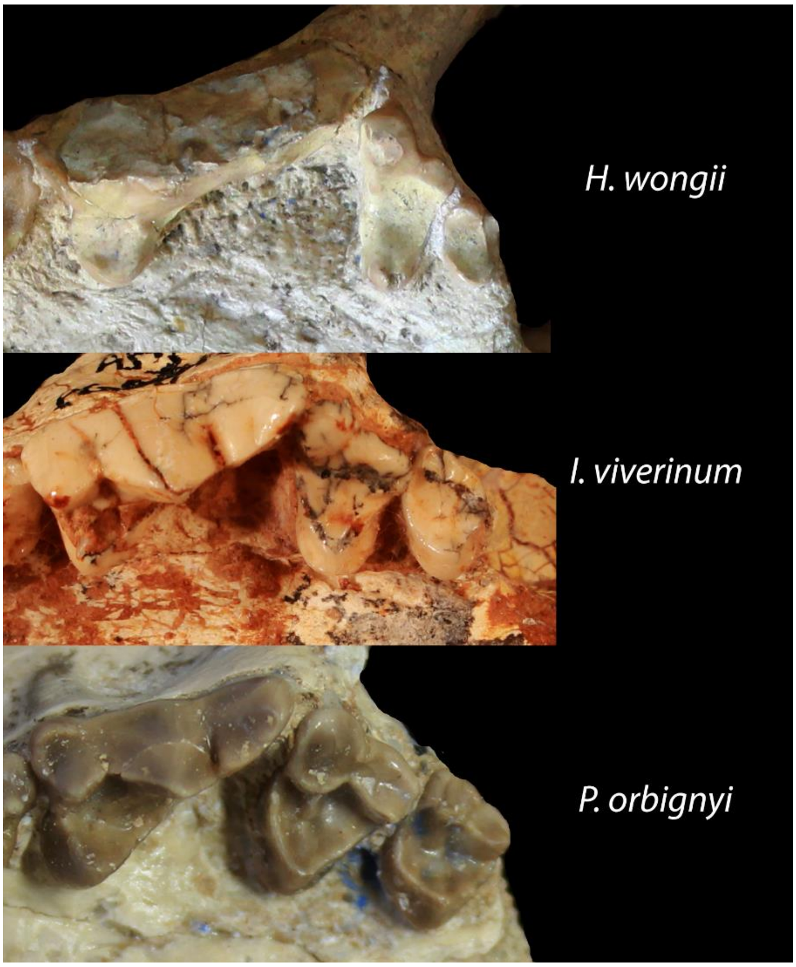


Fig. 54: Upper cheek teeth of *H. wongii*, *I. viverrinum* and *P. orbignyi*

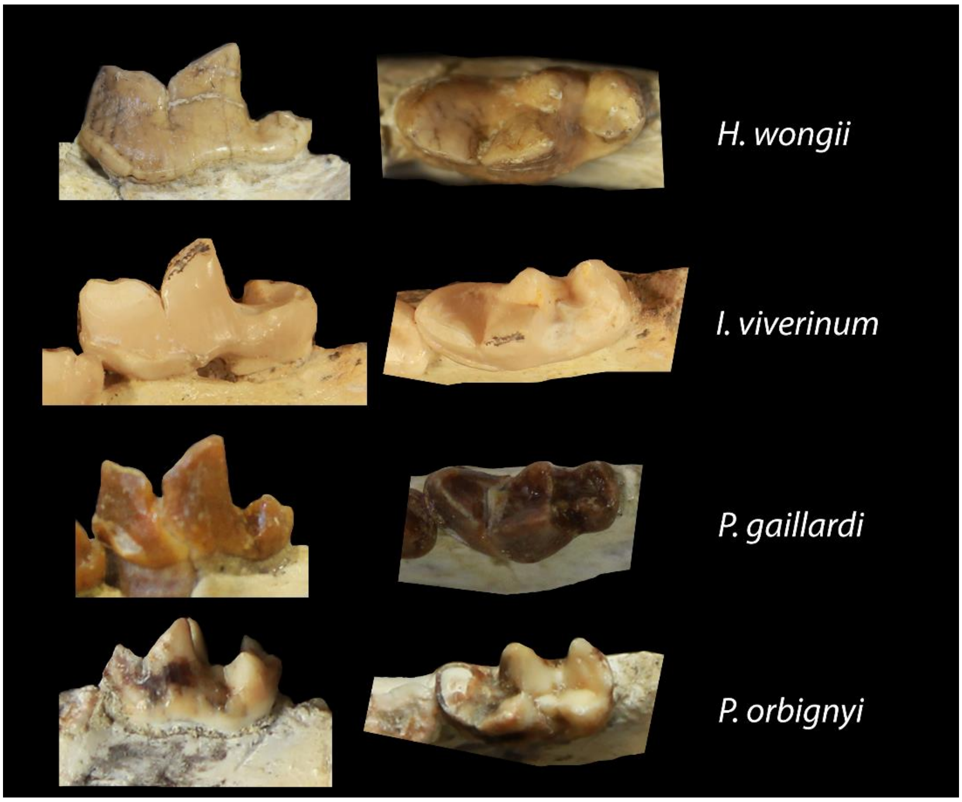


Fig. 55: m1 of *H. wongii*, *I. viverrinum*, *P. gaillardi* and *P. orbignyi*

[3] *Amphimachairodus giganteus, Paramachairodus orientalis, Metailurus major, Metailurus parvulus* & *Pristifelis attica*

During the Turolian, there were five species of felids in Pikermi: *Pristifelis attica*, *Metailurus parvulus*, *Metailurus major*, *Paramachairodus orientalis* and *Amphimachairodus giganteus* (Koufos, 2011) in successively increasing size (Fig. 56). As felids, all the species are here considered to be strict carnivorans. *Pristifelis* belongs to Felinae and the latter four species belong to Machairodontinae. The genus *Metailurus* is considered one of the most primitive lineages of felid sabertooths (Spassov & Geraads, 2014), *Amphimachairodus* was a large sabertooth in the size and body plan of *Smilodon* (Antón, 2013), while *Paramachairodus orientalis* is a scarcely known species in the size of *Metailurus major*, but with more advanced sabertooth adaptations (Salesa et al., 2010). *Pristifelis attica*, as a feline, is considered the most slender species, while the sabertooths were significantly more robust.

Using m1 length (Van Valkenburgh, 1990) to calculate the body mass for the five Pikermian felids, it is obvious that there is a gradual increase is size towards the most derived sabertooths. The only species that have similar body masses are *Paramachairodus orientalis* and *Metailurus major*.

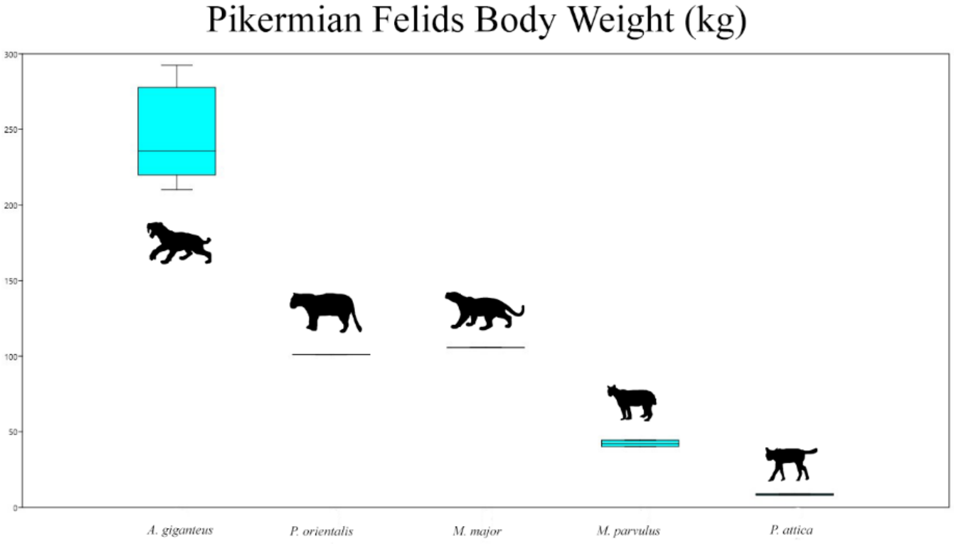


Fig. 56: Body mass of Pikermian felids

This difference in body mass affects also their bite force. In Fig. 57, it is visible that the bite force of *Amphimachairodus giganteus* is similar to the extant lions and tigers. *Metailurus major* had a canine bite force intermediate between *Panthera pardus* and *Panthera onca*, while *Metailurus parvulus* presents values similar to extant lynxes and caracals.

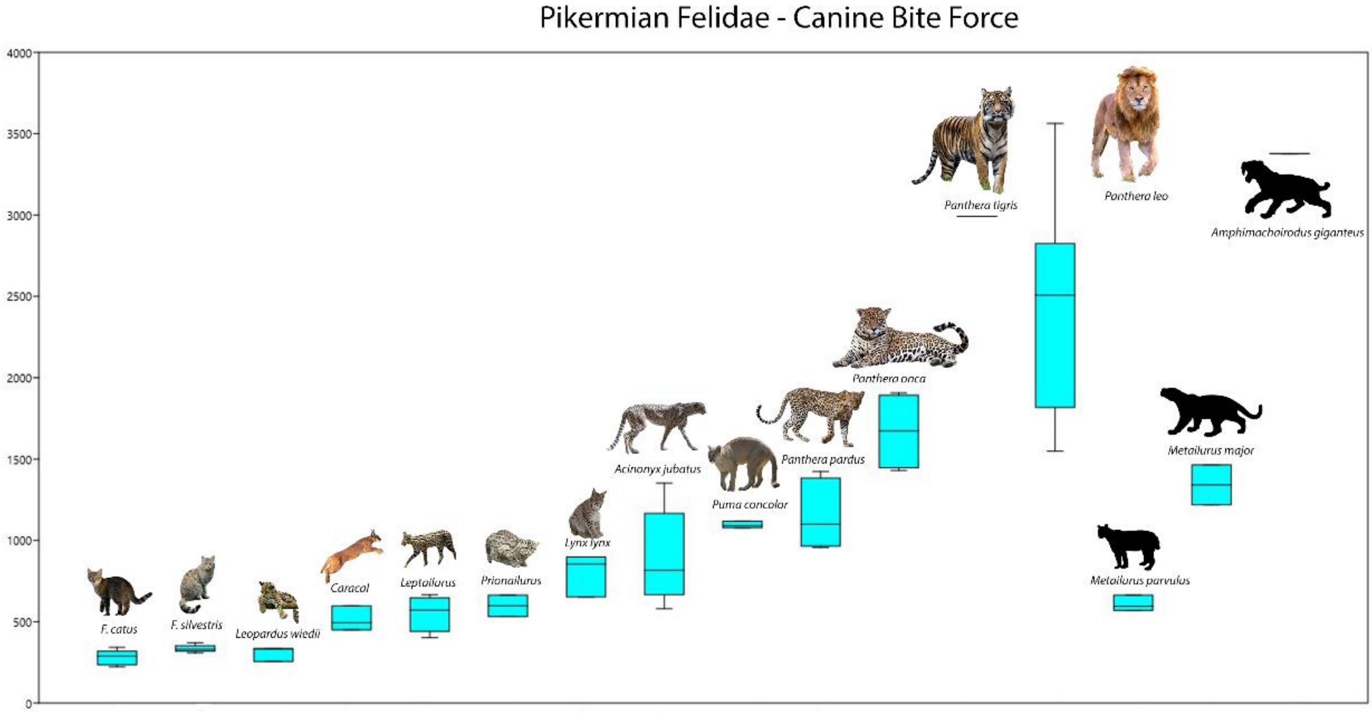


Fig. 57: Canine bite force of Pikermian felids and comparative extant Felidae

The most characteristic feature of sabertooths are their upper canines. The shape of the cross-section of the canines of the Pikermian felids (Fig. 58) follows the general trend of sabertooth evolution, where more evolved forms have more laterally compressed canines. This trait enables them to grow in height, but lowers the relative bending strength. The bending strength in the anteroposterior plane seems to be similar to the extant felids (Fig. 59). However, the bending strength in the mediolateral plane is lower, especially in *A. giganteus* (Fig. 60). The most primitive *M. parvulus* doesn't have significantly lower SxC, while *M. major* presents an intermediate state.

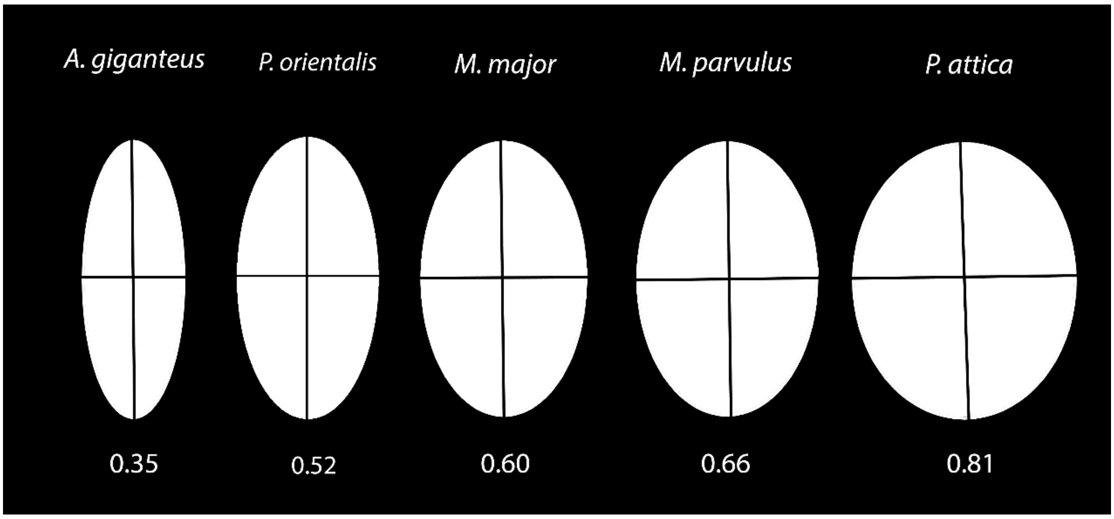


Fig. 58: Cross-section and the ratio of width to length for the upper canine of Pikermian felids. Data for *P. orientalis* by Salesa et al. (2010).

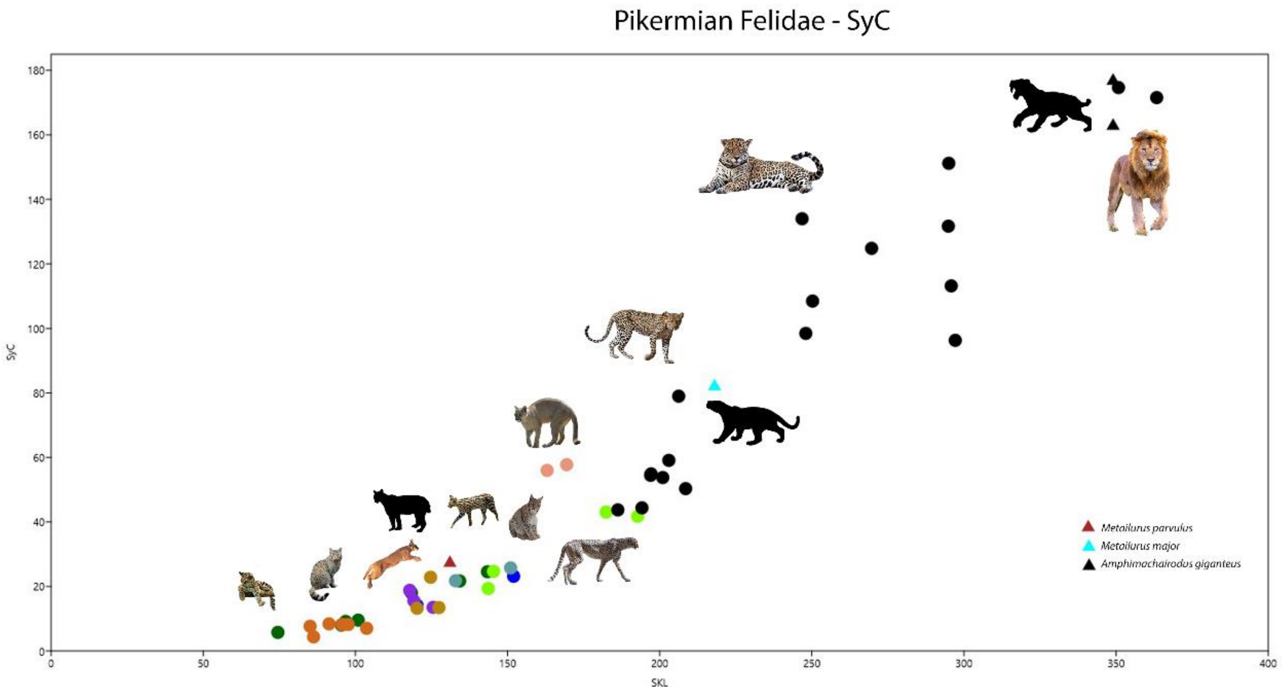


Fig 59: Canine anteroposterior bending strength in Pikermian and extant Felidae

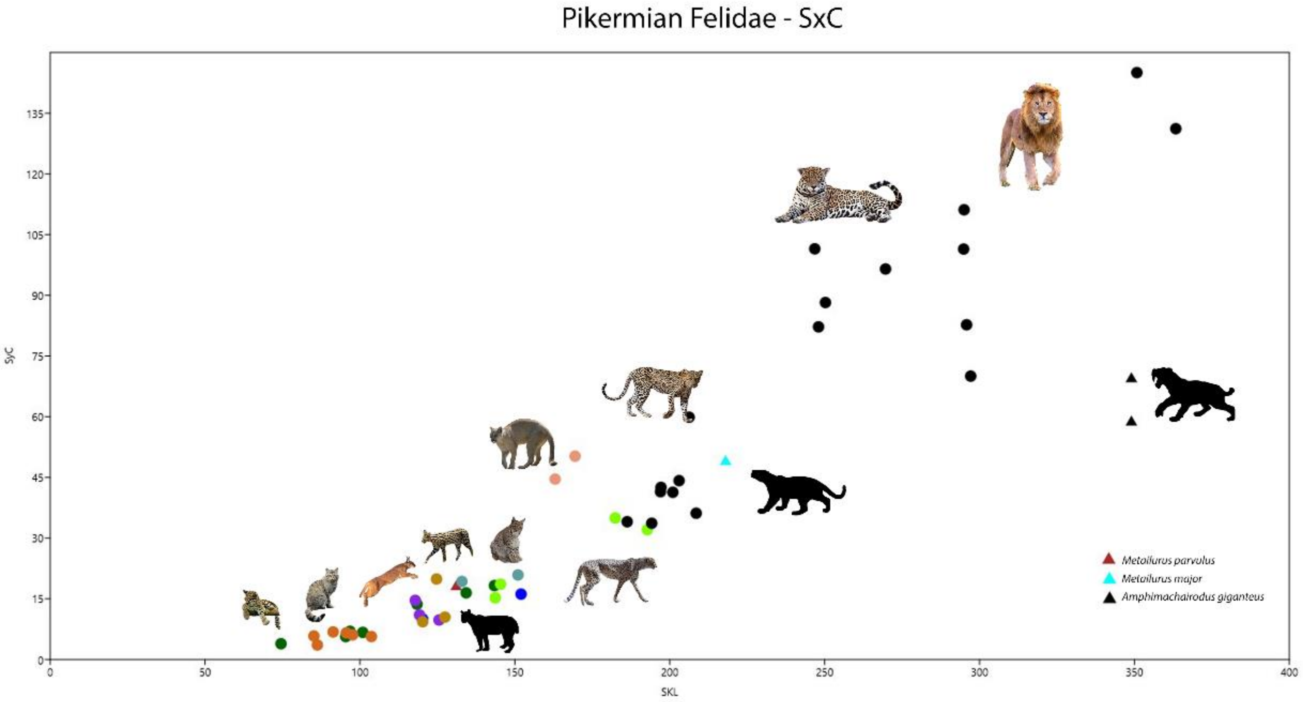


Fig 60: Canine mediolateral bending strength in Pikermian and extant Felidae

The relative rostrum width seems to be stable in all the felids. Therefore, it doesn't offer any results on their ecomorphology.

In general, machairodontines have similar or slightly higher values on their intercuspid notches than the pantherines. The difference is significant when comparing *Panthera leo* (snp3 & p4 average 8.75) with *Amphimachairodus giganteus* (snp3 & p4 14). This trait probably doesn't offer any ecomorphological results, but it definitely is one more tool in the arsenal of sabertooths jaws, in order to shear flesh.

It is believed that the most derived sabertooths had the ability to make a canine-shear bite. During this bite, the front teeth kept the victims neck steady, the lower jaw acted as a stabilizer and the upper canines were driven slowly in the neck of prey and then the neck drove the head backwards, shearing the victim's trachea (e.g. Antón, 2013). This function is connected with many traits in the skulls, mandibles, teeth and necks of the sabertooths. The mastoid region near the ear offers an attachment area for the muscle of the neck, which are responsible for the backword drive (Antón et al., 2004).

A comparison of mastoid musculature was made between the following species: *Puma concolor, Felis catus, Panthera leo, Amphimachairodus giganteus, Metailurus major* and *Metailurus parvulus*. These species reveal the differences between the three major subfamilies of Felidae (Felinae, Pantherinae & Machairodontinae). In the following paragraphs the mastoid region of all the aforementioned species will be described, focusing in possible differences in the mastoid musculature system, using the two main processes of the auditory region, the mastoid process and the paraoccipital process.

Puma concolor: The paraoccipital process is equal in size with the mastoid process. Both processes are reduced, very thin and peel-like, nearly adjusted to the auditory bulla. The paraoccipital process is not extended over the auditory bulla. It is slightly caudally inclined (approximately 10^{o}). The fossa between the paraoccipital process and the occipital condyle is oval-shape and deep. The reduction of the paraoccipital process creates larger space between itself and the occipital condyle.

The mastoid process is similar in size and shape with the paraoccipital process. It preserves a fold in the middle of its craniocaudal axis. A small surface between the two processes exists, but it is slightly rough.

The temporomandibular joint is almost vertical.

Felis catus: The morphology of the two processes in the domestic cat is almost similar with the case of the cougar. However, the paraoccipital process seems faintly more reduced, while the distance between the paraoccipital process and the occipital condyles is slightly smaller. The temporomandibular joint is forward-faced.

Panthera leo: The paraoccipital process is not peel-like (like in felines), but it projects approximately 10 mm from the auditory bulla. It is inclined caudally, approximately 50^{o}. In the plane of the ventral margin of the auditory bulla its width is 9 mm. A groove is present in its medial portion and a protuberance exists between the process and the occipital condyle. The fossa is deep and continuous towards the occipital condyle. The distance between the paraoccipital process and the occipital condyle is moderate.

The mastoid process is large, almost reaching the height of the auditory bulla. Its surface can be either smooth or rough. A slight groove can be seen in the ventral portion of the supraoccipital crest, which ends in the dorsal portion of the paraoccipital process.

Metailurus parvulus: The base of the paraoccipital process is bulb-like, but its tip is broken. It seems to be caudally inclined, as in the lion. Its base is closely situated to the highest plane of the auditory bulla, so it must have been extended over it. The fossa between the paraoccipital process and the occipital condyle is shallow.

The mastoid process is slightly enlarged, with its lateral-dorsal portion being rough, but not very broad. The articular surface of the mastoid process seems to be away from the bulla, near the lateral end of the nuchal crest.

The temporomandibular joint is almost similar with the pantherine morphotype.

Metailurus major: The paraoccipital process is smaller than in the lion and it is nearly horizontal. Its base is significantly broad. Its tip is broken, but it can be assumed that it extended at least 6 mm from the auditory bulla. This extension of the process reduces the distance between the process and the occipital condyle. The fossa is deep continuing towards the occipital condyle. The supraoccipital crest is laterally broken.

The mastoid process is developed and almost vertical to the paraoccipital process. It reaches the height of the auditory bulla. Its shape is completely different from the shape of the mastoid process of the lion. It is not as broad as in the lion, whereas it is laterally orientated, forming available attachment space cranially-dorsally. This space is significantly rough.

The temporomandibular joint seems slightly more vertical than in felines and pantherines, intermediate between *Metailurus parvulus* and *Amphimachairodus giganteus*.

Amphimachairodus giganteus: The paraoccipital process is short, completely horizontal and faintly hook-like. It is extended approximately 9 mm from the auditory bulla. The fossa between the paraoccipital process and the occipital condyle is relatively shallow, when compared with the fossa of *Metailurus major*.

The mastoid process is very robust. Its lateral-dorsal portion is similar with the one seen in the lion, extending laterally, and not as inclined as in *Metailurus*. A strong protuberance is present ventrally of the external auditory meatus. This protuberance is very robust, equal in size (or even slightly larger) with the main body of the mastoid process. Both tips are bulb-like, flattened and rough. The occiput is relatively high.

The temporomandibular joint is clearly more vertical than in any other species.

It is clear that there are three distinct groups in the felids: the felines (*Puma concolor* and *Felis catus*), the pantherine (*Panthera leo)* and the sabertooth (*Amphimachairodus giganteus*). It is interesting that *Metailurus* resembles a transition between *Felis* and *Amphimachairodus*, while *Metailurus major* is more derived than *Metailurus parvulus*.

It seems that the most clear differences, in terms of areas, between the four morphotypes are the caudal-lateral portion of the mastoid process (hosting the ventral part of *m. obliquus capitis cranialis*) and the cranial-lateral portion of the mastoid process (hosting the *m. sternomastoideus*).

Panthera leo and *Amphimachairodus giganteus* share a broad caudal-lateral portion of the mastoid process, resulting to larger attachment area for *m. obliquus capitis cranialis*. This particular muscle is considered to have the most major impact in the canine shear bite (Antón et al. 2004). It is, therefore, reasonable to be developed in *A. giganteus*. It is moderately developed in *Metailurus major*, but it doesn't preserve similar morphology with the two former species. It is oval-shaped and slender. The most special characteristic is that it is not directed laterally, but almost completely caudally. Therefore, *m. obliquus capitis cranialis* would form an almost right angle at the base of the mastoid process.

The cranial-lateral portion of the mastoid process is relatively larger in the lion and significantly larger in *A. giganteus*. In the lion it is visibly rough. The most special characteristic in *A. giganteus* is the protuberance cranially to the mastoid process. The attachment area of *m. sternomastoideus* seems to be continuous between the mastoid process and this protuberance, becoming significantly larger. There is no such protuberance in *Metailurus major*, but it is special that this area is inclined laterally and not cranially. In combination with the caudally inclined posterior area of the mastoid process, it seems that the whole process is inclined laterally-caudally.

The length and the direction of paraoccipital process also differ between the groups, but it doesn't seem to affect significantly the attachment area of the muscles. The only observable difference is the slightly smaller tip of the paraoccipital process in the felines, resulting to faintly smaller attachment area for *m. digastricus*.

The more vertical orientation of the temporomandibular joint in *A. giganteus* is reasonable, because, as a true sabertooth, it requires higher gape angle than primitive *Metailurus*, felines or lions. The almost vertical angle in *Puma concolor* can be possibly explained by intraspecific variation, a factor probably very important in such delicate and fragile structures.

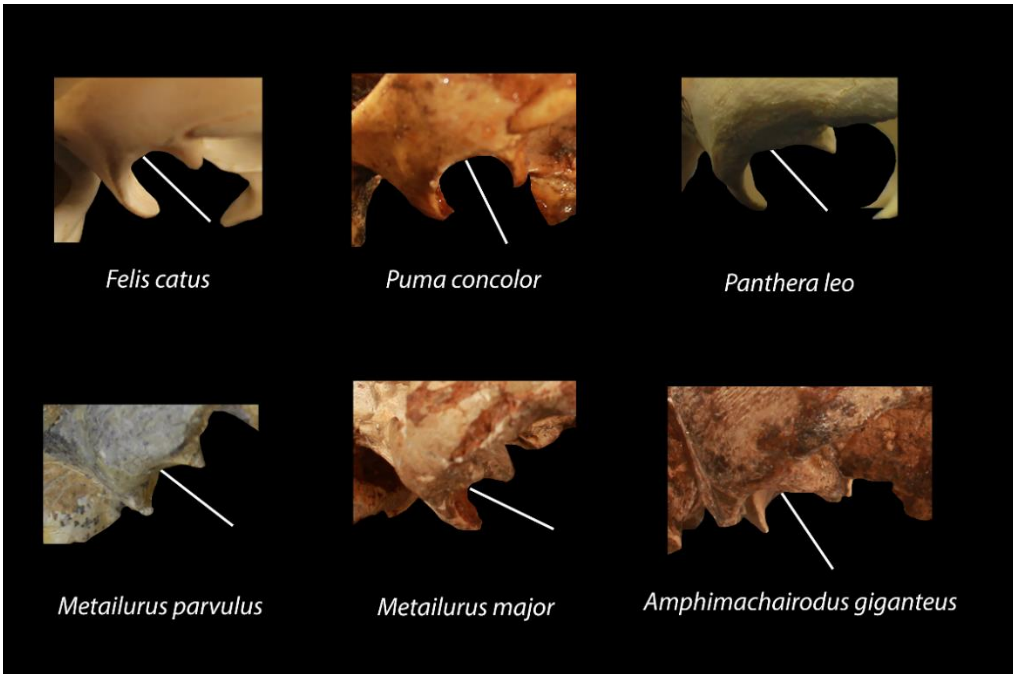


Fig. 61: Temporomandibular joint orientation in the studied felids.

Salesa et al. (2005) summarize the traits associated with canine-shear bite. In Table 11, the traits in primitive and derived machairodontines are resumed.

Table 11: (1) Upper canines (1 = elongated and flattened), (2) Mandibular symphysis (1 = vertical), (3) Coronoid process (1 = reduced), (4) Mastoid process (1 = antero-ventrally faced, 2 = and enlarged), (5) Paraoccipital process (1 = reduced), (6) Atlas (1 = backward projected wings and lengthened spinous processes), (7) Cervical vertebrae (1 = lengthened corpus) and (8) Cervical vertebrae transverse processes (1 = enlarged). Data based on: *M. parvulus* (this study & Roussiakis et al., 2006), *M. major* (this study and Kovatchev, 2001), *A. giganteus* (this study), *Y. garevskii* (Spassov & Geraads, 2014), *P. ogygia* (Salesa et al., 2005), *P. orientalis* (Salesa et al., 2010 and this study), *M. cultridens* (Christiansen & Adolfssen, 2007; Antón, 2013), *H. latidens* (Antón & Galobart, 1999), *M. aphanistus* (Antón et al., 2004) and *S. fatalis* (Werdelin, 2018).

Species/Characters	1	2	3	4	5	6	7	8
Metailurus parvulus	0	0	0	0	0	0	0	0
Metailurus major	0	0	0	0	0	0	0	0
Yoshi garevskii	0	1	?	1	0	?	?	?
Promegantereon ogygia	0.5	1	0.5	0.5	0.5	0	0.5	?
Paramachairodus orientalis	0.5	1	?	?	?	?	?	?
Machairodus aphanistus	1	0	0	0	0	?	?	?
Amphimachairodus giganteus	1	0	0.5	2	1	?	?	?
Megantereon cultridens	1	1	1	2	1	1	1	1
Homotherium latidens	1	1	1	2	1	1	1	1
Smilodon fatalis	1	1	1	2	1	1	1	1

It is clear that there are distinct differences between the studied species in several lineages. The species of *Metailurus* are the most primitive ones, with their close relative *Yoshi* preserving the first derived characters. *Promegantereon* and *Paramachairodus* act as an intermediate stage, between the metailurins and the derived sabertooths. It is interesting that the lineage of *Machairodus*-*Amphimachairodus* doesn't possess all of the traits (*Machairodus* don't even possess the majority of them), despite the fact that they were large-sized sabertooths. The Pleistocene species are the most derived, possessing all the characters associated with canine-shear bite.

Results: The studied species are able to coexist, because they differ in many characteristics. At first (with the exception of *M. major* and *P. orientalis*), they have different body sizes, providing them the ability to hunt different prey. This factor also affects bite force. The most interesting fact is that the four largest species represent gradual stages in sabertooth evolution, a fact seen in their upper canine shape and in their mastoid region. This differentiation probably was an ecologically dividing force, separating the species in their ability to chase prey and to perform a canine-shear bite.

[4] *Martes woodwardi, Sinictis pentelici, Promephitis lartetii, Parataxidea maraghana, Promeles palaeattica,* Mustelidae n. sp. & *Plioviverrops orbignyi*

The diversity of Turolian mustelids is very high, but most of the species are represented by very few specimens: *M. woodwardi* (2), *S. pentelici* (1), *E. laticeps* (only postcranial) etc. Therefore, their complete taxonomy and comparative ecology are not clear enough. This fragmentary nature doesn't allow for a comparison between all the species in every proxy. *Plesiogulo crassa* is also a mustelid in the Turolian, but its large size makes it inappropriate for study over interspecific competition. On the contrary, *Plioviverrops orbignyi* was added as this species is small enough to be compared ecologically with the mustelids.

The Mustelidae n. sp. has been found in Pikermi, during past excavations. Its code number is PA4879/91 and it consists of a skull with two associated hemimandibles. It has been previously labelled as *Sinictis pentelici*, but it actually is probably a member of Melinae and not Mustelinae. Some of its unique features are enough to consider it as (at least) a separate species.

Fig. 62: The skull and the two hemimandibles of Mustelidae n. sp. (PA4879/91) in occlusal and lateral view.

Using m1 length and skull length, the body masses of all the species were the following:

Table 12: Body masses of Turolian mustelids based on m1

Species	n	Body Mass based on m1	n	Body Mass based on SKL
Promeles palaeattica	6	4.8-9.1 kg	4	3.9-6.3 kg
Mustelidae n. sp.	1	3.9 kg	1	6.9 kg
Parataxidea maraghana	1	4.2 kg	1	4.6 kg
Martes woodwardi	2	4.3-5.4 kg	0	-
Sinictis pentelici	1	6.2 kg	0	-
Plioviverrops orbignyi	3	3.2-7.3 kg	0	-
Promephitis lartetii	1	2.1 kg	1	1.2 kg

The only size differentiation between the species is probably *Promephitis lartetii* which is clearly smaller than the other species. All the other taxa weight approximately 5 kg, confirming the problem of coexistence.

The bite force could be calculated only for *Parataxidea*, *Promeles* and *Plioviverrops* (Fig. 63). Both *Parataxidea* and *Promeles* have similar bite forces, between the main ranges of *Meles* and *Martes*. *Plioviverrops* has slightly lower values that fall into the range of *Martes*.

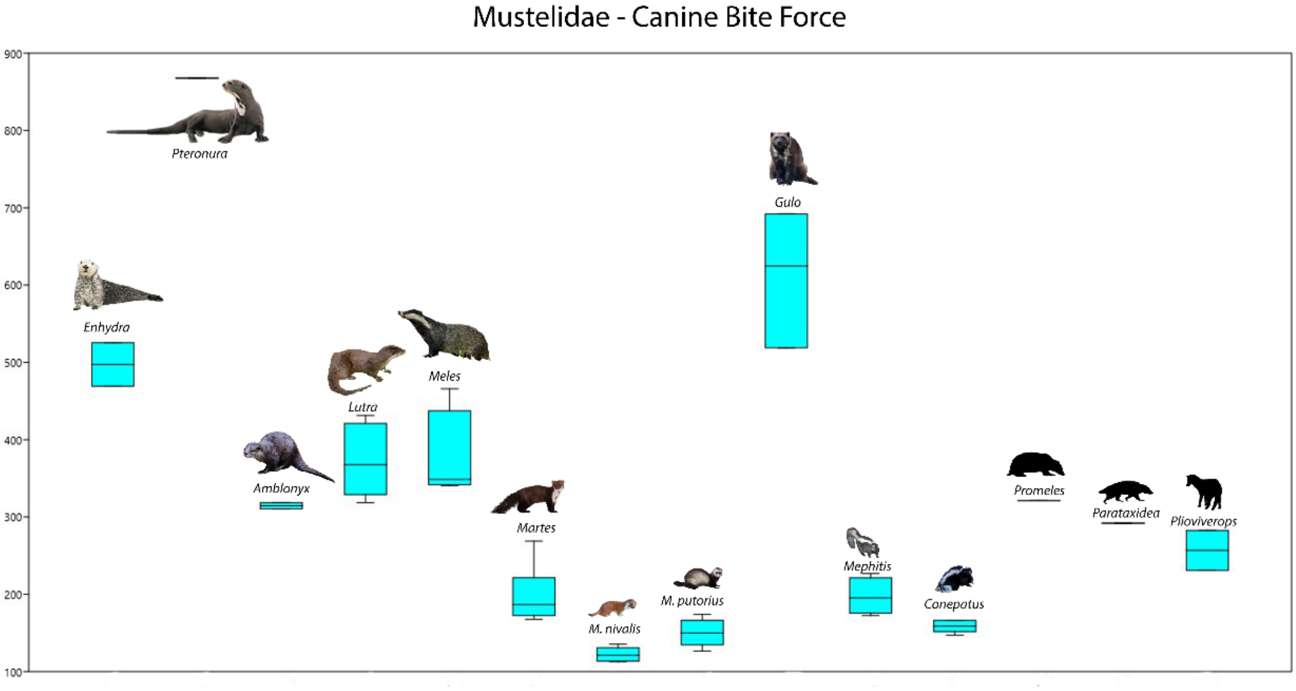


Fig. 63: Canine bite force for the studied mustelids

The upper canine bending strength could be measured only in *Promeles*, *Plioviverrops* and *Promephitis* (Fig. 64). Again *Promeles* fits between *Martes* and *Meles* and *Plioviverrops* is somewhat lower, fitting in the values of *Martes*. *Promephitis* has a relatively high value fitting with the higher borders of extant Mephitidae.

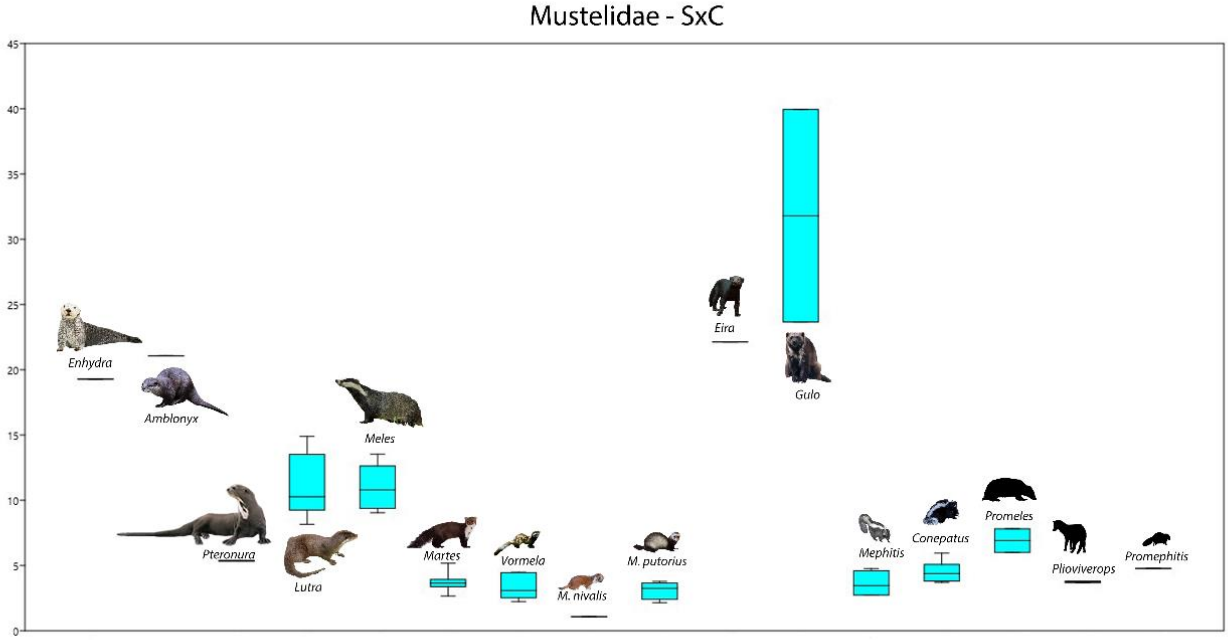


Fig. 64: Canine bending strength for the studied mustelids

The endocranial volume was calculated for *Promeles*, *Parataxidea* and *Plioviverrops*. *Promeles* again fits between *Martes* and *Meles*. *Parataxidea* has significantly higher value for endocranial volume, fitting with the ranges of *Meles* and *Eira*. *Plioviverrops* again seems to fit with *Martes* and *Mustela putorius*.

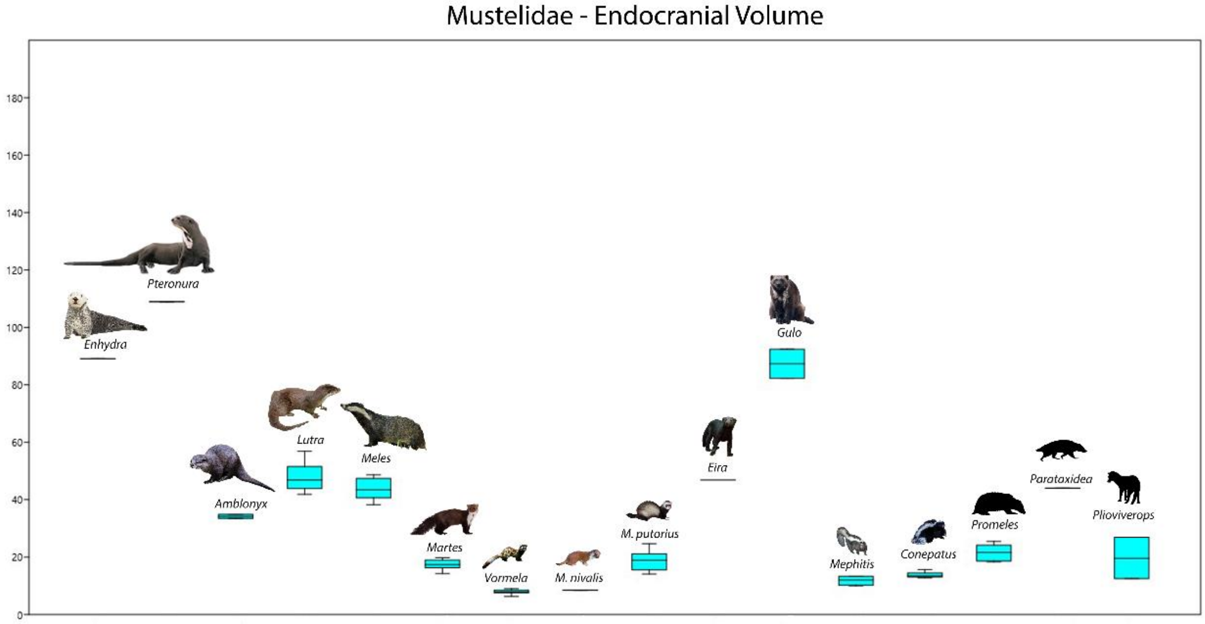


Fig. 65: Endocranial volume for the studied mustelids

The relative rostrum width of *Promeles* is similar to *Meles*, while the new species of Mustelidae has a relatively narrower rostrum, fitting in the values of *Martes*, but this is probably caused because of the deformation of the skull. *Plioviverrops* preserves high variability, but it preserves low values in general, again fitting with

Martes. *Promephitis* preserves very high value, near the highest borders of *Conepatus*.

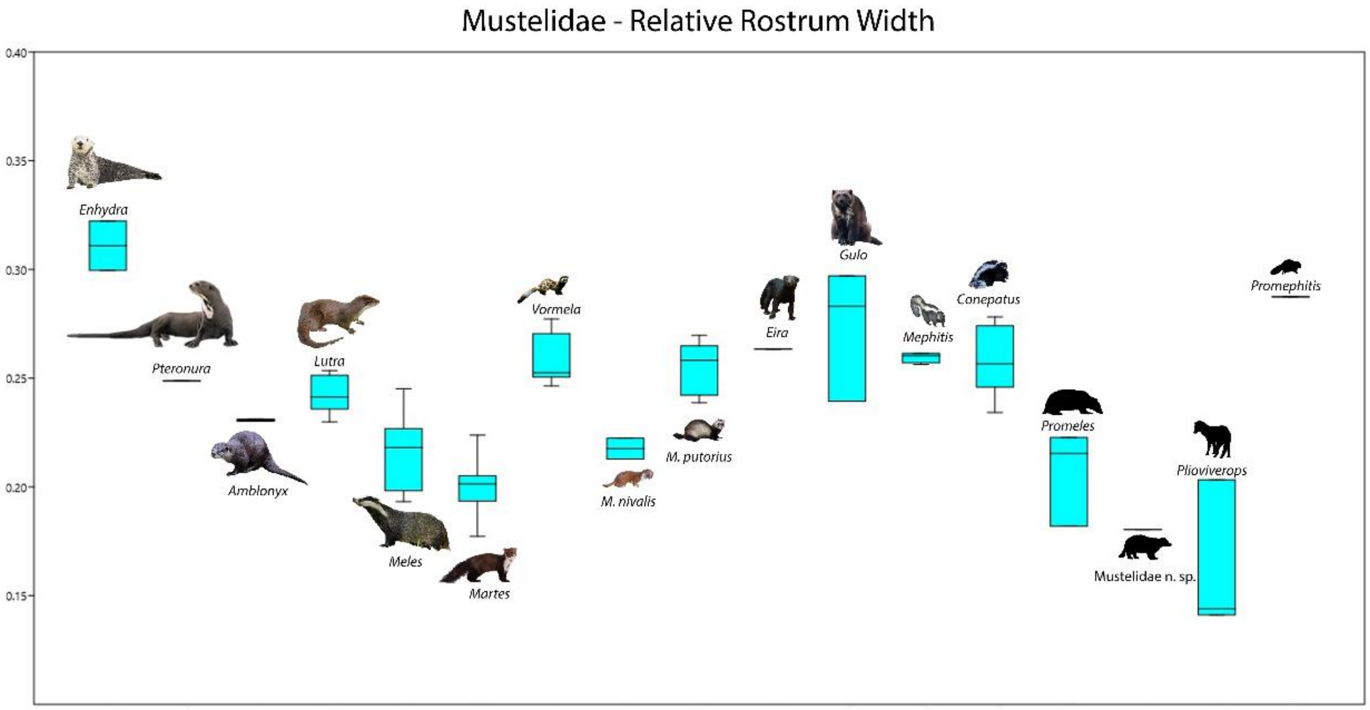

Mustelidae - Relative Rostrum Width

Fig. 66: Relative rostrum width for the studied mustelids

The most widely calculated value of Intercuspid notches was the sum of the notching scores for p4, which was calculated for *Promeles*, Mustelidae n. sp., *Plioviverrops*, *Sinictis* and *Promephitis*. There are no clear patterns in terms of dietary strategies. The values of *Promeles* fit between the ranges of *Martes* and *Mustela putorius*. The new species has lower values, similar with the extant *Meles*. *Plioviverrops* probably retains its ancestral hyaenid/viverrid trait, having high values of this proxy, indicating high carnassial function in p4. *Sinictis* has values similar to *Mustela putorius*. Finally, *Promephitis* has not extra cusps in its teeth, except for the main central cusp. The extant skunks have at least one small cusp in p4. This trait can be associated with insectivory, since the required function for killing and managing insects is not shearing, but piercing. Therefore, the accessory cusps are decreased and the central cusp is enhanced.

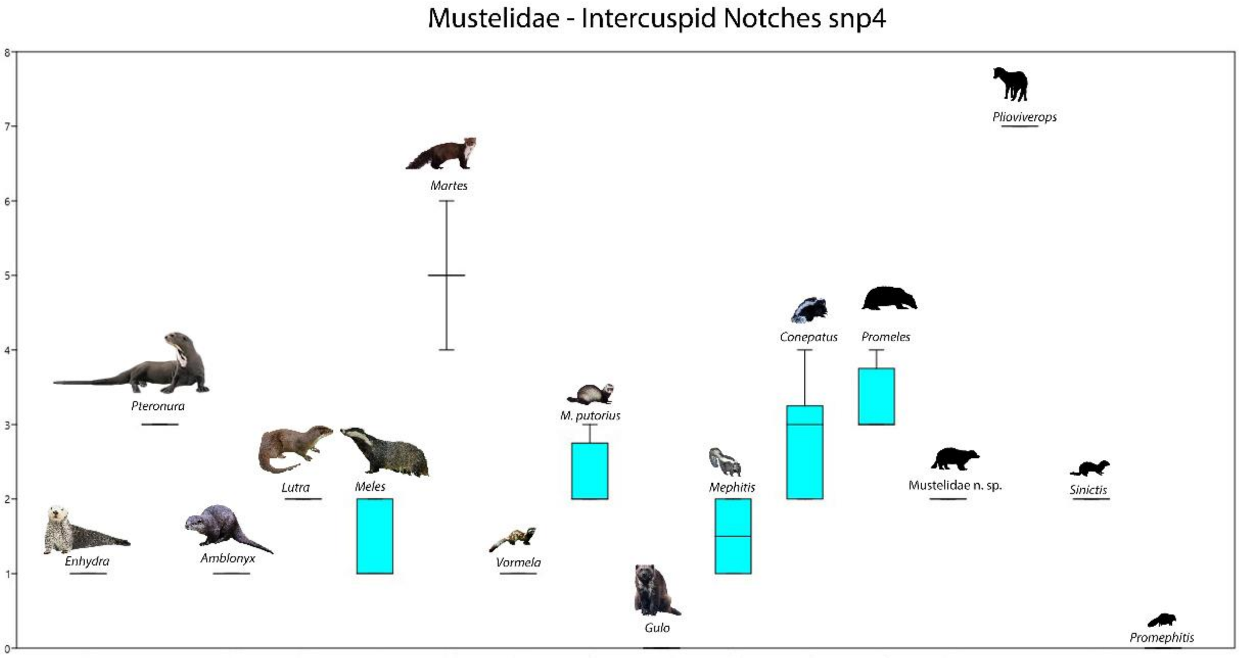


Fig. 67: Snp4 for the studied mustelids

The relative area of the upper cheek teeth (UGR) was calculated for the majority of species (Fig. 68). *Promeles* again has intermediate values between *Meles* and *Martes*, fitting better with *Meles*. The new species has lower values, fitting better with *Martes*. *Parataxidea* has very high values that fit with *Meles* and *Conepatus*. *Plioviverrops* has low value of UGR, fitting with the most carnivorous species, such as *Vormela* and *Mustela*. *Promephitis* has slightly lower value than *Mephitis*, fitting also to *Martes*.

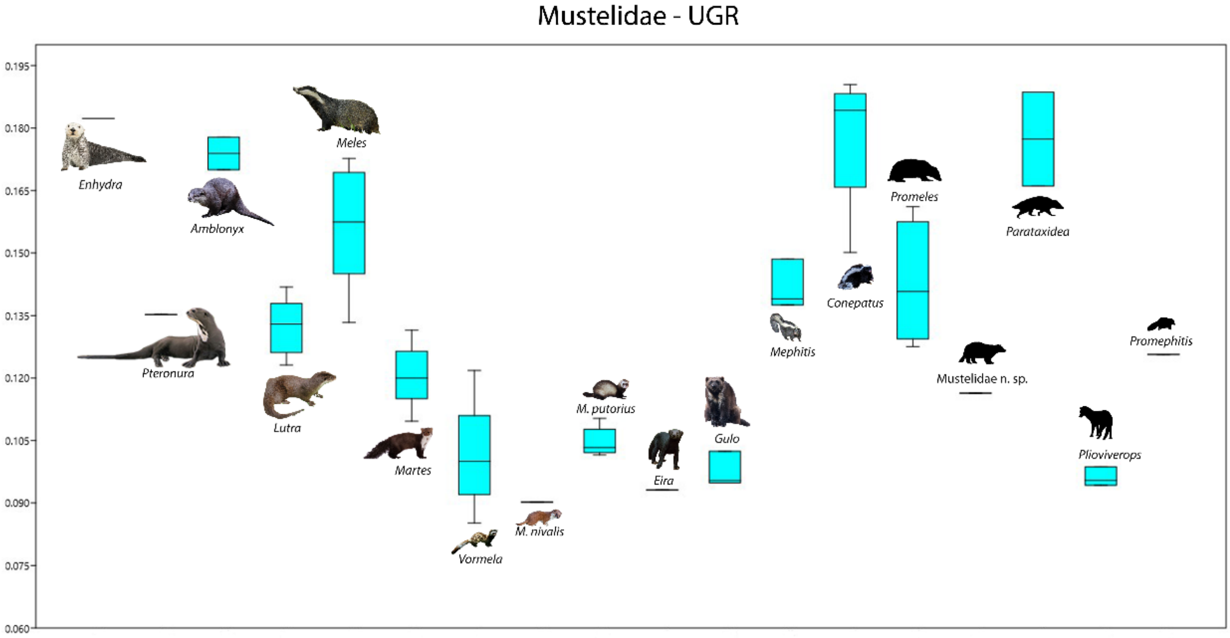


Fig. 68: UGR for the studied mustelids

The relative area of lower cheek teeth (LGR) was calculated for *Promeles*, *Sinictis* and *Promephitis* (Fig. 69). *Promeles* again fits between *Martes* and *Meles*. *Sinictis* has a very low value, comparable only with the mostly carnivorous *Mustela nivalis*. *Promephitis* has value similar to the extant *Mephitis*.

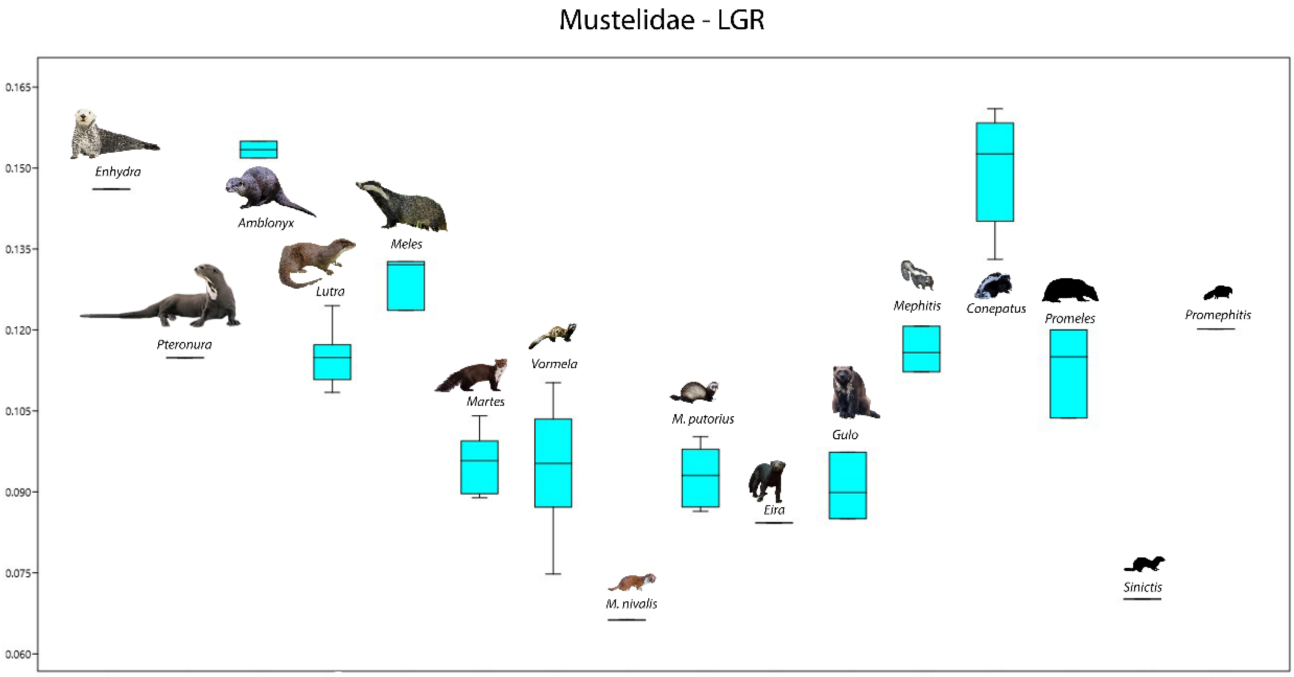


Fig. 69: LGR for the studied mustelids

The relative length of m1 talonid (M1BSZ) was calculated for *Promeles*, Mustelidae n. sp., *Plioviverrops*, *Sinictis* and *Promephitis*. *Promeles* presents very high values, but it also preserves high variability. These values can be explained by the contemporary shortening of the rostrum and the enhancing of m1 size in an allometric pattern. The new species of Mustelidae also has relatively high values, not reaching the levels of *Meles*. *Plioviverrops* has high values indicating a high percentage of meat in its diet. The same is true for *Sinictis* and *Promephitis*.

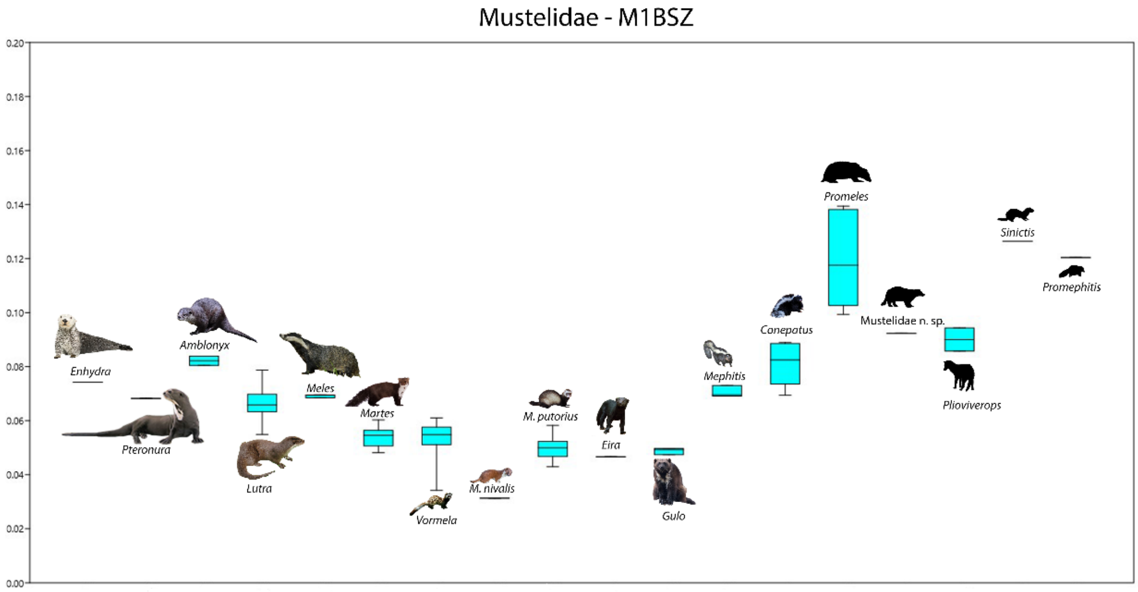


Fig. 70: M1BSZ for the studied mustelids

The PCA based on Popowics for the upper teeth interpreted 74.6% and 17.2% for PC1 and PC2 respectively, 91.8% in total. *Promeles* and *Parataxidea* again fit between *Martes* and *Meles*, with *Parataxidea* more closely associated to *Meles*. Again *Plioviverrops* fits close to the values of *Martes* and *Promephitis* fits into the range of extant Mephitidae.

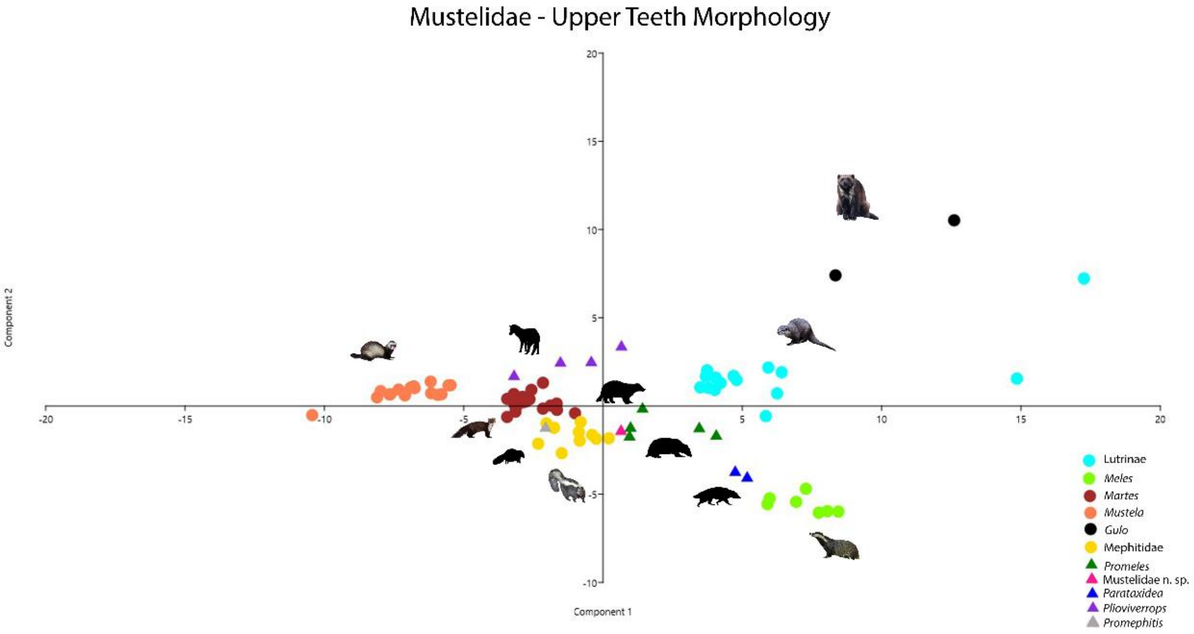


Fig. 71: PCA for the upper teeth of the studied mustelids

The PCA based on Popowics for the lower teeth interpreted 86.5% and 8.4% for PC1 and PC2 respectively, 94.9% in total. Again *Parataxidea* and *Promeles* fit between *Martes* and *Meles*, but now *Promeles* is more closely associated with *Meles*. This is caused because *Parataxidea* has very short m1, different from the elongated m1 of *Meles*. *Sinictis* also fits within this group. The new species fits better into the range of *Martes*, while *Promephitis* again fits into the range of extant skunks.

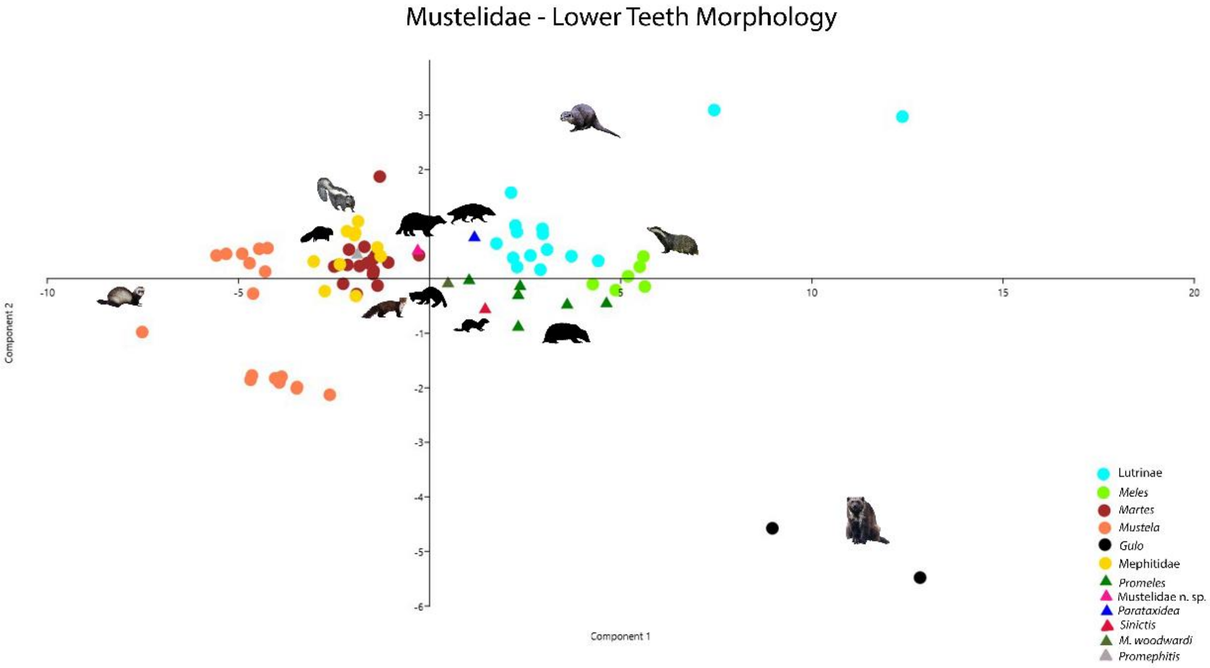


Fig. 72: PCA for the lower teeth of the studied mustelids

Because of the low number of specimens for the majority of species, a complete comparison on dental mesowear is not possible. However, some species present some interesting characters. Four of the nine *Promeles* specimens had extreme transverse wear, which was associated with extreme horizontal wear in only one specimen. On the other hand, there was one specimen (AMPG-No Nu), which had extreme horizontal wear and almost no transverse wear. One of the three specimens of *Parataxidea* (MTLA-283) also had extreme transverse wear, associated with only moderate horizontal wear. *Plioviverrops* and *Promephitis* also had mostly transversally worn molars, associated with moderate horizontal wear.

When looking at the morphology of the upper teeth it is clear that there is a cline between *Parataxidea* and *Plioviverrops*. *Plioviverrops* has the most restricted molars, reducing its grinding surfaces, while its P4 is very carnassiform. Probably the next step is *Promeles*, whose M1 is moderately enlarged, but its P4 is still carnassiform. In the new species M1 is also enhanced, but P4 is not so carnassiform as in *Promeles*, with more rounded metacone and wider protocone. A similar pattern is seen in *Promephitis*. Finally *Parataxidea* has a very large M1 and P4 has also formed a large grinding area.

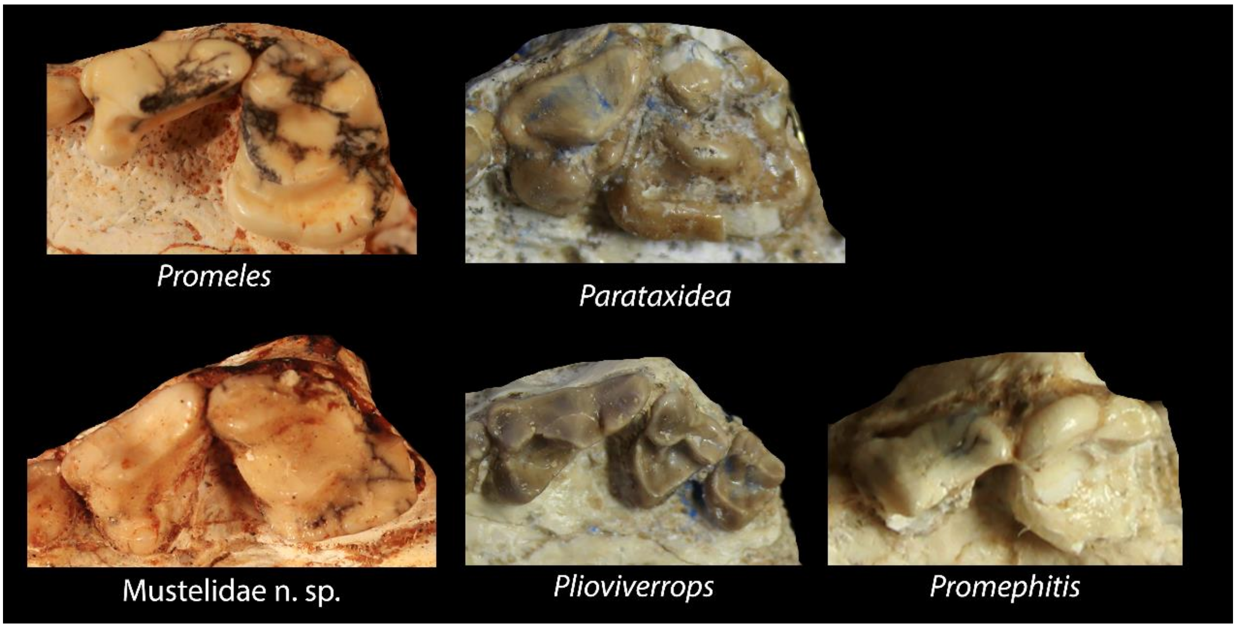


Fig. 73: Upper cheek teeth morphology of *Promeles*, *Parataxidea*, Mustelidae n. sp., *Plioviverrops* and *Promephitis*

The morphology of m1 in the mustelids is very informative since it includes both grinding and carnassial areas. In this tooth there is again a cline between *Martes* and *Parataxidea*. *Martes* has the largest trigonid, but the cingulum of the talonid is developed. The trigonid of *Sinictis* is slightly smaller, but there is no clear cingulum in the talonid. The m1 of *Plioviverrops* is typical of a small ictithere with significant carnassiform trigonid and with a wide talonid with high cusps. The next stage is probably the new species, which has a slightly reduced trigonid and a developed talonid. The same is visible in *Promeles*, but in a higher degree. Finally the m1 of *Parataxidea* has almost no carnassiform portion and resembles the bunodont molars of other omnivorous species.

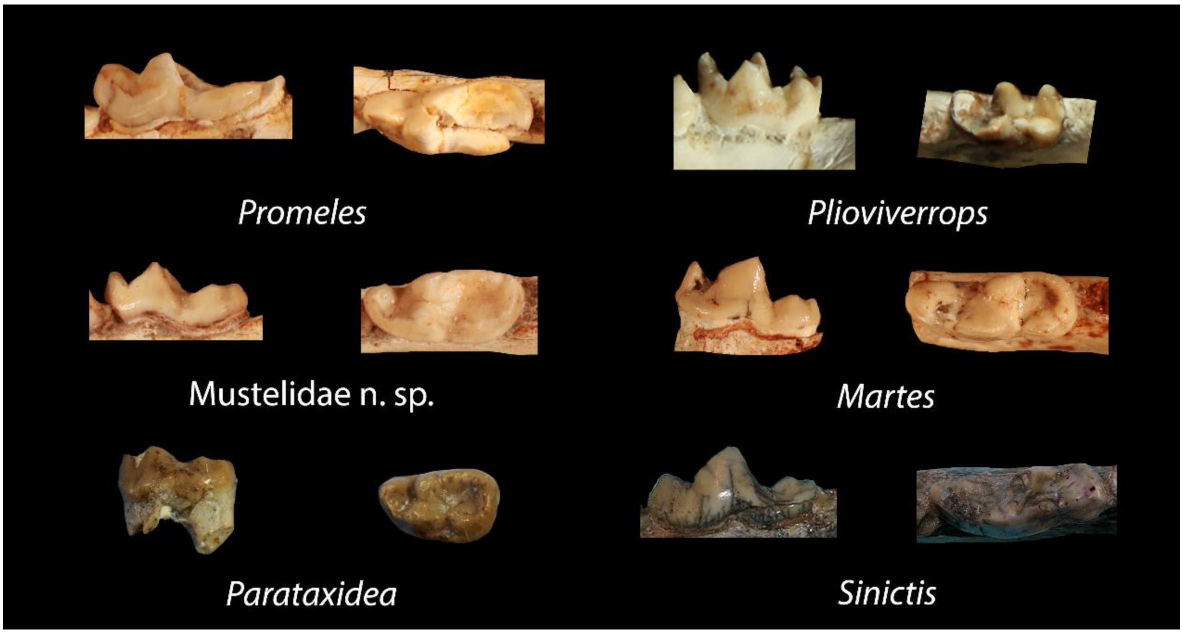


Fig. 74: Lower first molar morphology of *Promeles*, Mustelidae n. sp., *Parataxidea*, *Plioviverrops*, *Martes woodwardi* and *Sinictis pentelici*

Results: ***Promeles palaeattica*** is probably a species intermediate between the typical *Martes*-like mustelid and the extant badgers in terms of size and ecomorphology. This means that plant material was indeed a large percentage of its diet, but it probably retained the ability to hunt small prey like birds or rodents. A similar niche is proposed for both ***Parataxidea maraghana*** and **Mustelidae n. sp.**, with *Parataxidea* also preserving interesting features such as high endocranial volume and high-cusped premolars, probably associated with insectivory. ***Plioviverrops orbignyi*** probably had a niche similar to extant *Martes*, preferring plants as approximately 30-40% of its diet, but mainly hunting small prey, such as birds and small mammals. ***Sinictis pentelici*** and ***Martes woodwardi*** probably had similar roles with *Plioviverrops*, possibly being even more carnivorous. ***Promephitis lartetii*** seems to have a niche similar to extant skunks, with a diet based on insects and plants. Since no cranial material of ***Enhydriodon latipes*** is known, no comparison based on these proxies can be made. However, since all modern Lutrinae are fish-eaters and shell-eaters, it possibly occupied a similar niche.

Therefore, there are four groups of mustelids: the otter (*Enhydriodon*), the skunk (*Promephitis*), the *Martes*-like group (*Martes*, *Plioviverrops* and *Sinictis*) and the *Meles*-group (*Promeles*, *Parataxidea*, Mustelidae n. sp.). These groups occupy distinct niches, so they can coexist. However, the species inside the two latter groups occupied similar niches, so they must be competitive with each other. This fact explains the low abundance of *Sinictis*, *Martes*, Mustelidae n. sp. and *Parataxidea*, with *Promeles* and *Plioviverrops* being the most dominant species in each group. One explanation for this is that they were the more generalist species in terms of ecomorphology inside their groups, able to exploit more opportunities. This competition may explain the absence of *Promeles* in Samos and the absence of *Parataxidea* in Pikermi in the studied collections.

[5] *Homotherium latidens* & *Megantereon cultridens*

Unfortunately, there are only few remains of these Villafranchian sabertooths, in order to make a proper comparison based on specimens found in Greece. A great new skull of *Homotherium* has been found recently in Dafnero (Kostopoulos et al., 2019) and a publication has been submitted. However, there are a lot of data in literature, enough to make a short discussion.

At first, these two genera are not of the same size. The following boxplot can be made by comparing the m1 length values found in literature.

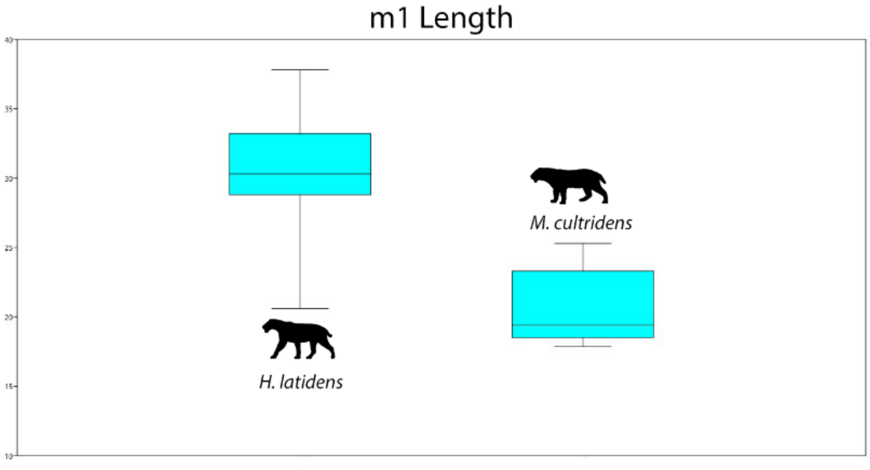


Fig. 75: m1 Length of *Homotherium latidens* and *Megantereon cultridens*. Data from: Antón et al. (2004), Christiansen & Adolfssen (2007), Palmqvist et al. (2007), Sardella & Iurino (2012), Serangeli et al. (2015) and present study.

However, the most interesting factor that differentiates these two genera is that *Homotherium* is considered a scimitar-toothed sabertooth, while *Megantereon* is considered a dirk-toothed sabertooth. These two morphotypes of sabertooths differ in the following characteristics: The scimitars had long, fine-serrated canines and short, powerful limbs, whereas the dirks had shorter, less-serrated canines and longer, thinner limbs (e.g. Martin, 1980; Martin et al., 2000).

These differences indicate a different way of life. Despite being larger, *Homotherium* is considered to be more cursorial than *Megantereon*, which is considered as an ambush predator, similar to the majority of heavily-built sabertooths (Antón, 2013).

Another distinguishing trait is the mechanics of their killing bite. Figueirido et al. (2018) have concluded that the killing bite of *Homotherium* was somewhat intermediate between the suffocating bite of extant felids and the instant canine-shear bite of the dirk-toothed sabertooths. This means that the canines of this genus were able to withstand more pressure during killing the prey than in *Megantereon*, which was more vulnerable to breakage.

Concluding, we can’t say that the two genera were feeding on different prey-targets. However, their different killing methods (both chase/ambush and semi-suffocation/canine-shear bite) may have provided different abilities on preying different species.

[6] *Chasmaporthetes lunensis* & *Pliohyaena perrieri*

These two hyenas coexisted in the early Villafranchian of Europe. *Chasmaporthetes lunensis* has been found in Greece only in the locality of Dafnero (Koufos, 1993) since today. *Pliohyaena perrieri* has also been found in very few localities in Greece: in Seklso, Gerakarou (Koufos, 2014) and Petralona Cave (Baryshnikov & Tsoukala, 2010). They were both large sized hyenas, so their coexistence is a matter for discussion.

Similar to the case of *Homotherium* and *Megantereon*, these two hyenas differed in their way of living and hunting. *Chasmaporthetes* is considered a cursorial, light-weighted hyena, able to chase down prey for a long distance, similar to today’s wolves or African wild dogs (e.g. Coca-Ortega & Pérez-Claros, 2019). In fact, it is the only species of Hyaenidae able to reach the Americas, and one important element for this transition probably was its cursorial lifestyle (Wang & Tedford, 2008). Antón et al. (2006) describe a very well-preserved skull of *C. lunensis*, pointing its similarities with extant *Lycaon*. They finally conclude that this species was probably a social hunter of medium-sized ungulates, retaining the ability to crack bones of carcasses.

On the other hand, *Pliohyaena perrieri* is one typical crocutoid hyena, with very large premolars, well-adapted to a scavenging lifestyle. It is thought that this species was also not as social as extant *Crocuta crocuta*, following a more solitary way of living, similar to *Hyaena hyaena* (Vinuesa et al., 2015).

Therefore, this case is in a way similar to the comparison between *Lycyaena* and *Adcrocuta*, with a cursorial and a crocutoid hyena. However, this time the cursorial species is thought to be social and the crocutoid solitary and not the opposite as it’s seen in the Turolian.

[7] *Canis apolloniensis, Canis etruscus, Canis arnensis, Lycaon lycaonoides, Vulpes praeglacialis*

The locality of Apollonia has offered a large amount of carnivoran fossils, including five species of canids (Koufos, 2018): *Vulpes praeglacialis*, *Lycaon lycaonoides*, *Canis etruscus*, *Canis arnensis* and *Canis apolloniensis*. *Canis apolloniensis* at the moment has been found only in Apollonia (Koufos & Kostopoulos, 1997). It is interesting how five species of canids, and especially three species of *Canis*, were able to coexist in the same locality.

At first, based on m1 length, there is a considerable size difference between the three genera (Fig. 76). The data for *Canis arnensis* were taken by Baryshnikov & Tsoukala (2010) and Bartolini Lucenti & Rook (2016). The data for *Lycaon lycaonoides* were taken by De Grossouvre et Stehlin (1912), Sotnikova (2001), Moullé et al. (2006), Madurell-Malapeira et al. (2013) and personal measurements. The data for *Vulpes praeglacialis* were taken by Baryshnikov & Tsoukala (2010) and present study.

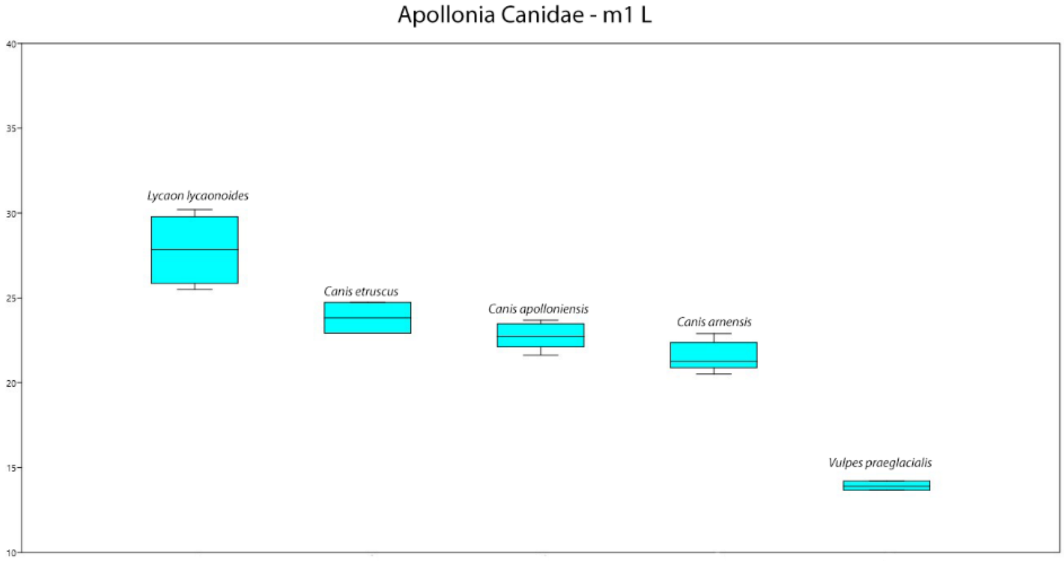


Fig. 76: m1 length as indicator of body mass in the canids of Apollonia

The bending strength of the upper canines of *Lycaon lycaonoides* and *Canis etruscus* fit well into the range of hypercarnivorans. *Canis arnensis* and *Canis apolloniensis* fit in the overlapping range between *Canis arnensis* and *Canis lupus* groups. *Vulpes praeglacialis* fits into the range of *Vulpes* group.

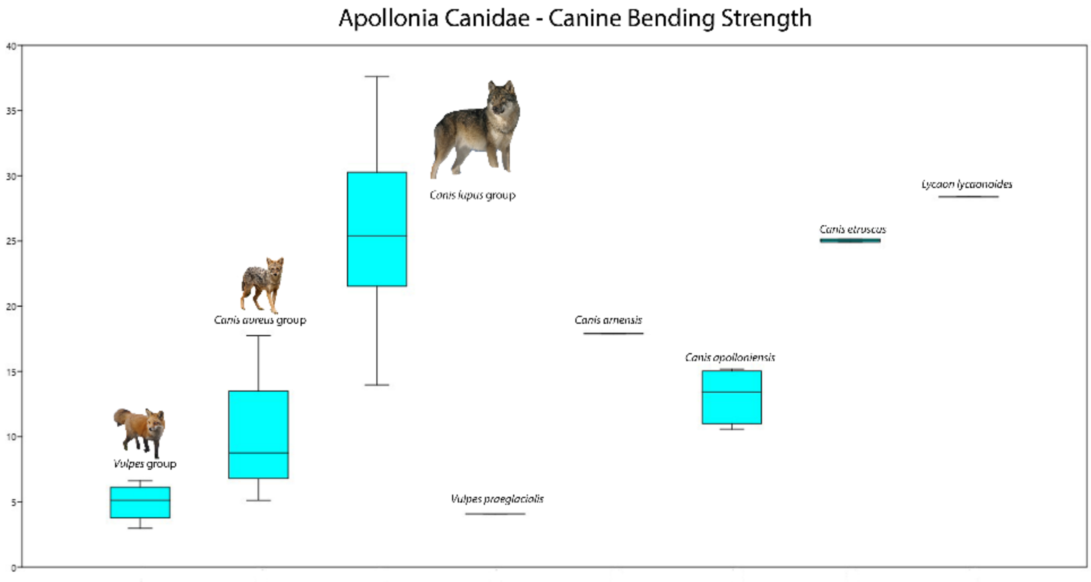


Fig. 77: Canine bending strength in Apollonia canids

The intercuspid notches of the extant canids offer some degree of ecomorphological differentiation (Fig. 78). The value of *Vulpes praeglacialis* fits better with the average of *Vulpes* group. *Canis apolloniensis* and *Canis etruscus* fit in the overlapping area between *Canis aureus* and *Canis etruscus* group, while *Lycaon lycaonoides* is clearly in the group of hypercarnivorans.

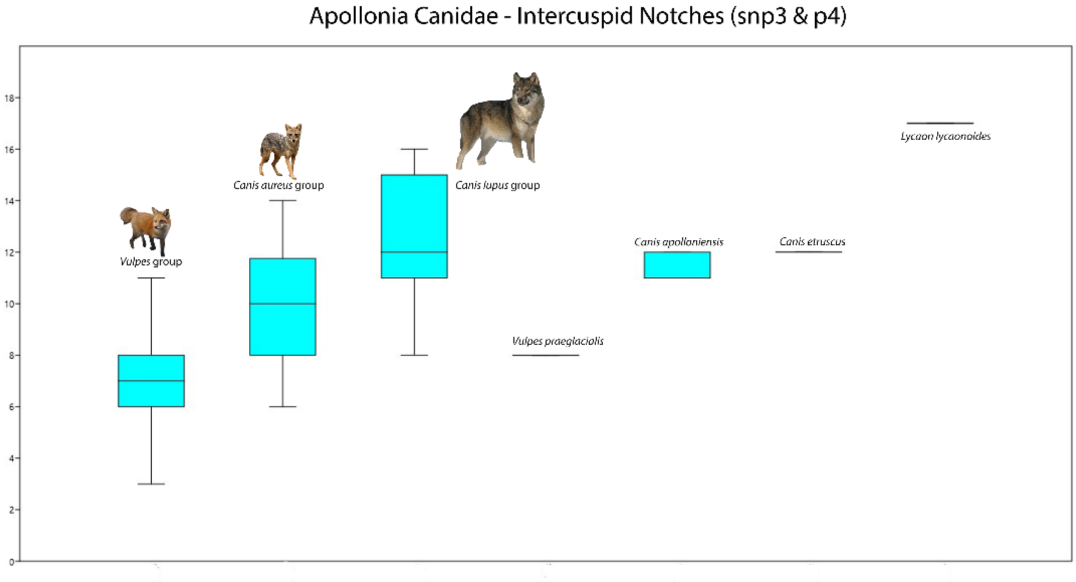


Fig. 78: Intercuspid Notches of Apollonia Canidae compared to extant canids

The only endocranial volumes available to calculate were those of one *Canis arnensis* (GER-45) and one *Canis etruscus* (APL-522), which were 68.9 ml and 74.9 ml respectively, intermediate between the values of extant black-backed jackals (*Canis mesomelas*) and coyotes (*Canis latrans*).

The rostrum width for *Canis etruscus* and *Canis arnensis* seems to fits into the lower values of *Canis aureus* group (Fig. 79).

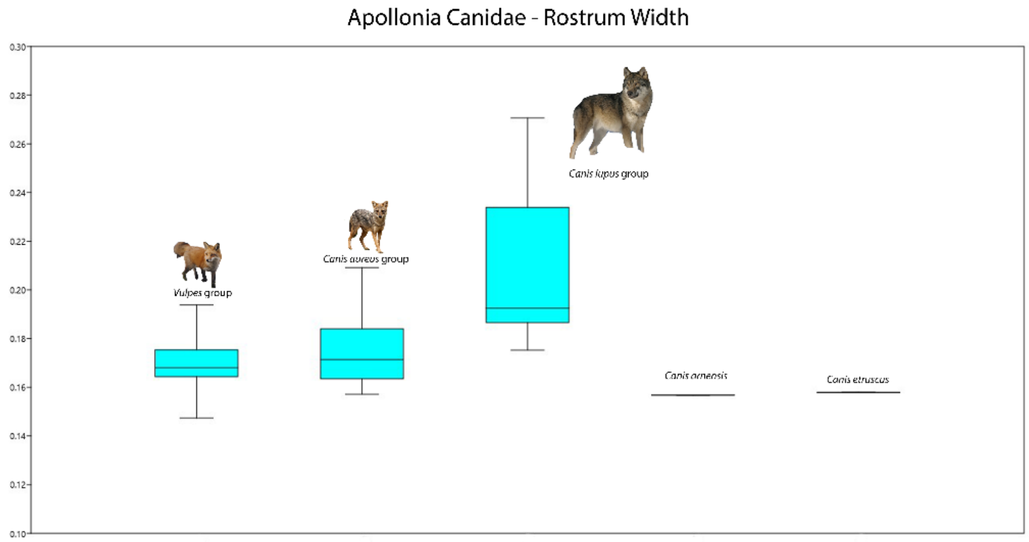


Fig. 79: Relative rostrum width for Apollonia canids

PC1 interpreted 96.1% and PC2 1.2% of total variance for the upper teeth morphometry based on Popowics (2003). It is obvious from Fig. 80 that *Lycaon lycaonoides* and *Canis etruscus* fit in the group of hypercarnivorans, while *Canis arnensis* and *Canis apolloniensis* fall into the borders between *Canis aureus* group and *Canis lupus* group.

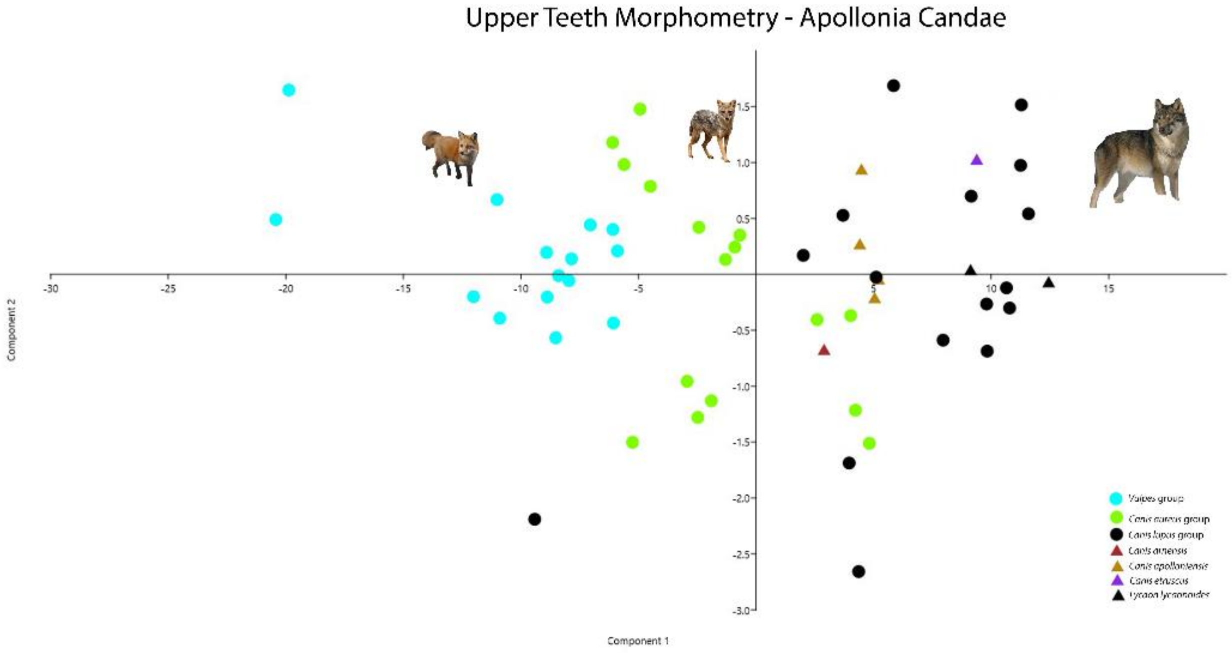


Fig. 80: PCA based on Popowics (2003) for the upper teeth of Apollonia canids

PC1 interpreted 97.1% and PC2 1.2% of total variance for lower teeth morphometry based on Popowics (2003). Again *Lycaon lycaonoides* fits well into the group of hypercarnivorans, while *Canis arnensis* and *Canis apolloniensis* fit in the borders between the groups of *Canis aureus* and *Canis lupus*. *Vulpes praeglacialis*, reasonably, fits into the range of *Vulpes* group.

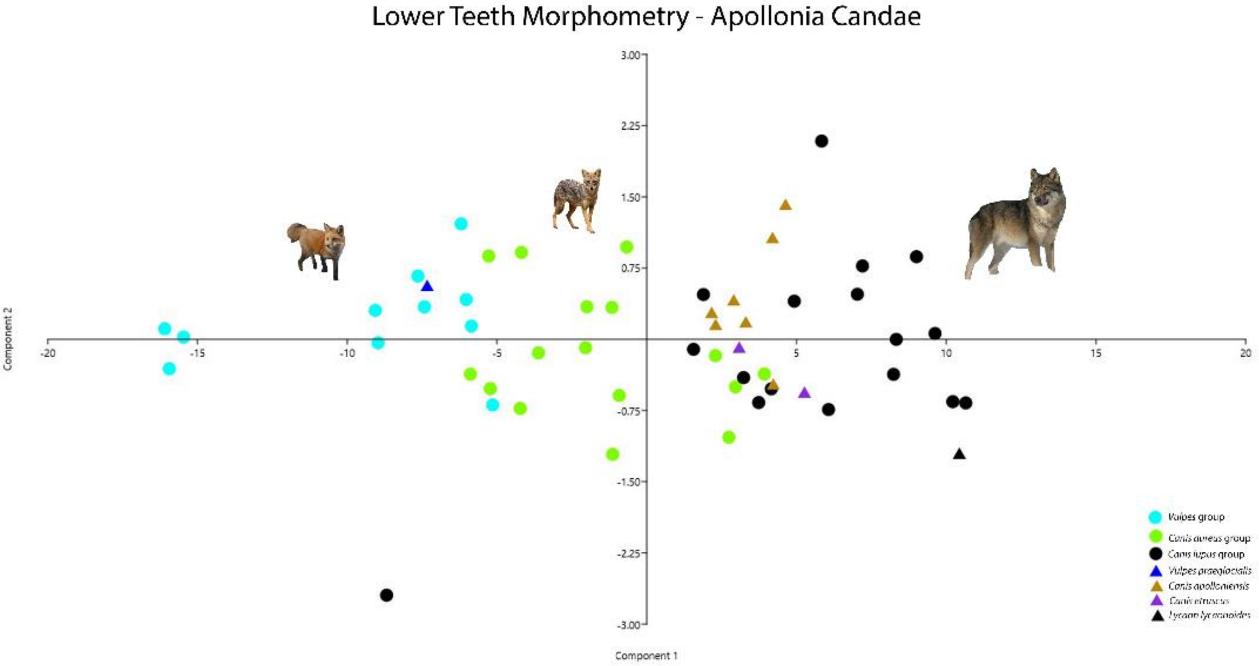


Fig. 82: PCA based on Popowics (2003) for the lower teeth of Apollonia canids

The only parameter proposed by Sacco & Van Valkenburgh (2004) that had differentiating value in canids was M1BSZ (Fig. 82). It is clear that *Vulpes praeglacialis* falls into the upper part of the range of *Vulpes* group, *Canis apolloniensis* and *Canis etruscus* fall into the overlapping range of *Canis aureus* and *Canis lupus* groups, while *Lycaon lycaonoides* exceeds the range of extant hypercarnivorans.

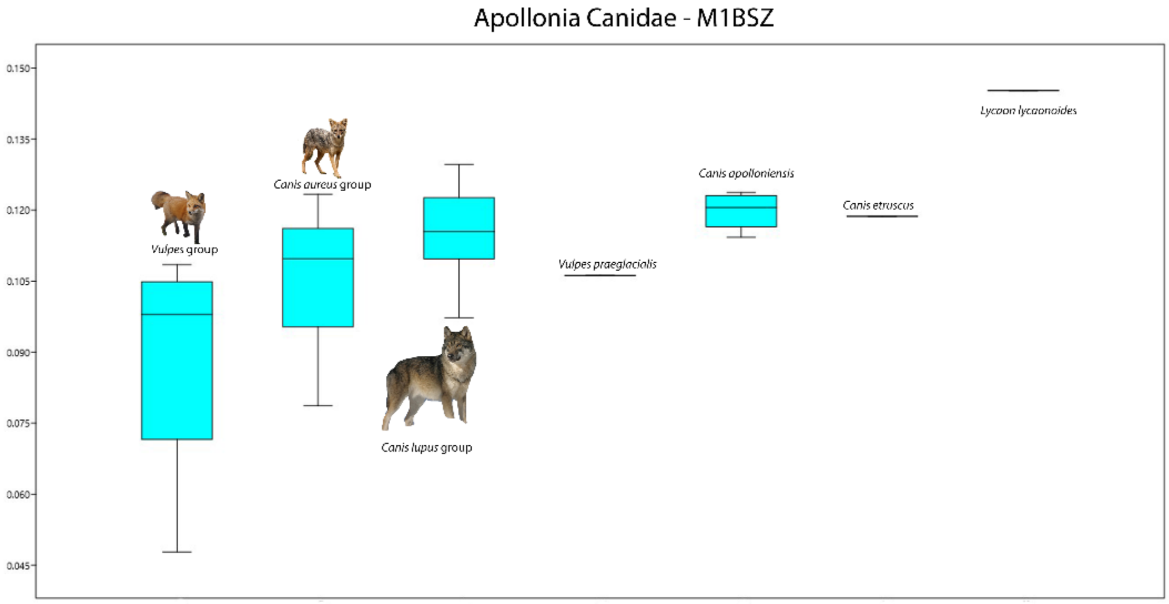


Fig. 82: M1BSZ for Apollonia Canidae

No particular patterns of dental wear were observed. It seems that in all species of *Canis* in Apollonia, transverse and horizontal wear have equal value, indicating that all the species were fed both in meat and bones/plants. The only specimen of particular interest is APL-1, which is assigned to *Canis apolloniensis* (Fig. 83). This specimen preserves extreme wear and possibly belongs to an old individual, which (at least) in the end of its life probably fed on the remains of carcasses.

Fig. 83: *Canis apolloniensis* (LGPUT-APL-1) preserving extreme wear

Results: ***Vulpes praeglacialis*** seems to be similar ecologically with the extant foxes being an opportunistic, meat-based omnivore. ***Lycaon lycaonoides***, on the other end, seems to be a typical hypercarnivoran, relevant to extant *Lycaon* and *Canis lupus*. The three species of *Canis* probably represent a small cline between the *Canis aureus* and *Canis lupus* groups. ***Canis arnensis*** fits better in the range of *Canis aureus*, ***Canis etruscus*** in the group of *Canis lupus* and ***Canis apolloniensis*** probably fits in an intermediate position. These results agree with the already-known differentiation of *C. arnensis* and *C. etruscus* (e.g. Cherin et al., 2013). Despite this gradual differentiation, it is very likely that these species had close ecological niches. Therefore, they should have competed with each other. Today in USA *Canis rufus*, *Canis latrans* and *Canis lupus* coexist with four species of *Vulpes* and two of *Urocyon* forming a similar carnivoran assemblage. A perhaps more similar case is the region of North Africa, where *Lycaon pictus*, *Canis lupus*, *Canis aureus*, *Canis lupaster* and four species of foxes are found (IUCN Red List - www.iucnredlist.org). It is possible that these small-medium sized canids have evolved a variety of adaptations, not visible in their skeleton, in order to coexist, e.g. their circadian rhythm (Loveridge & Macdonald, 2003).

Temporal Study of Ecologically Similar Species

[1] *Promeles palaeattica, Meles dimitrius* & *Meles meles*

The Turolian form of a badger is *Promeles palaeattica*, a relatively common species in Greece and especially in Pikermi (Roussiakis, 2002). This form is replaced by the Villafranchian form *Meles dimitrius*, which and finally the extant *Meles meles*. However, the revision of Villafranchian badgers (Madurell-Malapeira et al., 2011) suggests that the specimens of *Meles dimitrius* must be seperated in *Meles thorali* (specimens from Gerakarou) and *Meles meles atavus* (specimens from Apollonia). The herein studied specimens of *M. dimitrius* come from Apollonia.

From the following figures and tables it is clear that the two genera are quite distinct. *Promeles* is a much more primitive taxon in many parameters, while *Meles dimitrius* seems to fit close or into the ranges of *Meles meles*.

At first there is a clear size difference between *Promeles* and *Meles* as can be seen in Fig. 84. Based on skull length (Van Valkenburgh, 1990) the weight of *Promeles* is estimated to be between 4 and 12 kg, with the average being 6.7 kg (n=7), lower than the average value for extant *Meles meles* (≈10 kg).

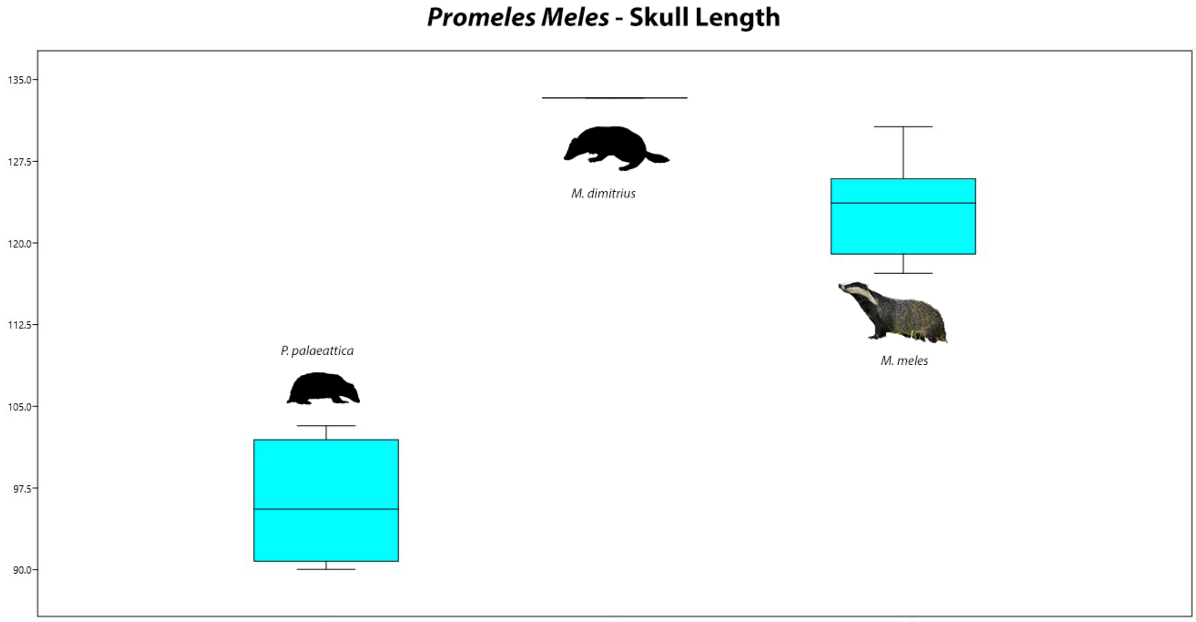


Fig. 84: Skull length of *P. paleattica*, *M. dimitrius* and *M. meles*

The relative width of the rostrum seems to be stable since the Turolian in badgers (Fig. 85).

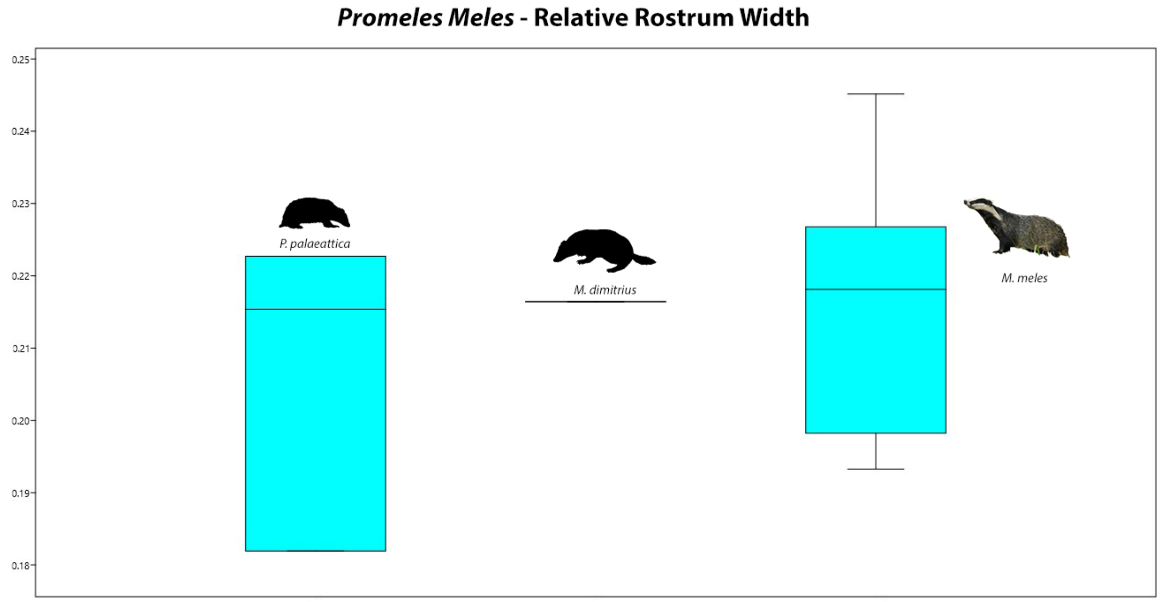


Fig. 85: Relative rostrum width of *P. paleattica*, *M. dimitrius* and *M. meles*

There is a succession through *P. palaeattica*, *M. meles* and *M. dimitrius* in Bite Force (Fig. 86). However, the only available data for the Bite Force of *M. dimitrius* were only from APL-544, which seems to be an extremely robust individual, in terms of sagittal crest development and zygomatic width. Therefore, it probably does not represent the average value of Bite Force for the whole species, but a relatively high value.

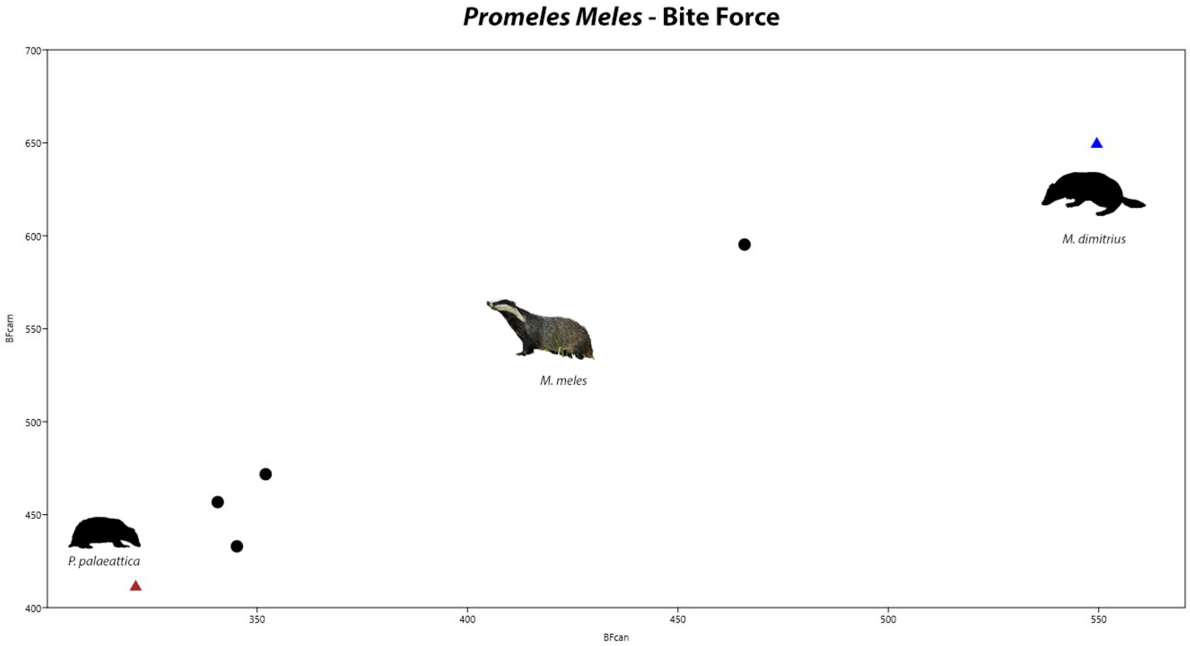


Fig. 86: BFcan and BFcarn of *P. paleattica*, *M. dimitrius* and *M. meles*

The canine bending strength of *P. palaeattica* is clearly lower than in *Meles*, while the value for *M. dimitrius* falls into the range of *M. meles* (Fig. 87).

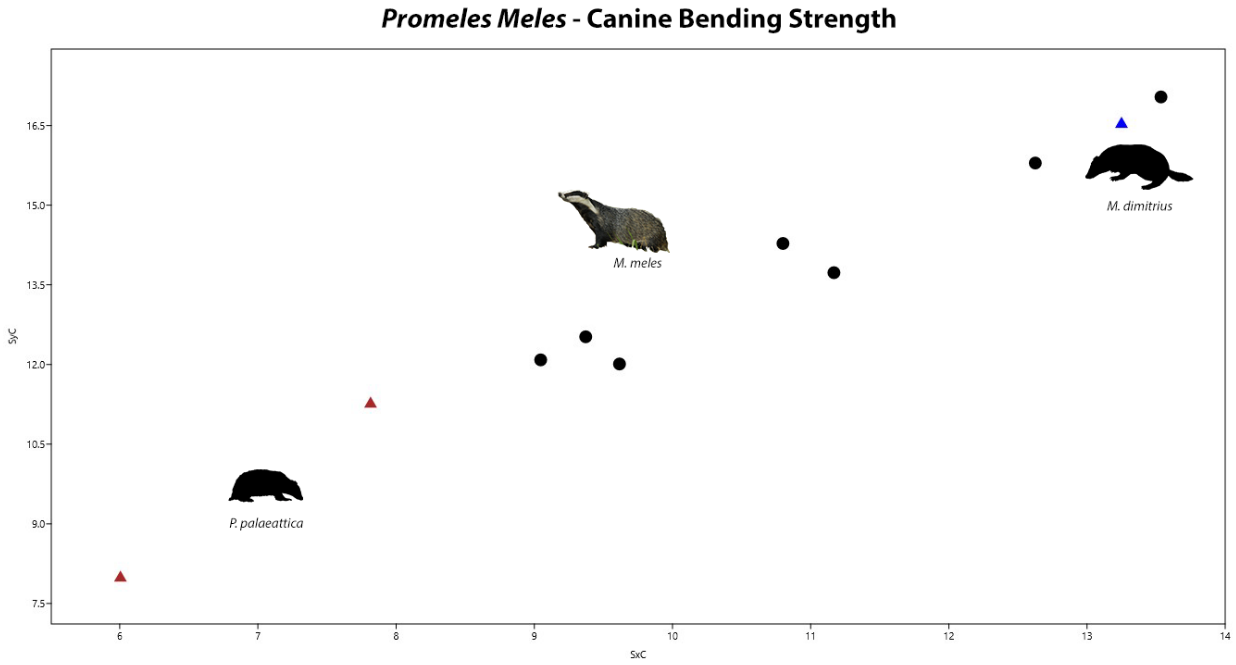


Fig. 87: SxC and SyC of *P. paleattica*, *M. dimitrius* and *M. meles*

The Dental Mesowear of all the species seem to have a similar pattern: the extreme transverse wear is very frequent, indicating a high percentage of plant material in the diet, while the horizontal wear is mostly low indicating a decreased carnassial function of the teeth (Table 13).

Table 13: Dental Mesowear patterns in *P. paleattica*, *M. dimitrius* and *M. meles*

Species	**n**	**Transverse**			**Horizontal**			**Premolars**
		1	**2**	**3**	**1**	**2**	**3**	
Promeles palaeattica	8	0.25	0.25	0.5	0.75	0.13	0.13	0.38
Meles dimitrius	4	0.25	0.5	0.25	0.75	0.25	0	0.25
Meles meles	9	0.11	0.66	0.33	0.56	0.33	0.11	0.44

The relative area of the upper (UGR) and the lower cheek teeth (LGR) seems to be enhanced in *Meles*, while it is not so developed in *Promeles*. The ranges are wide, but the averages and the minimums & maximums show a clear trend (Figs. 88 & 89).

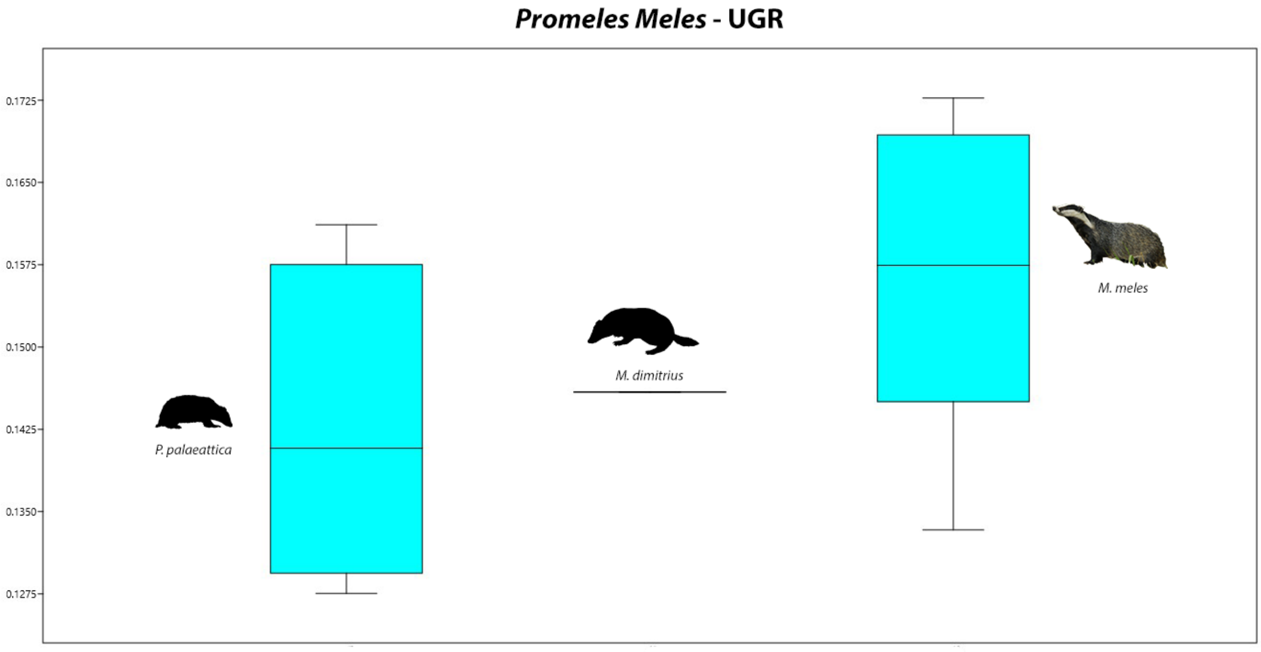


Fig. 88: UGR of *P. paleattica*, *M. dimitrius* and *M. meles*

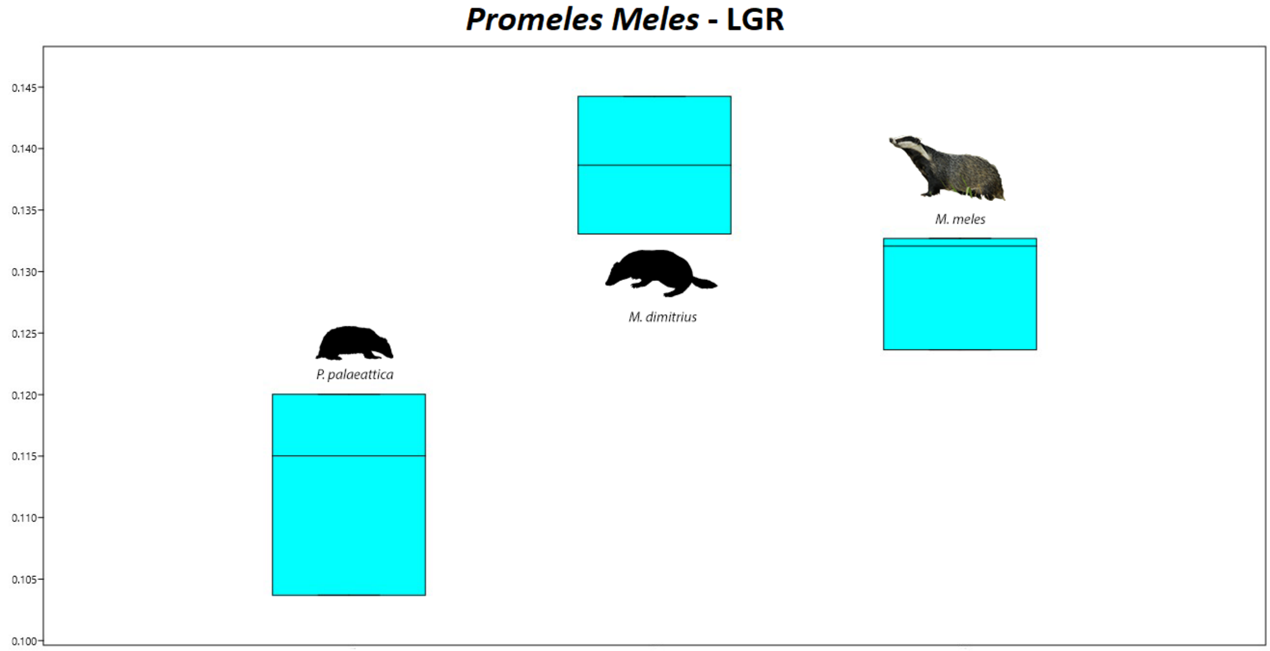


Fig. 89: LGR of *P. paleattica*, *M. dimitrius* and *M. meles*

The relative length of m1 (M1BSZ) seems to be reduced in *Meles*, indicating a decrease in carnassial function (Fig. 90). It is interesting that *Promeles* preserves a very wide range on this parameter.

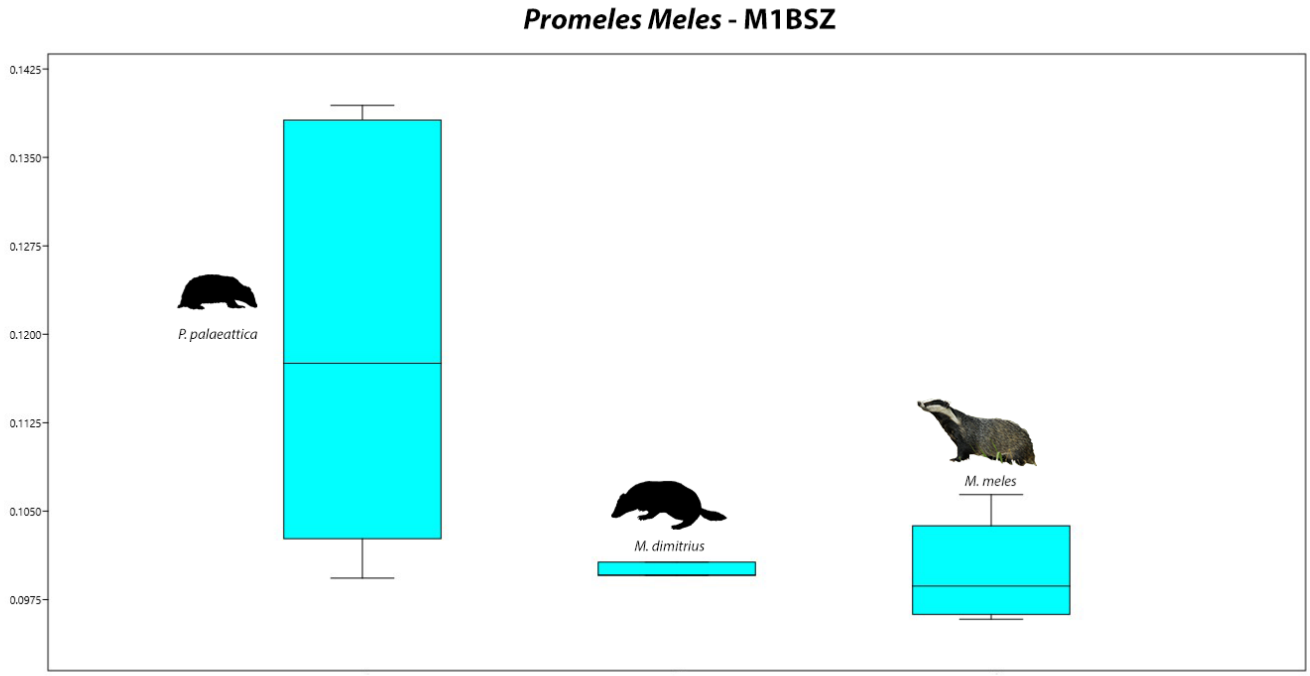


Fig. 90: M1BSZ of *P. paleattica*, *M. dimitrius* and *M. meles*

The upper teeth metrical PCA based on Popowics resulted in a final 95.3% interpretation of total variability (PC1 90.9% and PC2 4.5%). *Promeles* is clearly homogenous in the upper teeth, such as *Meles meles*. *Meles dimitrius* falls near the borders of *Meles meles* range.

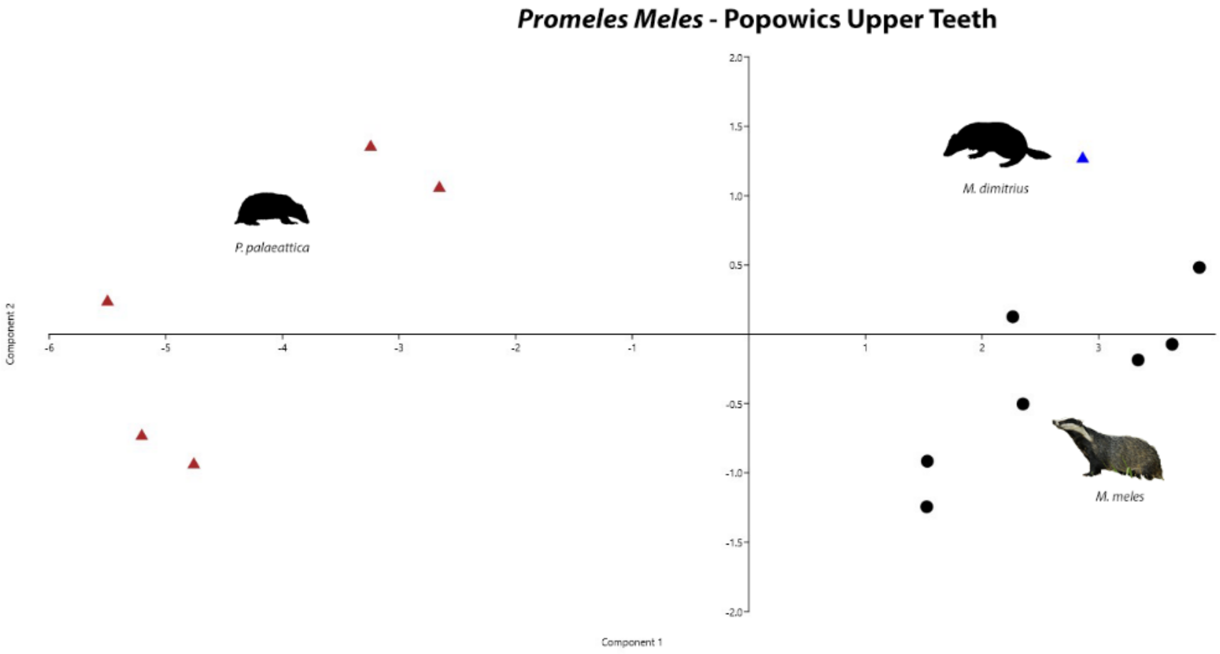


Fig. 91: PCA on the upper teeth of *P. paleattica*, *M. dimitrius* and *M. meles*

The lower teeth metrical PCA based on Popowics resulted in a final 92.6% interpretation of total variability (PC1 75.3% and PC2 17.3%). Again (as in M1BSZ) *Promeles'* m1 seems to be variable and homogenous as in the upper teeth. *Meles meles* is homogenous, while *M. dimitrius* seems to form a separate group.

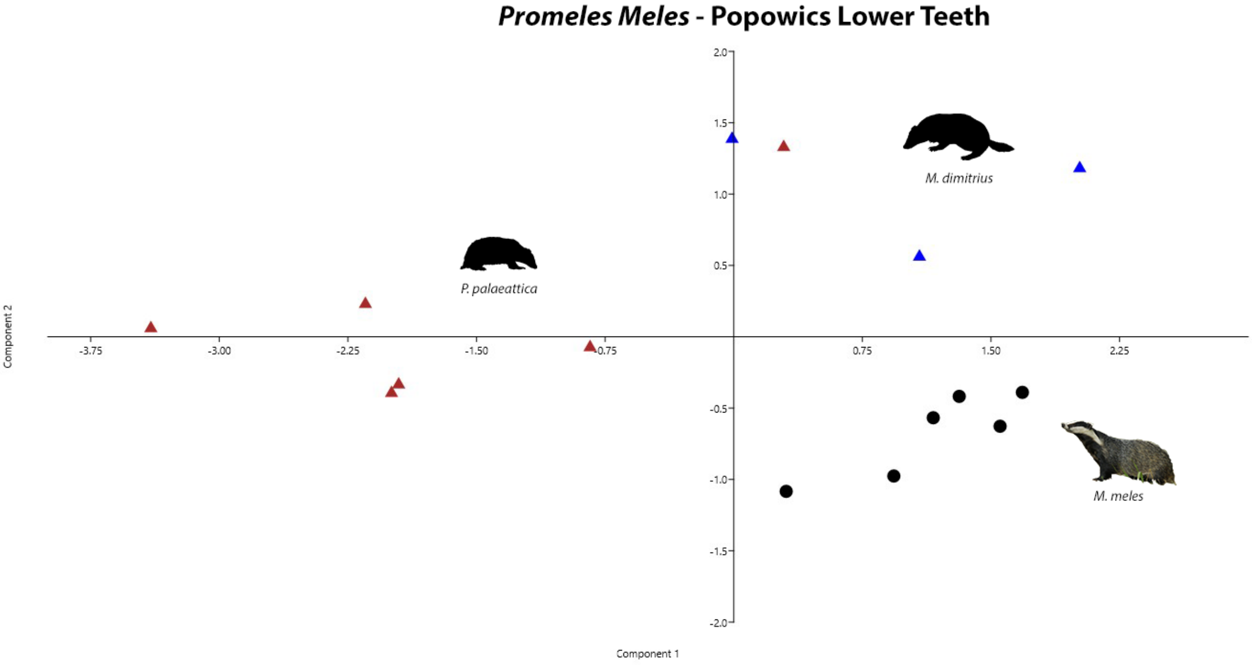


Fig. 92: PCA on the lower teeth of *P. paleattica*, *M. dimitrius* and *M. meles*

Finally, the cheek teeth morphology (Fig. 93) preserves clear that *Promeles* is more primitive than *Meles*. In *Promeles* P4 is longer and its protocone retains the plesiomorphic form seen in Mustelinae, while in *Meles* P4 is shorter and the protocone is widened to form an additional grinding surface. M1 is relatively much shorter in *Promeles*, being intermediate between the 8-shaped M1 of Mustelinae and the enlarged M1 of *Meles*. The talonid of m1 seems to be slightly shorter in *Promeles*, in comparison to *Meles*. All these characters indicate that the teeth of *Promeles* were not so well adapted to grinding plant material in comparison to *Meles*.

The teeth of *Meles dimitrius* do not differ significantly from *Meles meles*. It is possible that the grinding surfaces of P4 and m1 are slightly larger in *Meles dimitrius* as indicated also by LGR (Fig. 89).

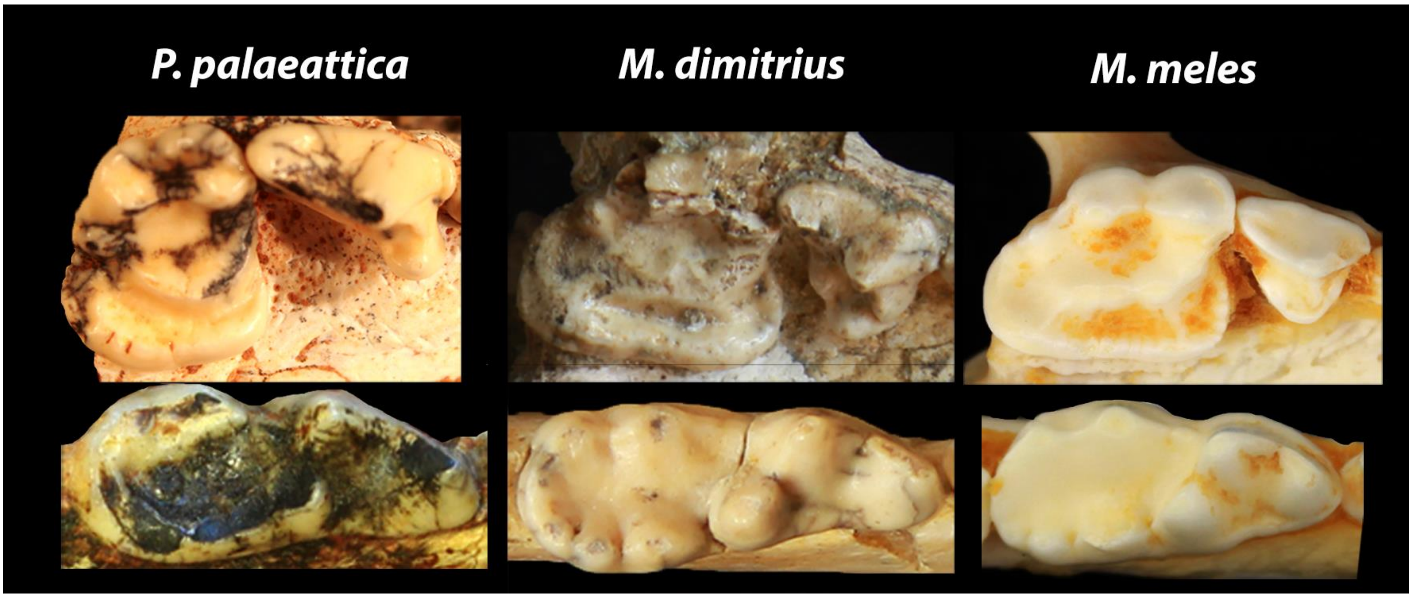


Fig. 93: Upper and lower cheekteeth morphology of *P. palaeattica, M. dimitrius* and *M. meles*

<u>Results</u>: It is clear that *Promeles* is a clearly distinct taxon from *Meles* based on many parameters. In basic terms, it is smaller, with lower bite force and canine bending strength and its cheek teeth represent an intermediate stage between the Mustelinae and extant *Meles*. Therefore, we can assume that ***Promeles palaeattica*** had an intermediate (but again important) percentage of plant material in its diet between these two groups. ***Meles dimitrius*** is similar to ***Meles meles*** ecomorphologically. It is possible that it had even higher percentage of plant material in its diet than *M. meles*. In conclusion, the badgers' evolution is characterized by two main axes: the size enlargement (affecting also bite force and bending strength) and the enhancement of grinding areas associated with an increase of plant material in their diet.

[2] *Nyctereutes donnezani* → *Nyctereutes megamastoides* → *Nyctereutes procyonoides*

The modern racoon dogs (*Nyctereutes procyonoides*) are small, racoon-like, fox-sized canids, occurring in eastern Asia as native and in central-eastern Europe as introduced. The genus *Nyctereutes* colonized Asia from North America with *N. tingi* being the first species found in China in 5.5-3.0 Mya (Wang & Tedford, 2008). The next species of this line is *N. donnezani* of the Pliocene, *N. megamastoides* in the Villafranchian and finally today's *N. procyonoides*. In this chapter the major trends of the evolution of the three last species of *Nyctereutes* will be studied.

The first visible trend is the total body size reduction, here interpreted by the skull length (Fig. 94).

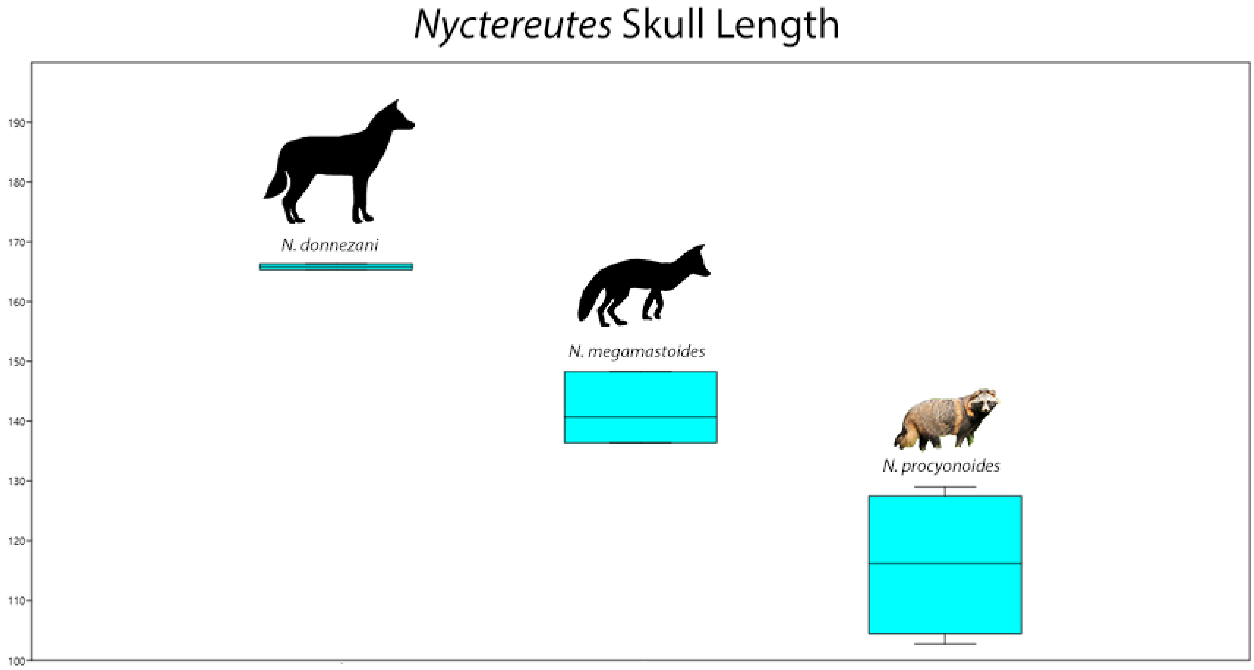


Fig. 94: Skull Length of *Nyctereutes* over evolution

Together with skull length, the bite force (Fig. 95) and the endocranial volume (Fig. 96) seem to decrease throughout evolution. It is interesting however, that the specimen Σ-384 preserves an endocranial volume of 67 mL, larger even from *N. donnezani*.

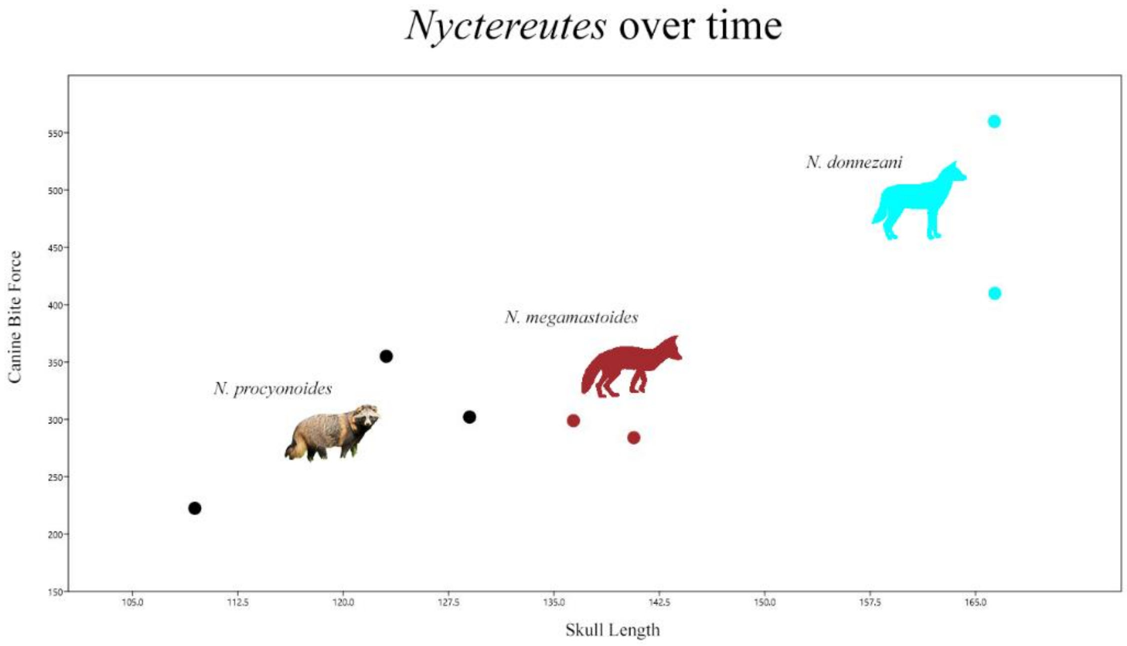


Fig. 95: Bite Force of *Nyctereutes* over evolution in correlation to the skull length

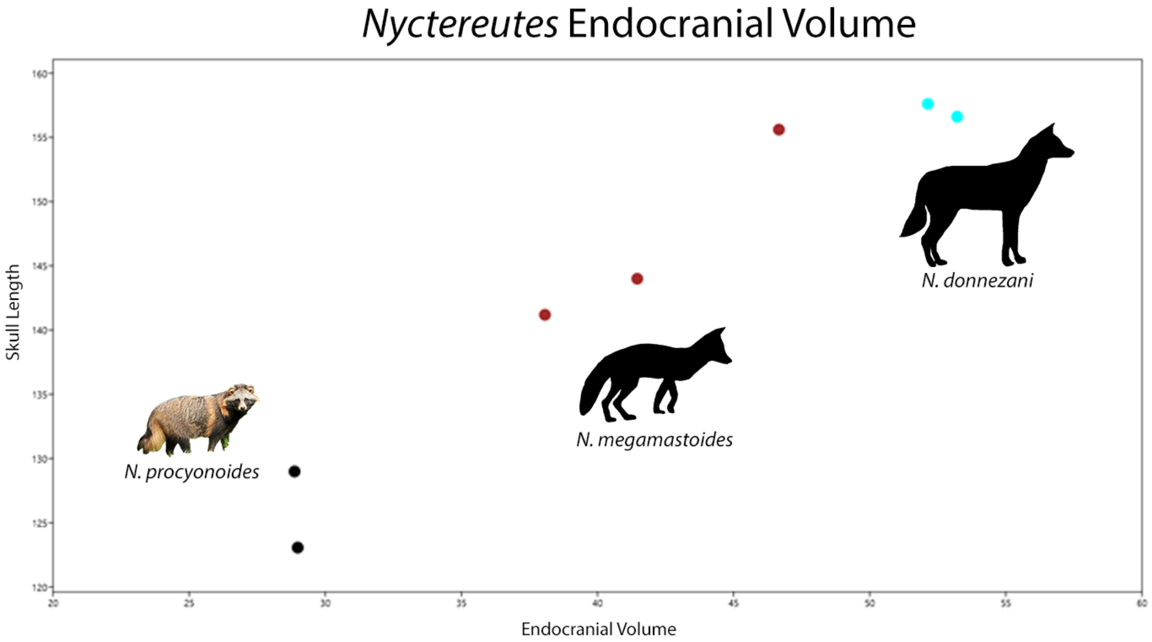


Fig. 96: Endocranial Volume of *Nyctereutes* over evolution in correlation to the skull length

The index of the rostrum width divided by the skull length seems to change throughout geological time with the older species having wider rostra and the younger species having narrower rostra (Fig. 97).

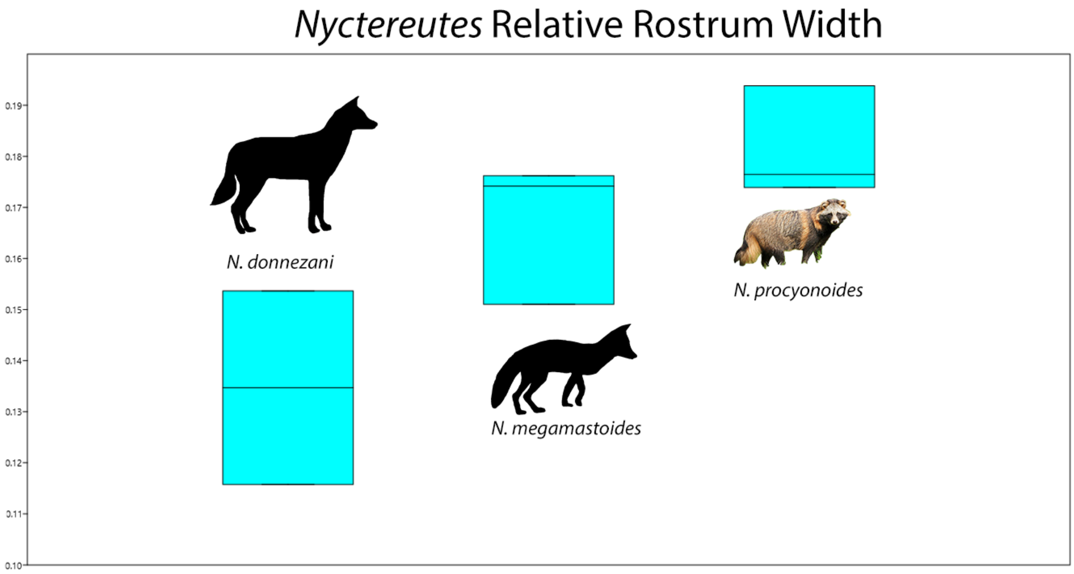


Fig. 97: Relative rostrum width of the genus *Nyctereutes* throughout evolution

While looking at the succession of the teeth morphology in the three species, some more trends are visible. In fact, it seems that the step between *N. donnezani* and *N. megamastoides* is more significant than the step between *N. megamastoides* and *N. procyonoides*. At first the enlargement of the talonid in m1, which can be connected with the enhancement of grinding functions associated with consuming plant material. The P4 of *N. donnezani* has a strong cingulum and a more robust and round protocone, while in the two next species there is no cingulum and the protocone is weaker and more triangular. Both M1 and M2 have changed from the plesiomorfic state seen in *N. donnezani* to rounded, low cusped teeth with weaker metacone and paracone and wider hypocone and protocone. All these traits are connected with the preference on plant material instead of meat.

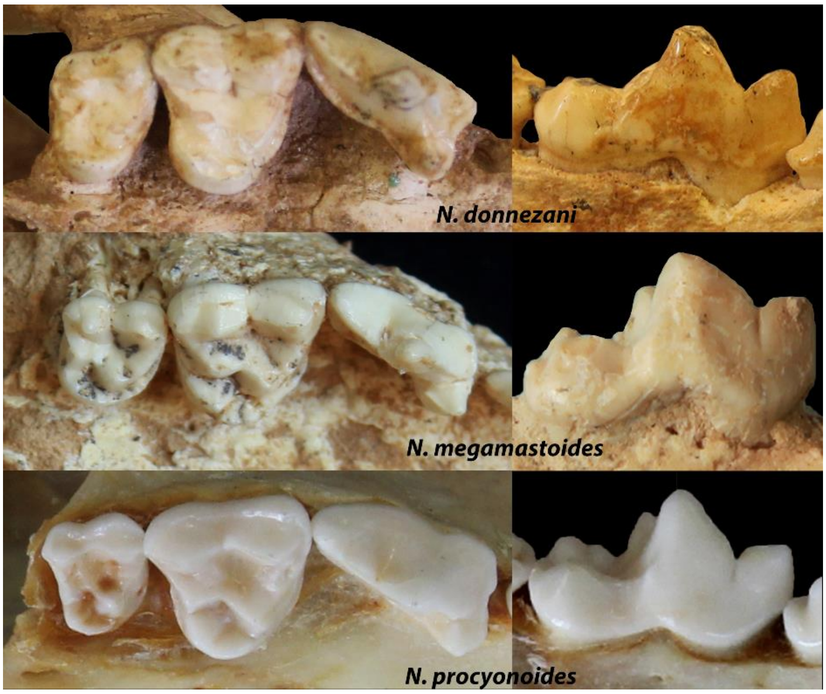


Fig. 98: Upper and lower cheek teeth of *N. donnezani*, *N. megamastoides* and *N. procyonoides*

Results: It is clear from the aforementioned data that the genus *Nyctereutes* has followed an evolutionary path of size reduction and plant-based omnivory since Pliocene. The most probably scenario is that ***Nyctereutes donnezani*** was an opportunistic omnivore, which preferred plants as approximately 30% of its diet, similar e.g. with extant *Canis mesomelas* or *Canis adustus*, which also are of similar size. The most significant transition was made with ***Nyctereutes megamastoides***, which probably had a diet already similar with extant ***Nyctereutes procyonoides***: an omnivore with variable percentages of plant material ranging from 30 to 70% of its diet, probably depending on the seasonal availability of certain food sources. This fact can also be seen in the extreme transverse wear of the teeth of DFN-17 (Fig. 99), indicating significant grinding function on upper molars. However, *N. megamastoides* was slightly larger than extant racoon dogs and had a relatively narrower rostrum. These results are similar to those made by Bartolini Lucenti et al. (2016).

Fig. 99: Teeth wear in DFN-17

[3] *Dinocrocuta gigantea/salonicae* → *Adcrocuta eximia* → *Pliohyaena perrieri* → *Pachycrocuta brevirostris* → *Crocuta crocuta/spelaea*

The ecological connection of these species has already been studied by many authors (e.g. Werdelin & Solounias, 1991). Since the Vallesian, Old World was dominated by some bone-cracking hyena. The Vallesian *Dinocrocuta* was replaced by *Adcrocuta*, which was the most common carnivoran in the Turolian of Greece. The Pliocene-Villafranchian form of *Pliohyaena* was a slightly smaller species, but the Villafranchian-Pleistocene *Pachycrocuta* was the largest member of the family Hyaenidae *sensu stricto* (Turner & Antón, 1996). Finally the Pleistocene *Crocuta* was a very successive genus occupying nearly all the Old World (e.g. Klein & Scott, 1989; Louys et al., 2007). However, none of these hyenas managed to reach America, probably due to the competition with the established bone-cracking dogs (Wang & Tedford, 2008). The only genus of hyena ever able to colonize America was *Chasmaporthetes*, an intermediate form between the classic bone-crushers and the ictitheres (Wang & Tedford, 2008).

All of these genera are represented in the fossil record of Greece. *Dinocrocuta gigantea* has been found in Pentalophos with a right mandible of a juvenile (PNT-70). There is also a right maxilla (M11413) in the Natural History Museum of London (M11413), which was published by Andrews (1918) as a separate species, *Dinocrocuta salonicae*. This specimen comes from Diavata, a locality possibly the same with Pentalophos (Koufos, 2011). The genus *Dinocrocuta* is typical of the Vallesian of the Balkans, leading to the determination of the term *Dinocrocuta*-event by Koufos (2003).

Fig. 100: The specimens of *Dinocrocuta* from Greece: (a) *Dinocrocuta gigantea* (PNT-70), (b) *Dinocrocuta salonicae* (M11413). Not in scale.

Probably the most common carnivoran in the fossil record of Greece is *Adcrocuta eximia*. This species is mentioned in both the Vallesian and the Turolian. Its extremely high frequency probably indicates that it was social like the modern spotted hyenas. It is found in the faunas of Halmyropotamos, Pikermi, Samos, Ravin de la Pluie, Xirochori, Ravin de Zouaves, Prochoma, Vathylakkos, Perivolaki and Kerassia (Koufos, 2011). There is a contradiction on its presence in Dytiko. Koufos (1987, 2011) states that these specimens belong to a separate species, *Chasmaporthetes bonisi*, while Werdelin & Solounias (1991) believe that these specimens actually belong to *Adcrocuta eximia*. Similar to the *Dinocrocuta*-event, Koufos (2003) recognised an *Adcrocuta*-event in the Turolian.

Fig. 101: Complete skull and mandible of *Adcrocuta eximia* from Pikermi. Not in scale.

Pliohyaena perrieri is the rarest of the true crocutoid hyenas in the fossil record of Greece. It has only been referred in Sesklo, Gerakarou and Petralona Cave (Koufos, 1992; Symeonidis, 1992; Baryshnikov & Tsoukala, 2010) with very scarce remains. The wear of the teeth in both Sesklon and Gerakarou specimens is extreme, revealing its ossifragous habits. It is considered as typical species from the Late Ruscinian until the Late Villafranchian by Koufos & Kostopoulos (2016).

Fig. 102: The material of *Pliohyaena perrieri* from Sesklon (a) and Gerakarou (b). Not in scale

The classical giant hyaena of the Villafranchian, *Pachycrocuta brevirostris*, is more common than *Pliohyaena*. It is mentioned in the faunas of Gerakarou, Apollonia, Kalamoto, Livakkos and Karnezeika (Koufos, 2014; Kokotini et al., 2019). Unfortunately the material is rather fragmentary. It is considered as typical species of Late and Epi Villafranchian by Koufos & Kostopoulos (2016).

Fig. 103: Material of *Pachycrocuta* from Apollonia, Gerakarou, Libakkos and Karnezeika. Not in scale

Finally, the genus *Crocuta* dominated Old World since the beginning of the Ice Ages. It is present in many cave faunas in Greece, which however are not well known. The faunas of Petralona seems to include two subspecies: *Crocuta crocuta praespelaea* and *Crocuta crocuta petralonae* (Baryshnikov & Tsoukala, 2010). The species *Crocuta spelaea* has also been found in Greece in Haliakmonas (Melentis, 1966).

Fig. 104: Mandible of *Crocuta crocuta* from Petralona Cave. Source: Baryshnikov & Tsoukala (2010).

[4] *Amphimachairodus giganteus, Paramachairodus orientalis, Metailurus major, Homotherium latidens, Megantereon cultridens, Panthera gombaszoegensis* & *Panthera leo, Panthera pardus*

Similar to the case of bone-crushing hyenas, from the Turolian until Holocene Greece hosted several species of large felids. As mentioned in a previous section, the Turolian of Greece yielded 5 species of felids. Three of them, *Metailurus major*, *Paramachairodus orientalis* and *Amphimachairodus giganteus,* were species of over 50 kg and hunters of large prey (Fig. 105).

Fig. 105: Material of *Amphimachairodus giganteus* (a), *Paramachairodus orientalis* (b) and *Metailurus major* (c) from Halmyropotamos (a,c) and Pikermi (b). Not in scale.

The second era of felids dominance is the Villafranchian, when two species of sabertooths (*Homotherium latidens* and *Megantereon cultridens*) and one large pantherine (*Panthera gombaszoegensis*) are found. At this time, there is also *Lynx issiodorensis,* an ancestral species of modern lynxes, which was also of great size.

Fig. 106: Material of *Panthera gombaszoegensis* (a), *Megantereon cultridens* (b) and *Homotherium latidens* (c) from Greece.

Finally, the Late Pleistocene and even the Holocene of Greece were the last period with large felids in Greece. Lion and leopard remains have been found in many caverns, some of them offering plenty of material such as Petralona and Vraona (Nagel, 1995; Baryshnikov & Tsoukala, 2010). The presence of lions is also mentioned in many myths of ancient Greece.

Today the largest species of felid in Greece is the wildcat, *Felis silvestris*. The presence of Eurasian lynx, *Lynx lynx*, is questionable, despite the fact that approximately 100 years ago, there were references of this species even in central Greece.

Species Profiles

The following section summarizes all the ecomorphological characteristics of the species studied during this project. These characteristics are accompanied by a taxonomic scheme and a stratigraphic-geographic range of every species. Every profile categorizes the respective species in (at least) one of the dietary categories determined and predicts its possible prey species, pointing to a modern analogue.

Family Felidae FISCHER VON WALDHEIM, 1817
Subfamily Felinae FISCHER VON WALDHEIM, 1817
Genus *Pristifelis* SALESA, ANTÓN, MORALES & PEIGNÉ, 2012
Pristifelis attica (WAGNER, 1857)

Stratigraphical range: MN10-MN13

Geographical Range: Greece, Turkey, Iran?, Italy?, Spain, Germany, Moldova, Hungary and China?

Localities: Pikermi (Roussiakis, 2002), Vathylakkos 3 (Arambourg & Piveteau, 1929; Koufos, 2000), Samos (de Beaumont, 1961; Koufos, 2000), Akkasdagi (de Bonis, 2005), Kinik, Karain (Schmidt-Kittler, 1976), Middle Maragheh, Upper Maragheh (Mecquenem, 1925; NOW, 2007; the Maragheh specimens are considered by Salesa et al., 2012 to belong to Styriofelis vallesiensis), Valdecebro 5, Venta del Moro, Brisighella (as cf.), Dorn Dörkheim, Taraklia, Sömeg (NOW, 2016) and Shansi-Loc. 49 (Zdansky, 1924; de Beaumont, 1961)

Table 14: Ecomorphological characteristics of *Pristifelis attica*

Body Mass		6-10 kg
Canine W/L %		81%
Endocranial Volume		25-30 mL
Sum Intercuspid Notches		15
Rostrum Width / Skull Length		22%
Dental Mesowear	**T**	1
	H	1-2

Dietary Category: 1-2

Diet: Rodents (e.g. *Parapodemus*, *Micromys*), hares (*Prolagus*, *Alilepus*), insectivores (*Schizogalerix*), birds, reptiles and fish.

Sociality: Solitary

Modern analogue: *Felis libyca*

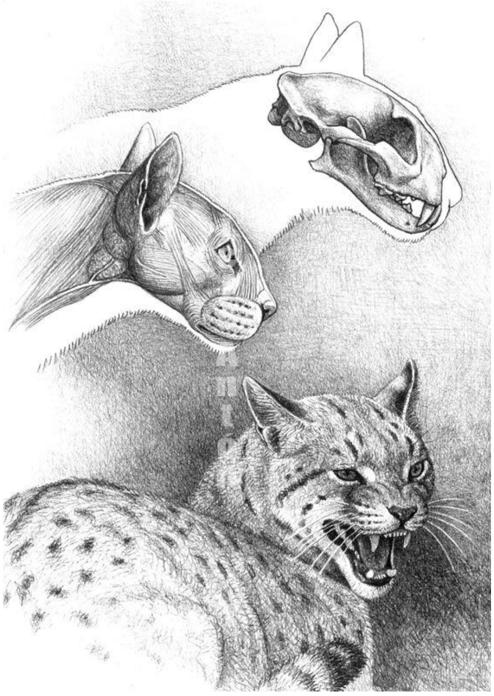


Fig. 107: *Pristifelis attica*. Source: alchetron.com. Artist: M. Antón

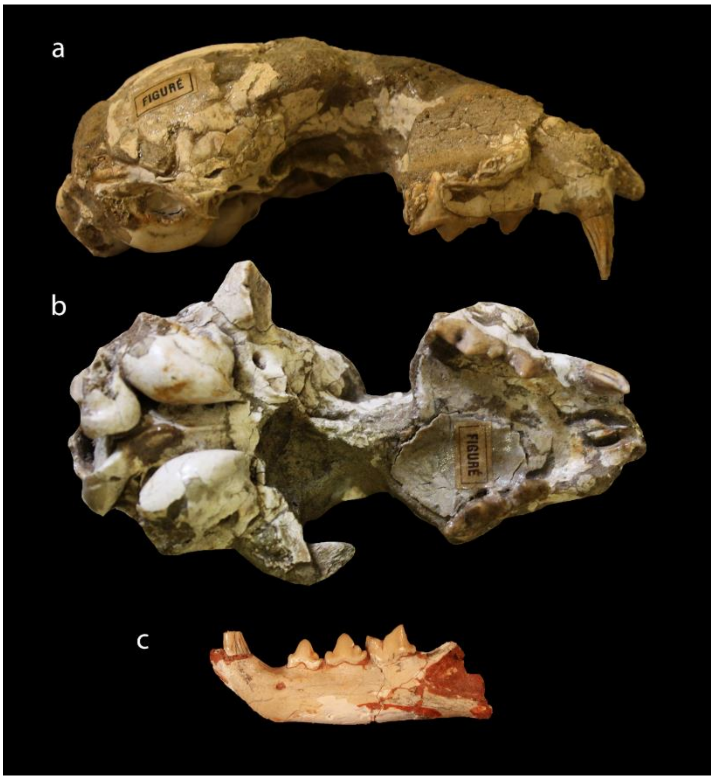


Fig. 108: skull (MNHN-SLQ-935) and mandible (AMPG-PG01/107) of *Pristifelis attica*. Not in scale.

Family Felidae FISCHER VON WALDHEIM, 1817
Subfamily Felinae FISCHER VON WALDHEIM, 1817
Genus *Lynx* KERR, 1792
Lynx issiodorensis (CROIZET & JOBERT, 1828)

Stratigraphical range: MN15-MNQ20

Geographical Range: Greece, Turkey, Bulgaria, Italy, France, Spain, Romania, Russia, Ukraine, Georgia, Hungary, Kazakhstan, Tadzhikistan, China, Mongolia, USA and South Africa?

Localities: Tourkovounia 3-5 (Symeonidis & de Vos, 1976), Apollonia 1 (Koufos, 1992), Volax ? (Sickenberg, 1968), Mt. Perrier, Etouaires, (Kurtén, 1978), Pantalla (Cherin et al., 2013), South Africa (Hendey, 1974), USA (Schultz & Martin, 1972), Tsao Chuang, Fan Tsun, Mafang, Hsia Chang, Beregovaia, Loc. 32, Lantian, IVPP, Nihowan, Shamar (Kurtén & Werdelin, 1984), Pyrgos, Varshets, Odessa Catacombs, Kosyakino, Udunga, Pietris, Graunceanu, St Vallier, Perpignan, Roccaneyra, Pardines, Vialette, Triversa, Villaroya, Piedrabuena, Layna, La Gloria, La Calera, El Rincón, La Puebla de Valverde, Kislang, Gólyazi, Halta, Kvabebi, Esekartkan, Kuruksaj (NOW, 2016)

Table 15: Ecomorphological characteristics of *Lynx issiodorensis*. Data from Kurtén (1978), Cherin et al. (2013) and this study

Body Mass		16-36 kg
Canine W/L %		78%
Sum Intercuspid Notches		16
Rostrum Width / Skull Length		27%
Dental Mesowear	**T**	1
	H	1-3

Dietary Category: 3

Diet: Medium sized ruminants (*Gazella*, *Gazellospira*, *Gallogoral*, *Cervus*), hares (*Lagurodon*), small horses, birds.

Sociality: Solitary

Modern analogue: *Puma concolor*

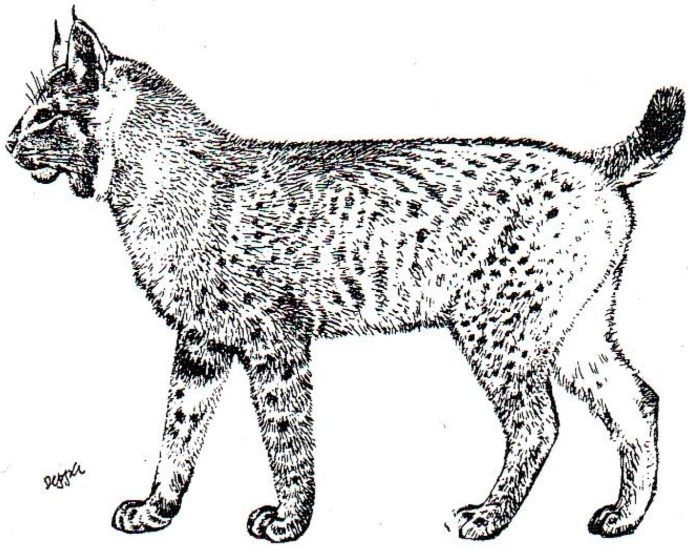


Fig. 109: *Lynx issiodorensis*. Source: Kurtén (1978). Artist: H. Pepper

Fig. 110: Material of *Lynx issiodorensis*: (a) APL-543, (b) APL-14 and (c) TB-960. Not in scale

Family Felidae FISCHER VON WALDHEIM, 1817
Subfamily Pantherinae POCOCK, 1917
Genus *Panthera* OKEN, 1816
Panthera gombaszoegensis (KRETZOI, 1938)

Stratigraphical range: MN17-MNQ24

Geographical Range: Greece, Italy, Bulgaria, Georgia, Russia, France, Spain, Germany, Netherlands, England, Hungary, Croatia, Saudi Arabia and Western Sahara

Localities: Karnezeika (Kokotini et al., 2019), Halykes, Gerakarou (Koufos, 2014), Petralona, Dmanisi, Olivola, Pantalla, Villa Spinola, Slivnitsa, Csarnota, Kislang, Tegelen, Monte Argentario, Villany 3-5-12, Betfia VII-1 & XIII, Erpfingen 2, Langenboom, Strmica, Pirro Nord, Sima del Elefante, Venta Micena, Ubeidya, Trlica, Akhakalaki, Monte Peglia, Tsymbal, Untermassfeld, Penal, Slivia, Vallonet, Maasvlakte, An Nafud, Cal Guardiola, Vallparadis, Holstejn 1-Chlum, Huescar, Somssichhegy II, Westbury-sub-Mendip, Pakefield, Trinchera Dolina 5-6-8, Artenac I, L'Escale, Chateau Breccia 4-3, Grotte XIV, Mosbach 2, Süssenborn, Hundsheim, Koněprusy C718, Stránska Skála, Thomas Quarry 1 & 3, La Belle-Roche, La Nauterie I-14, Betfia V, Gombaszög, Swanscombe, Vertesszöllös II, Uppony I-4-7-8-10, Biśnik Cave 19ad, Kudaro Cave 1-5 & 3-6, Coudoulous II, Azé-Aiglons, Villereversure, Rabenstein (Marciszak, 2014)

Table 16: Ecomorphological characteristics of *Panthera gombaszoegensis*. Data from Koufos (1992), Marciszak (2014) and this study

Body Mass		70-180 kg
Canine W/L %		88.0%
Rostrum Width / Skull Length		26.3%
Endocranial Volume		150 mL
Dental Mesowear	**T**	1-3
	H	1

Dietary Category: 3

Diet: Medium-large sized ruminants (*Croizetoceros*, *Eucladoceros* and *Cervus*), horses, boars.

Sociality: Solitary

Modern analogue: *Panthera onca*

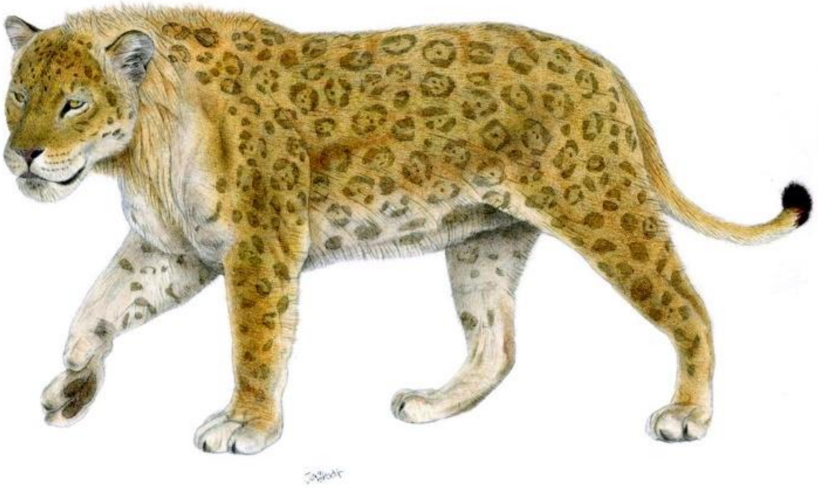


Fig. 111: *Panthera gombaszoegensis*. Source: flickr.gr.

Fig. 112: The skull of *Panthera gombaszoegensis* from Gerakarou (LGPUT-GER-165). Not in scale

Family Felidae FISCHER VON WALDHEIM, 1817
Subfamily Machairodontinae GILL, 1872
Tribe Metailurini DE BEAUMONT, 1964
Genus *Metailurus* ZDANSKY, 1924
Metailurus parvulus (HENSEL, 1862)

Stratigraphical range: MN10-MN13

Geographical Range: Greece, Moldavia, Spain, France, Italy, Turkey and Iran

Localities: Pikermi, Halmyropotamos, Chomateres, Kerassia, Samos, Ravin de la Pluie (Koufos, 2011), Chimishlija, Los Mansuetos, Arquillo, Montredon, Kinik, Gravitelli, Maraghah (NOW, 2016)

Table 17: Ecomorphological characteristics of *Metailurus parvulus*.

Body Mass		40-45 kg
Canine W/L %		66%
Canine Bite Force		550-670 N
Carnassial Bite Force		950-1050 N
Rostrum Width / Skull Length		30-35%
Endocranial Volume		50-70 ml
Sum Intercuspid Notches		15
Dental Mesowear	**T**	1
	H	1-2

Dietary Category: 3

Diet: Small-medium sized ruminants (*Gazella*, *Pliocervus*, *Dorcatherium*), young hipparions, *Mesopithecus*, *Hystrix*, birds (*Pavo*) and reptiles.

Sociality: Solitary

Modern analogue: *Caracal caracal* / *Lynx lynx*

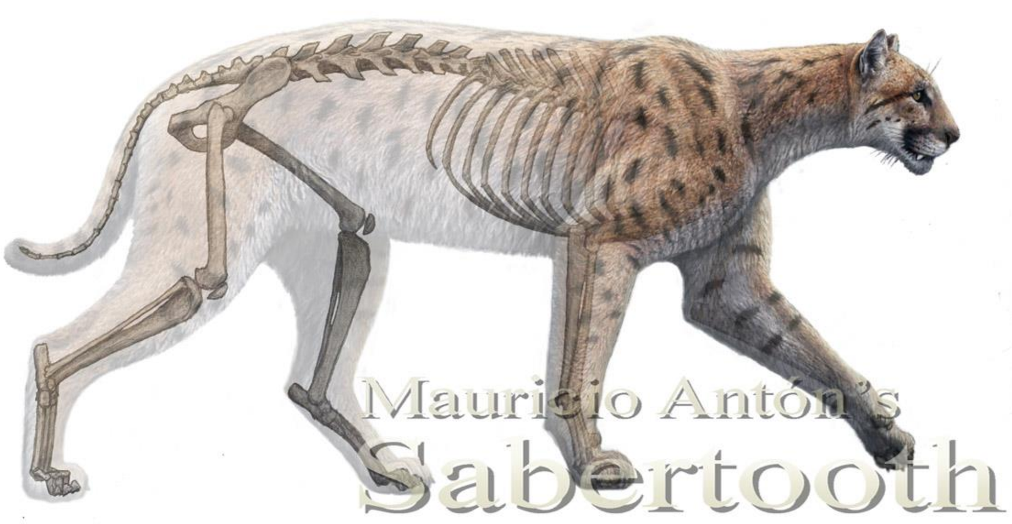


Fig. 113: *Metailurus parvulus*. Source: chasingsabertooths.wordpress.com. Artist: M. Antón

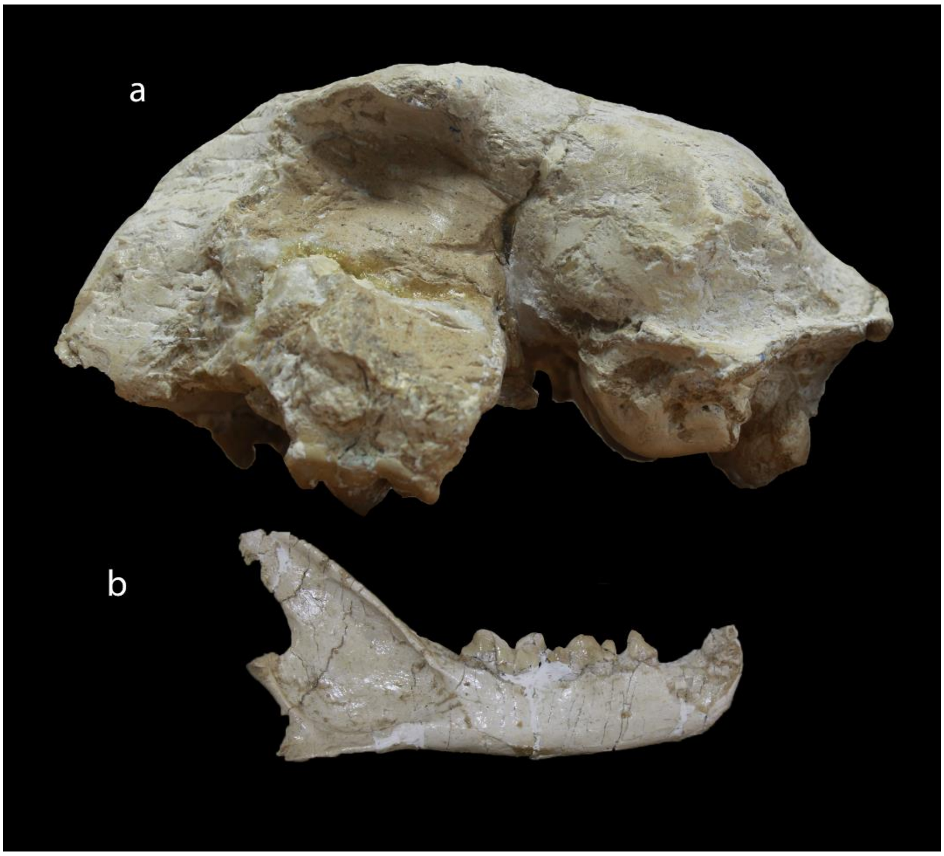


Fig. 114: Material of *Metailurus parvulus* from (a) Samos (NHMA-MTLA-234) and (b) Kerassia (AMPG-K1/210). Not in scale

Family Felidae FISCHER VON WALDHEIM, 1817
Subfamily Machairodontinae GILL, 1872
Tribe Metailurini DE BEAUMONT, 1964
Genus *Metailurus* ZDANSKY, 1924
Metailurus major ZDANSKY, 1924

Stratigraphical range: MN12-MN13

Geographical Range: Greece, Italy, Spain, Iran and China

Localities: Pikermi, Halmyropotamos, Samos?, Alfacar, Concud, Tai-Chia-Kou, Yushe (Roussiakis, 1996), Cerro de la Garita, Baccinello V3, Maragheh (NOW, 2016)

Table 18: Ecomorphological characteristics of *Metailurus major*.

Body Mass		50-100 kg
Canine W/L %		60%
Canine Bite Force		1200-1450 N
Carnassial Bite Force		1900-2300 N
Rostrum Width / Skull Length		24-26%
Endocranial Volume		85-115 ml
Sum Intercuspid Notches		11
Dental Mesowear	**T**	1-2
	H	1-3

Dietary Category: 3

Diet: Medium-large sized ruminants (*Pliocervus*, *Protragelaphus*, *Tragoportax*), *Microstonyx*, *Hipparion*, *Mesopithecus*, young giraffes (*Helladotherium*, *Palaeotragus*), *Pliohyrax*, *Hystrix*.

Sociality: Solitary

Modern analogue: *Panthera pardus*

Fig. 115: *Metailurus major*. Source: Antón (2013). Artist: M. Antón

Fig. 116: *Metailurus major* from (a) Pikermi (AMPG-PA1257/91) and (b) Halmyropotamos (AMPG-HAL1967/1). Not in scale

Family Felidae FISCHER VON WALDHEIM, 1817
Subfamily Machairodontinae GILL, 1872
Genus *Paramachairodus* PILGRIM, 1931
Paramachairodus orientalis (KITTL, 1887)

Stratigraphical range: MN11-MN13

Geographical Range: Greece, Spain, Iran, Northern Macedonia, Hungary, Germany, Moldova and Ukraine

Localities: Pikermi, Silata, Thymiana B? (Koufos, 2011), Crevillente-15, Crevillente-16, Puente Minero, Concud. Maragheh (Salesa et al., 2010), Titov Veles, Chobruchi, Polgradi, Dorn Dorkheim, Taraklia, Chimishlija, Novo-Elizavetovka (NOW, 2016)

Table 19: Ecomorphological characteristics of *Paramachairodus orientalis*. Data from Salesa et al. (2010) and this study

Body Mass		80-100 kg
Canine W/L %		48-56%
Sum Intercuspid Notches		8
Dental Mesowear	**T**	1
	H	1-3

Dietary Category: 3

Diet: Medium-large sized ruminants (*Pliocervus*, *Protragelaphus*, *Tragoportax*), *Microstonyx*, *Hipparion*, *Mesopithecus*, young giraffes (*Helladotherium*, *Palaeotragus*), *Pliohyrax*, *Hystrix*.

Sociality: Solitary

Modern analogue: *Panthera onca*

Fig. 117: The holotype of *P. orientalis* (NHMW 2007z0172/0001). Source: Salesa et al. (2010)

Family Felidae FISCHER VON WALDHEIM, 1817
Subfamily Machairodontinae GILL, 1872
Genus *Megantereon* CROIZET & JOBERT, 1828
Megantereon cultridens (CUVIER, 1824)

Stratigraphical range: MN15-MN17

Geographical Range: Greece, France, Spain, Georgia, Romania and Tadzhikistan

Localities: Volax, Apollonia, Makineia (Koufos, 2014), Dmanisi, Saint Vallier, Etouaires, Pardines, Chilhac, Senéze, Villaroya, La Puebla de Valverde, Graunceanu, Kuruksaj (NOW, 2016)

Table 20: Ecomorphological characteristics of *Megantereon cultridens*. Data from Palmqvist et al. (2007) and this study

Body Mass		50-120 kg
Canine W/L %		37-60%
Dental Mesowear	**T**	1
	H	3

Dietary Category: 3

Diet: Medium-large sized ruminants (*Croizetoceros*, *Eucladoceros*, *Cervus*), horses, boars.

Sociality: Solitary

Modern analogue: *Panthera onca*

Fig. 118: *Megantereon cultridens*. Source: Antón (2013). Artist: M. Antón

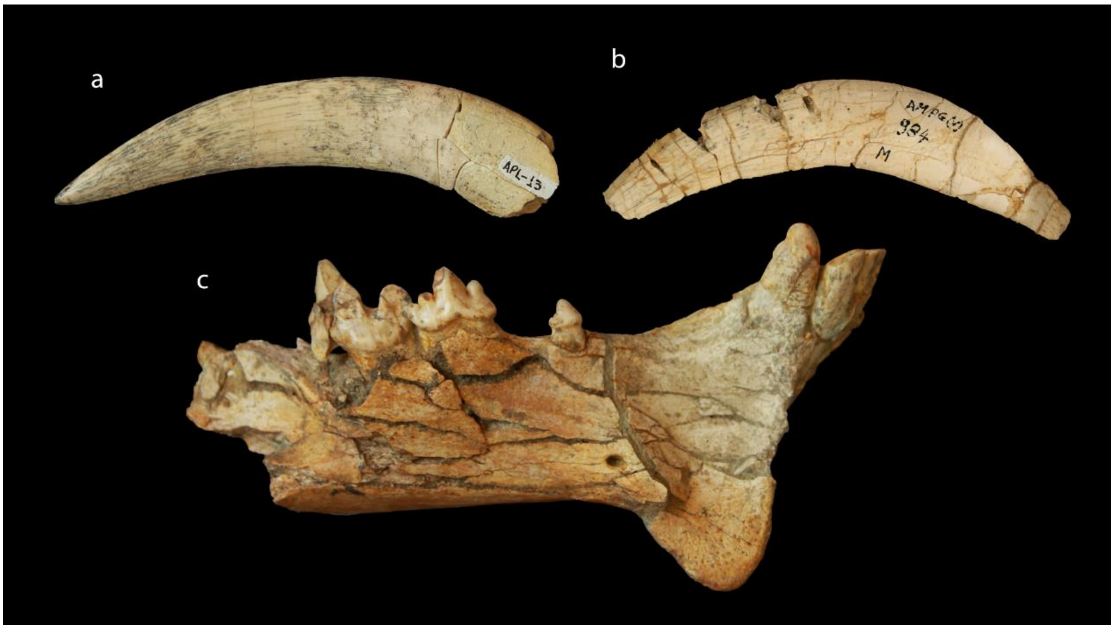


Fig. 119: *Megantereon cultridens* from Apollonia (a: LGPUT-APL-13; c: LGPUT-APL-12) and Makineia (AMPG-M984). Not in scale

Family Felidae FISCHER VON WALDHEIM, 1817
Subfamily Machairodontinae GILL, 1872
Genus *Homotherium* FABRINI, 1890
Homotherium crenatidens (WEITHOFER, 1889)

Stratigraphical range: MN14-MN18

Geographical Range: Greece, Bulgaria, Italy, France, Spain, Hungary, Romania, Ukraine, Georgia, Tadzhikistan

Localities: Sesklon, Tourkovounia, Milia, Livakkos (Koufos, 2014), Dmanisi, Slivnitsa, Odessa Catacombs, Saint Vallier, Triversa, Villaroya, La Puebla de Valverde, Kislang, Graunceanu, Kuruksaj (NOW, 2016)

Table 21: Ecomorphological characteristics of *Homotherium crenatidens*. Data from Ballesio (1963)

Body Mass		>150 kg
Canine W/L %		40%
Dental Mesowear	**T**	1
	H	1-3

Dietary Category: 3

Diet: Medium-large sized ruminants (*Croizetoceros*, *Eucladoceros*, *Cervus*), horses, boars.

Sociality: Solitary

Modern analogue: *Panthera leo*

A similar niche is proposed for *Homotherium latidens*.

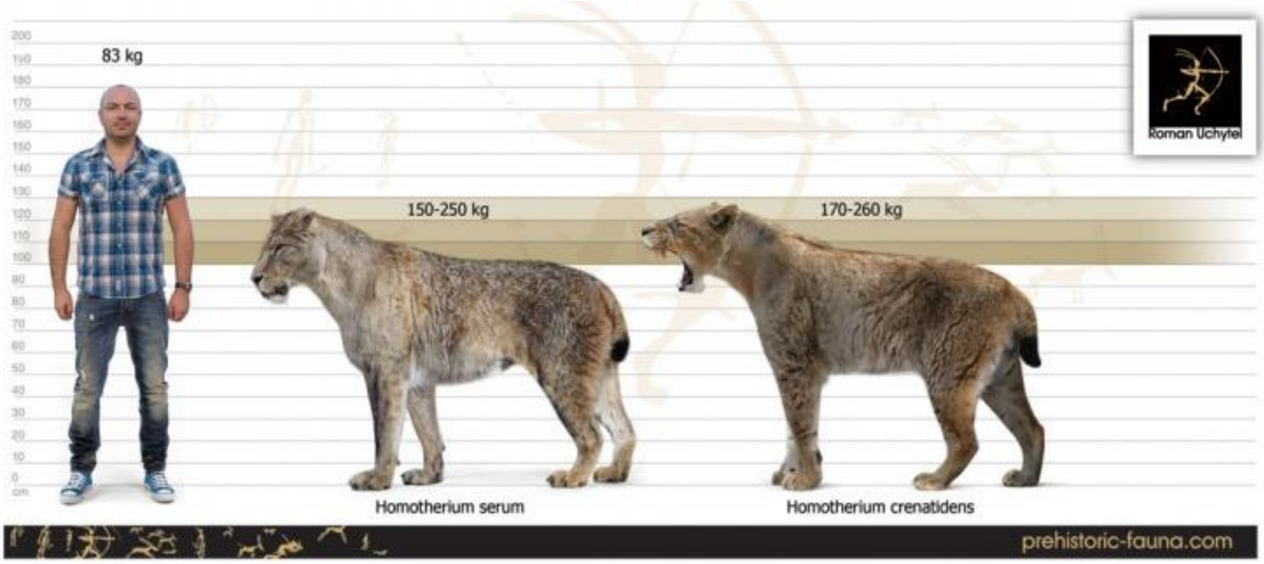


Fig. 120: *Homotherium serum* and *H. crenatidens*. Source: prehistoricfauna.com Artist: R. Uchytel

Family Felidae FISCHER VON WALDHEIM, 1817
Subfamily Machairodontinae GILL, 1872
Genus *Amphimachairodus* KRETZOI, 1929
Amphimachairodus giganteus (WAGNER, 1848)

Stratigraphical range: MN10-MN13

Geographical Range: Greece, Spain, France, Hungary, Turkey and Iran

Localities: Pikermi, Ravin-X, Halmyropotamos, Kerassia, Ravin des Zouaves 5, Samos, Thermopigi? (Koufos, 2011), Las Casiones, Cerro de la Garita, Crevillente-2, Los Mansuetos, Concud, Venta del Moro, Arquillo, Terassa, Milagros, Crevillente 16, Los Aljezares, Mt. Luberon, Baltavar, Chalta, Maragheh (NOW, 2016)

Table 22: Ecomorphological characteristics of *Amphimachairodus giganteus*.

Body Mass		>150 kg
Canine W/L %		33-43%
Canine Bite Force		3378 N
Carnassial Bite Force		4614 N
Endocranial Volume		234 mL
Sum Intercuspid Notches		14
Relative Rostrum Width		22%
Dental Mesowear	**T**	1
	H	1-3

Dietary Category: 3

Diet: Large sized ruminants (*Tragoportax*, *Palaeoryx*), *Hipparion*, young giraffes (*Helladotherium*, *Samotherium*), *Microstonyx, Pliohyrax*, *Hystrix*

Sociality: Solitary

Modern analogue: *Panthera tigris*

Fig. 121: *Amphimachairodus giganteus*. Source: Antón (2013). Artist: M. Antón

Fig. 122 : *Amphimachairodus giganteus* from Halmyropotamos (a: HAL1967/5) and Pikermi (b: AMPG-PG01/100). Not in scale.

Family Hyaenidae Gray, 1821
Subfamily Ictitheriinae Trouessart, 1897
Genus *Plioviverrops* Kretzoi, 1938
Plioviverrops orbignyi (Gaudry & Larteti, 1856)

Stratigraphical Range: MN11-MN12

Geographical Range: Greece and Spain

Localities: Pikermi, Ravin des Zouaves 5, Prohoma-1, Vathylakkos-2,3, Perivolaki, Samos, Kerassia (Koufos, 2011), Los Aljezares (NOW, 2016)

Table 23: Ecomorphological characteristics of *Plioviverrops orbignyi*.

Body Mass		3.5-7.3 kg
Canine Sx/Sy		3.7/5.5
Canine Bite Force		230-280 N
Carnassial Bite Force		380-520 N
Endocranial Volume		20-27 mL
Sum Intercuspid Notches		8
Relative Rostrum Width		14-20%
M1BSZ		0.09
M2SZ		0.06
UGR		0.09-0.10
Dental Mesowear	**T**	1-3
	H	1-2

Dietary Category: 9

Diet: Rodents (e.g. *Parapodemus*, *Micromys*), insectivores (*Schizogalerix*), birds, reptiles, insects, plant material between 30-50% (fruits, seeds, fungi).

Sociality: Solitary

Modern analogue: *Martes foina*

Fig. 123: *Plioviverrops orbignyi*. Source: tsaagan.tumblr.com. Artist: J. Lacerda

Fig. 124: *Plioviverrops orbignyi* from (a) Samos (NHMA-MTLB-170)
and (b) Perivolaki (LGPUT-PER-1). Not in scale.

Family Hyaenidae GRAY, 1821
Subfamily Ictitheriinae TROUESSART, 1897
Genus *Protictitherium* KRETZOI, 1938
Protictitherium gaillardi (GAUDRY & LARTETI, 1856)

Stratigraphical Range: MN4-MN10

Geographical Range: Greece, France, Germany, Spain, and Turkey

Localities: Antonios, La Grive (Koufos, 2011), Contres MN5, Bizian, Castelnau-d'Arbieu, Pontlevoy, Langenau 1, Can Llobateres I, Can Ponsic, Arroyo del Val, Paracuellos 3, Castell de Barberu, Santiga, Simorre, Terassa, Handir?, Pasalar (NOW, 2016)

Table 24: Ecomorphological characteristics of *Protictitherium gaillardi*

Body Mass		≈5 kg
M1BSZ		0.11
Dental Mesowear	**T**	1
	H	1

Dietary Category: 9

Diet: Rodents (e.g. *Parapodemus*, *Micromys*), insectivores (*Schizogalerix*), birds, reptiles, insects, plant material between 10-25% (fruits, seeds, fungi).

Sociality: Solitary

Modern analogue: *Genetta genetta*

A similar niche is proposed for all the species of *Protictitherium*.

Fig. 125: *Protictitherium* spp. Source: carnivora.net Artist: M. Antón

Fig. 126: *Protictitherium gaillardi* from Malartic (a: MNHN-SML-453; b: MNHN-SML-1194). Not in scale

Family Hyaenidae GRAY, 1821
Subfamily Ictitheriinae TROUESSART, 1897
Genus *Ictitherium* WAGNER, 1848
Ictitherium viverrinum (ROTH & WAGNER, 1854)

Stratigraphical Range: MN10-MN13

Geographical Range: Greece, France, Spain, Germany, Northern Macedonia, Moldova, Slovakia, Georgia, Ukraine, Turkey, Iran, Kazakhstan, Kirgizija and China

Localities: Pikermi, Ravin des Zouaves-5, Prochoma-1, Vathylakkos-3, PER?, Samos? (Koufos, 2011), Montredon, Vösendorf, Belka, Chobruchi, Grebeniki, Novoelisavetovka, Titov Veles, Loc 12, Loc 31, Chen Chia Mao Kou, Chen Kou, Chin Kou, Chou Chia Kou, Huan Lou Kou, Liao Wan Kou, Nan Ho, Ta Tung Kou, Yan Mu Kou (Werdelin & Solounias, 1991), Milagros, Borsky Svaty Jur, Middle Sinap, Bazaleti, Maragheh, Saty Lower, Ortok, Lufeng, Junggar-botamoyin, Junggar-Ganqikairixi (NOW, 2016)

Table 25: Ecomorphological characteristics of *Ictitherium viverrinum*.

Body Mass		10-16 kg
Canine Sx/Sy		12/16
Canine Bite Force		520-873 N
Carnassial Bite Force		853-1479N
Endocranial Volume		45-65 mL
Sum Intercuspid Notches		10-15
Relative Rostrum Width		14-22%
M1BSZ		0.10-0.12
M2SZ		0.36-0.53
LGR		0.06-0.07
UGR		0.09
Dental Mesowear	**T**	1-3
	H	1-3

Dietary Category: 9-10

Diet: Small-medium sized ruminants (*Gazella*, *Pliocervus*, *Dorcatherium*), young hipparions, *Mesopithecus*, hares (*Prolagus*, *Alilepus*), rodents (*Parapodemus*, *Micromys*, *Hystrix*), *Pliohyrax*, birds (*Pavo*), reptiles, plant material between 20-40% (fruits, seeds, fungi).

Sociality: Social

Modern analogue: *Canis mesomelas*

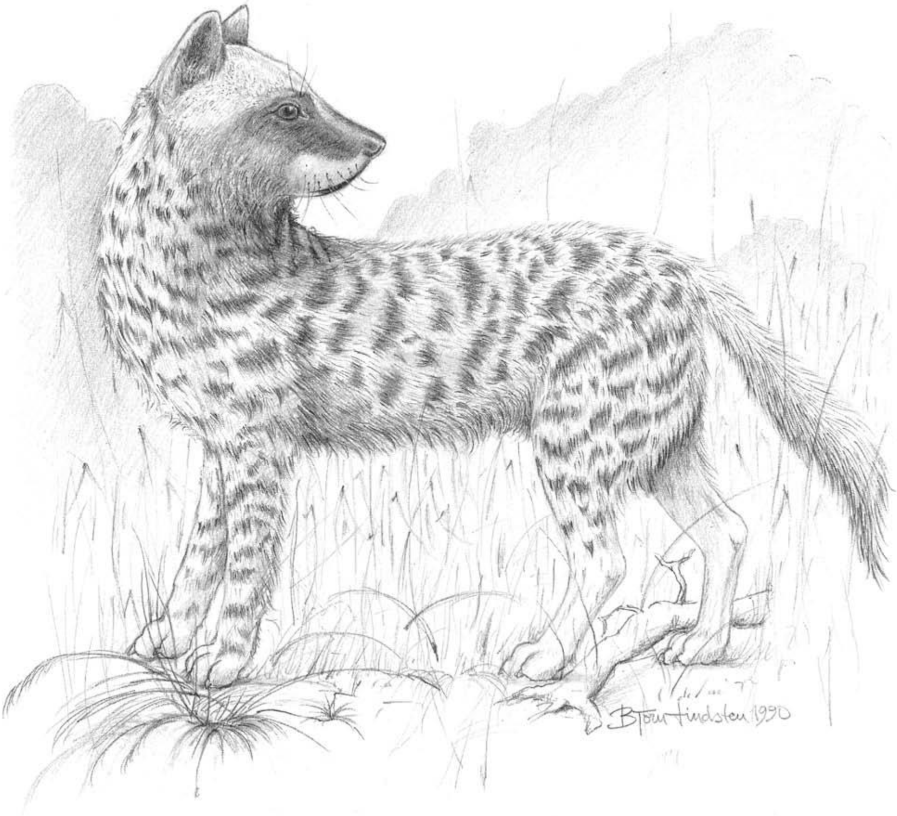


Fig. 127: *Ictitherium viverrinum*. Source: Werdelin & Solounias (1991).

Fig. 128: *Ictitherium viverrinum* from Pikermi (NHMUK-M8981).

Family Hyaenidae Gray, 1821
Subfamily Ictitheriinae Trouessart, 1897
Genus *Hyaenotherium* Semenov, 1989
Hyaenotherium wongii (Zdansky, 1924)

Stratigraphical Range: MN10-MN12

Geographical Range: Greece, Turkey, Germany, Ukraine, Iran, Kazakhstan and China

Localities: Pikermi, Ravin des Zouaves-1, Ravin des Zouaves-5, Vathylakkos 2-3, Samos (Koufos, 2011), Höwenegg, Akin, Bota-Mojnak, Cherevichnoe, Grebeniki, Maragheh, Tie Chia Kou, Loc 35, Loc 43, Yan Mu Kou, Chen Chia Mao Kou, Huan Lou Kou, Loc 110, Nan Liang Kou, Loc 115, Loc 116, Chao Tsu Kou, Chin Kou, Chou Chia Kou, Fu Ku Hsien, He Tsui Chu, His Mao Kou, Hsiao Kou Chan, Hsin Yao, Jen Tse Kou, Kou Chia Ta, Kuer Shan, Lao Yeh Mao Kou, Liao Wan Kou, Lou Wan Kou, Lu Kao Ling, Ma Chi Liang Kou, Nan Hao Hsia, Nan Ho, Pai Tao Tsun, Tu Kou (Werdelin & Solounias, 1991), Hobanpinar (AS_42), Kemiklitepe A-B, Botamojnak, Saty Lower (NOW, 2016)

Table 26: Ecomorphological characteristics of *Hyaenotherium wongii*.

Body Mass		20-23 kg
Canine Sx/Sy		19-20/28-30
Canine Bite Force		560-795 N
Carnassial Bite Force		995-1330 N
Endocranial Volume		80-90 mL
Sum Intercuspid Notches		13
Relative Rostrum Width		17-19%
M1BSZ		0.10-0.11
M2SZ		0.34-0.44
LGR		0.50-0.65
UGR		0.07-0.08
Dental Mesowear	**T**	1-3
	H	1-3

Dietary Category: 9

Diet: Medium sized ruminants (*Pliocervus*, *Gazella*), hipparions, *Pliohyrax*, *Amphiorycteropus*, *Hystrix*, *Mesopithecus*, birds (*Pavo*), plant material 10-25% (fruits, seeds, fungi)

Sociality: Social

Modern analogue: *Canis latrans*

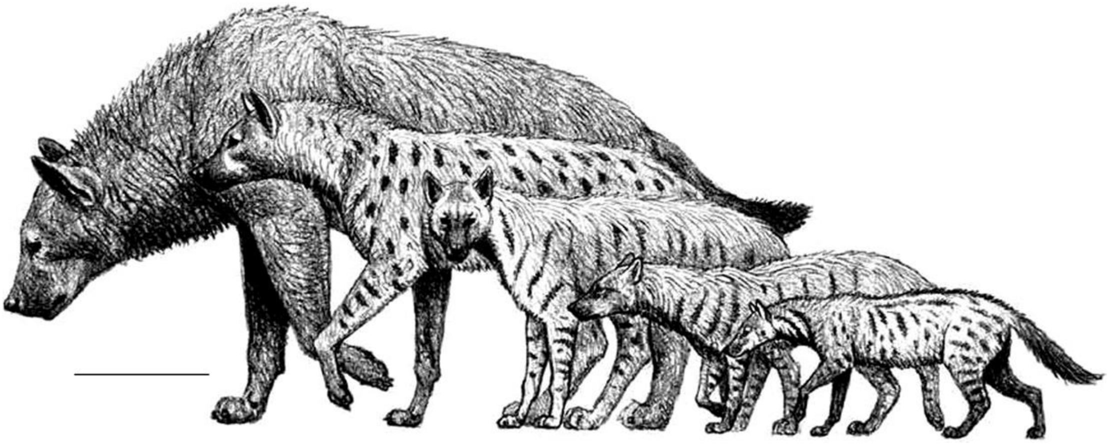


Fig. 129: From left to right: *Adcrocuta eximia*, *Hyaenotherium wongii*, *Ictitherium viverrinum*, *Protictitherium crassum*, *Plioviverrops orbignyi*. Source: Turner et al. (2008). Artist: M. Antón

Fig. 130: *Hyaenotherium wongii* from Samos (a:NHMA-MTLA-200, b: NHMA-MTLB-171) . Not in scale.

Family Hyaenidae GRAY, 1821
Subfamily Hyaeninae GRAY, 1821
Genus *Lycyaena* HENSEL, 1863
Lycyaena chaeretis (GAUDRY, 1861)

Stratigraphical Range: MN10-MN13

Geographical Range: Greece, Italy, Spain and Moldova

Localities: Pikermi, Samos (Koufos, 2011), Cerro de la Garita, Valdecebro 5, Los Mansuetos, Arquillo, Brisighella, La Roma, Taraklia (NOW, 2016)

Table 27: Ecomorphological characteristics of *Lycyaena chaeretis*. Data from Roussiakis (1996) and present study.

Body Mass		≈35 kg
Canine Bite Force		1200 N
Carnassial Bite Force		2080 N
Endocranial Volume		127 mL
Sum Intercuspid Notches		10-11
P3 W/L		0.60-0.61
p4 W/L		0.46-0.52
Relative Rostrum Width		22%
Dental Mesowear	**T**	1-3
	H	1-3

Dietary Category: 3

Diet: Medium-large sized ruminants (*Pliocervus*, *Tragoportax*, *Palaeotragus*), *Hipparion*, *Pliohyrax*, *Hystrix*, birds.

Sociality: Solitary

Modern analogue: *Hyaena hyaena*

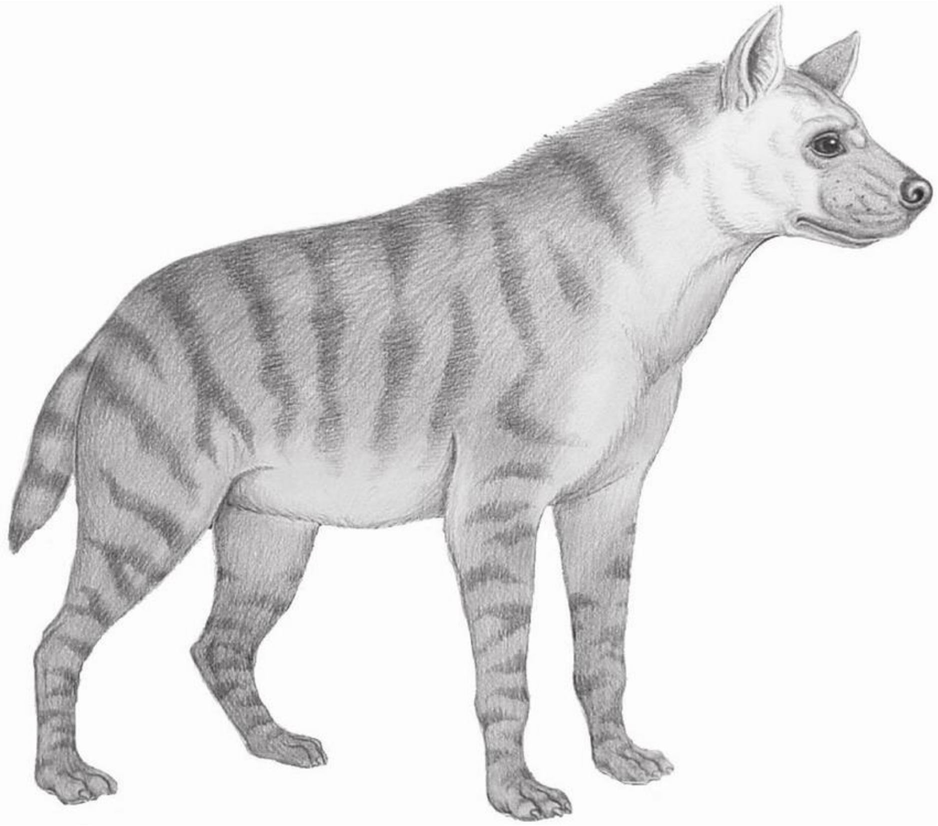


Fig. 131: *Lycyaena chaeretis*. Source: Sardella (2008). Artist: M. Sami

Fig. 132: *Lycyaena chaeretis* from Pikermi (a: NHMUK-M8978; b: NHMUK-M8979). Not in scale.

Family Hyaenidae GRAY, 1821
Subfamily Hyaeninae GRAY, 1821
Genus *Chasmaporthetes* HAY, 1921
Chasmaporthetes lunensis (DEL CAMPANA, 1914)

Stratigraphical Range: MN14-MN17

Geographical Range: Greece, Italy, Spain, France, Germany, Turkey, Ukraine, Russia, Tadzhikistan, Mongolia and China

Localities: Dafnero 1 (Koufos, 2014), Inferno, Olivola, Triversa, La Puebla de Valverde, Layna, Villaroya, Etouaires, Pardines, Roccaneyra, Senèze, St. Vallier, Erpfinger Höhle, Neulingen, Schernfeld, Beregovaia, Odessa Catacombs, Gülyazi, Shamar, Loc A, Dongancun, Hsia-Chuang, Malancun, Ma Tzu Kou, Niu Wa Kou, Ouniwa, Zhaohuangcun (Werdelin & Solounias, 1991), Kuruksaj, El Rincon, Chalta (NOW, 2016)

Table 28: Ecomorphological characteristics of *Chasmaporthetes lunensis*. Data from Antón et al. (2006), Coca-Ortega & Pérez-Claros (2019) and present study.

Body Mass		≈40 kg
P3 W/L		58-65%
p4 W/L		48-51%
Relative Rostrum Width		28%
Dental Mesowear	**T**	1-3
	H	1-3

Dietary Category: 3

Diet: Medium-large sized ruminants (*Gazellospira*, *Croizetoceros*, *Eucladoceros*) boars, horses.

Sociality: Social (Antón et al., 2016)

Modern analogue: *Lycaon pictus*

Fig. 133: *Chasmaporthetes lunensis*. Source: Antón et al. (2016). Artist: M. Antón

Fig. 134: *Chasmaporthetes lunensis* from Dafnero (a: LGPUT-DFN-75; b: 109; c: 111; d: 117; e: 194). Not in scale.

Family Hyaenidae GRAY, 1821
Subfamily Hyaeninae GRAY, 1821
Genus *Adcrocuta* KRETZOI, 1938
Adcrocuta eximia (ROTH & WAGNER, 1854)

Stratigraphical Range: MN10-MN13

Geographical Range: Greece, Bulgaria, Northern Macedonia, France, Spain, Rumania, Hungary, Austria, Germany, Turkey, Moldova, Georgia, Ukraine, Kazakhstan, Iran, Libya, Kirgizia, Tadzhikistan, Afghanistan, Pakistan and China

Localities: Halmyropotamos, Xirochori-1, Ravin de la Pluie, Ravin des Zouaves-1, 5, Prochoma-1, Vathylakkos-3, Samos, Perivolaki, Kerassia (Koufos, 2011), Kalimantsi, Titov Veles, Mt Leberon, Baltavar, Polgradi, Cimislia, Arquillo de la Fontana, Concud, Los Aljezares, Los Mansuetos, Masia del Barbo, Pena del Macho, Piera, Amasya Coban Pinar, Karain, Kavak Dere, Kinik, Kuyutarla, Mahmutgazi, Mugla, Bazalethi, Belka, Cherevinchnoe, Grebeniki, Novajaemetovka, Novoelisavetovka, Novoukrainka, Pavlodar, Starokondakovo, Chobruchi, Taraklia, Maragheh, Sahabi, Hasnot, Loc 12, Tie Chia Kou, Loc 31, San Chia Liang Kou, Loc 44, Yan Mu Kou, Chen Chia Mao Kou, Huan Lou Kou, Loc 110, Loc 114n, Ma Hua Tan, Loc 115, Chao Tsu Kou, Chang Chia Chuang, Chin Kou, Chou Chia Kou, Chou Fen Ta, Hsiao Kou Shan, Hsin Yao, Kou Chia Ta, Liao Wan Kou, Ma Chi Liang Kou, Nan Hao Hsia, Nan Ho, Pai Tao Tsun, Ta Tung Kou, Tung Ta Ling, Ta Tsun, Wang Lou Kou (Werdelin & Solounias, 1991), Tudorovo, Csakvar, Kemiklitepe A-B, Villadecavalls, Puente Minero, Kohfidisch, Dorn Dörkheim, Udabno II, Tiraspol, Grossulovo, Amasya, Kalmakpaj, Dzhuanaryk, Karabastuz, Molayan, Sor, Lantian-Koujiacun (NOW, 1991)

Table 29: Ecomorphological characteristics of *Adcrocuta eximia*. Data from Roussiakis (1996) and present study.

Body Mass		≈60-70 kg
Canine Sx/Sy		90-120/110-150
Canine Bite Force		1100-2400 N
Carnassial Bite Force		1700-3500 N
Endocranial Volume		130-200 mL
Sum Intercuspid Notches		10-13
P3 W/L		0.60-0.73
p4 W/L		0.54-0.65
Relative Rostrum Width		21-29%
Dental Mesowear	**T**	1-3
	H	1-3

Dietary Category: 3-5

Diet: Medium-large sized ruminants (*Pliocervus*, *Tragoportax*, *Palaeotragus*), hipparions, *Pliohyrax*, *Amphiorycteropus*, *Hystrix*, birds

Sociality: Social

Modern analogue: *Crocuta crocuta*

Fig. 135: *Adcrocuta eximia*, *Amphimachairodus giganteus* and a gomphothere. Source:pinterest.com
Artist: V. Simeonovski

Fig. 136: *Adcrocuta eximia* from Pikermi (a: NHMUK-M8966, adult; b: NHMUK-M8968, sub-adult; c: NHMUK-8980, juvenile). Not in scale

Family Hyaenidae GRAY, 1821
Subfamily Hyaeninae GRAY, 1821
Genus *Pliohyaena* KRETZOI, 1938
Pliohyaena perrieri (CROIZET & JOBERT, 1828)

Stratigraphical Range: MN14-MN20

Geographical Range: Greece, Bulgaria, Italy, France, Spain, Germany, Austria, Great Britain, Netherlands, Slovakia, Romania, Ukraine, Russia, Georgia, Tunisia, Turkey, Tadzhikistan and China

Localities: Sesklon, Gerakarou (Koufos, 2014), Petralona (Baryshnikov & Tsoukala, 2010), Hullabrunn, Hajnačka, Ardé, Etouaires, Es-Taliens, L' Escale, Lunel-Viel, Montmaurin, Montsaunes, Senèze, Serrat d'En Vacquer, St. Vallier, Vallonet, Erpfinger Höhle, Greusnach, Gundersheim, Mauer, Mosbach, Red Crag, Montipoli, Olivola, Tasso, Tegelen, La Calera II, La Puebla de Valverde, Layna, Villaroya, Kuruksai, Navorukho, Odessa Catacombs, Aïn Brimba, Gülyazi, Yassiörren, Haiyan, Hsia Chwang, Hsingyangcun, Ichuangtsun, Malancun, Nihowan, Niu Wa Kou, Wangianggou, Yinjiao, Zhangwagou (Werdelin & Solounias, 1991), Varshets, Sarikol Tepe, Perpignan, La Gloria 4, Graunceanu. Dmanisi, Udunga, Kuruksaj, Gaozhuang (NOW, 2016)

Table 30: Ecomorphological characteristics of *Pliohyaena perrieri*.
Data from Vinuesa et al. (2014, 2015), Coca-Ortega & Pérez-Claros (2019) and present study.

Body Mass		≈60 kg
Endocranial Volume		130-145 mL
P3 W/L		65-77%
p4 W/L		47-63%
Relative Rostrum Width		14-16%
Dental Mesowear	**T**	1-3

Dietary Category: 3-5

Diet: Medium-large sized ruminants (*Gazellospira*, *Croizetoceros*, *Eucladoceros*, young *Mitilanotherium*), boars, horses.

Sociality: Social

Modern analogue: *Crocuta crocuta*

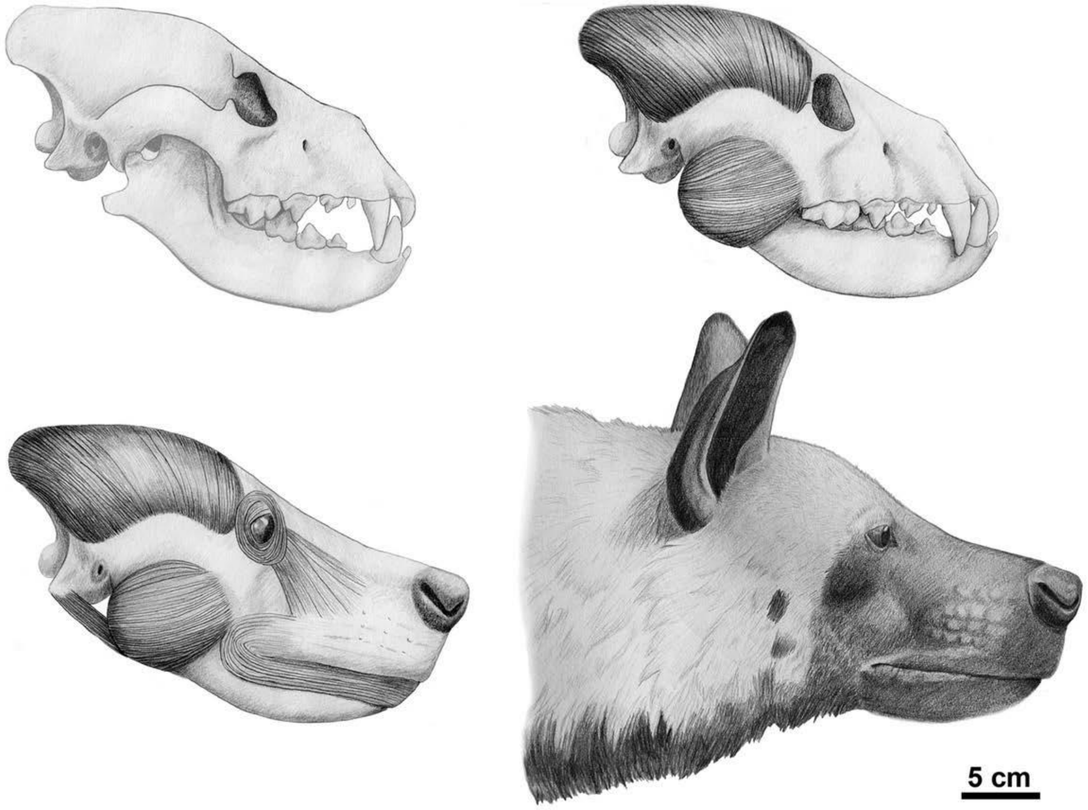


Fig. 137: *Pliohyaena perrieri*. Source: Vinuesa et al. (2014).

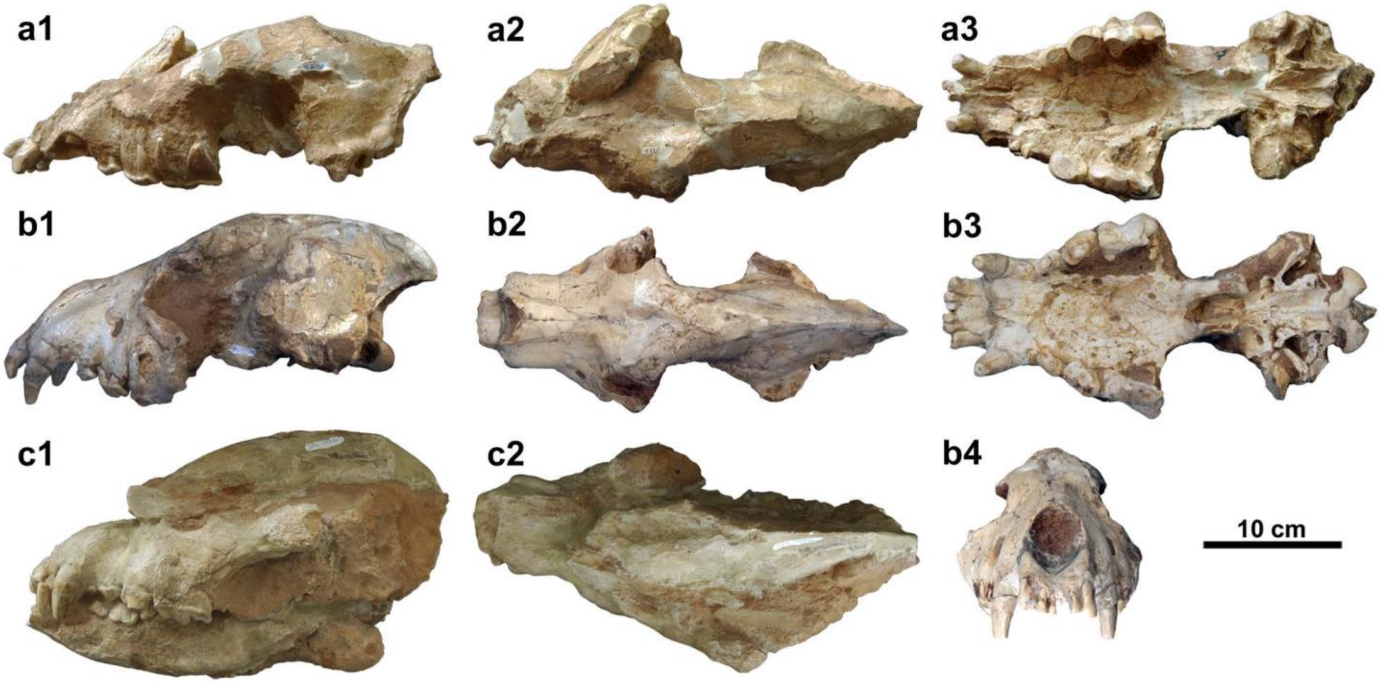


Fig. 138: *Pliohyaena perrieri* from Villarroya and La Puebla de Valverde. Source: Vinuesa et al. (2014)

Family Hyaenidae GRAY, 1821
Subfamily Hyaeninae GRAY, 1821
Genus *Pachycrocuta* KRETZOI, 1938
Pachycrocuta brevirostris (GERVAIS, 1850)

Stratigraphical Range: MN16-MN20

Geographical Range: Greece, Northern Macedonia, Italy, France, Spain, Germany, Great Britain, Slovakia, Hungary, Russia, Tadzhikistan, Kirgizia, Pakistan, India, Indonesia, Mongolia and China

Localities: Gerakarou, Apollonia, Kalamoto, Livakkos (Koufos, 2014), Foggia, Olivolla, Tasso, Stránska Skála, Meiningen, Sainzelles, Süssenborn, Würzburg-Schalksberg, Cromer Forest Bed, Gombaszög, Manastrirec, Jamu District, Siwaliks, Haro River, Sangiran, Chang Chih Hsien, Choukoutien Loc 1, Fu Min Hsien, Haiyan, Nihowan (Werdelin & Solounias, 1991), Casablanka, Zasukhino 3, Lakhuti 2, Tepke , Kopala 2 (NOW, 2016)

Table 31: Ecomorphological characteristics of *Pachycrocuta brevirostris*
Data from Palmqvist et al. (2011), Coca-Ortega & Pérez-Claros (2019) and present study.

Body Mass		≈100 kg
P3 W/L		65-77%
p4 W/L		63-71%
Dental Mesowear	**T**	1-3
	H	1-3

Dietary Category: 3-5

Diet: Medium-large sized ruminants (*Gazellospira*, *Croizetoceros*, *Eucladoceros*, young *Mitilanotherium*), boars, horses.

Sociality: Social

Modern analogue: *Crocuta crocuta*

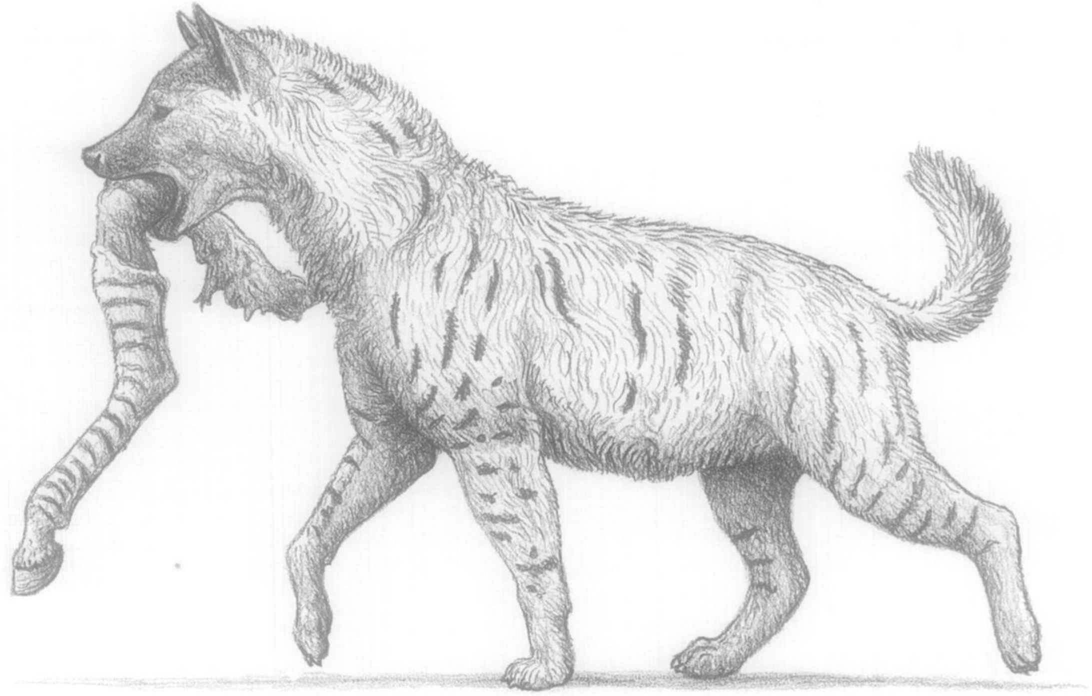


Fig. 139: *Pachycrocuta brevirostris*. Source: Turner & Antón (1996). Artist: M. Antón

Family Percrocutidae WERDELIN & SOLOUNIAS, 1991
Genus *Dinocrocuta* SCHMIDT-KITTLER, 1976
Dinocrocuta gigantea (SCHLOSSER, 1903)

Stratigraphical Range: MN9-MN12

Geographical Range: Greece, Bulgaria, Spain, Georgia, Mongolia, Tibet and China

Localities: Pentalophos-1 (Koufos, 2011), Tientsin, Shansi, Tibetfluss (Schlosser, 1903), Biru, Tianzhu, Hezheng, Latian, Fugu (Zhang, 2005), Aljezar B, Blagoevgrad, Nessebar, Eldari I, Natlismtsemeli I, Altan-Teli (NOW, 2016)

Table 32: Ecomorphological characteristics of *Dinocrocuta gigantea*
Data from Koufos (1995), Deng & Tseng (2010) and present study.

Body Mass		300+ kg
P3 W/L		71.4%
p4 W/L		51-60%
Dental Mesowear	**T**	1-3
	H	1-3

Dietary Category: 3-5

Diet: Medium-large sized ruminants (*Palaeotragus*, *Protoryx*, *Ouzocerus*), *Hipparion*, *Chilotherium*

Sociality: ?

Modern analogue: *Crocuta crocuta*

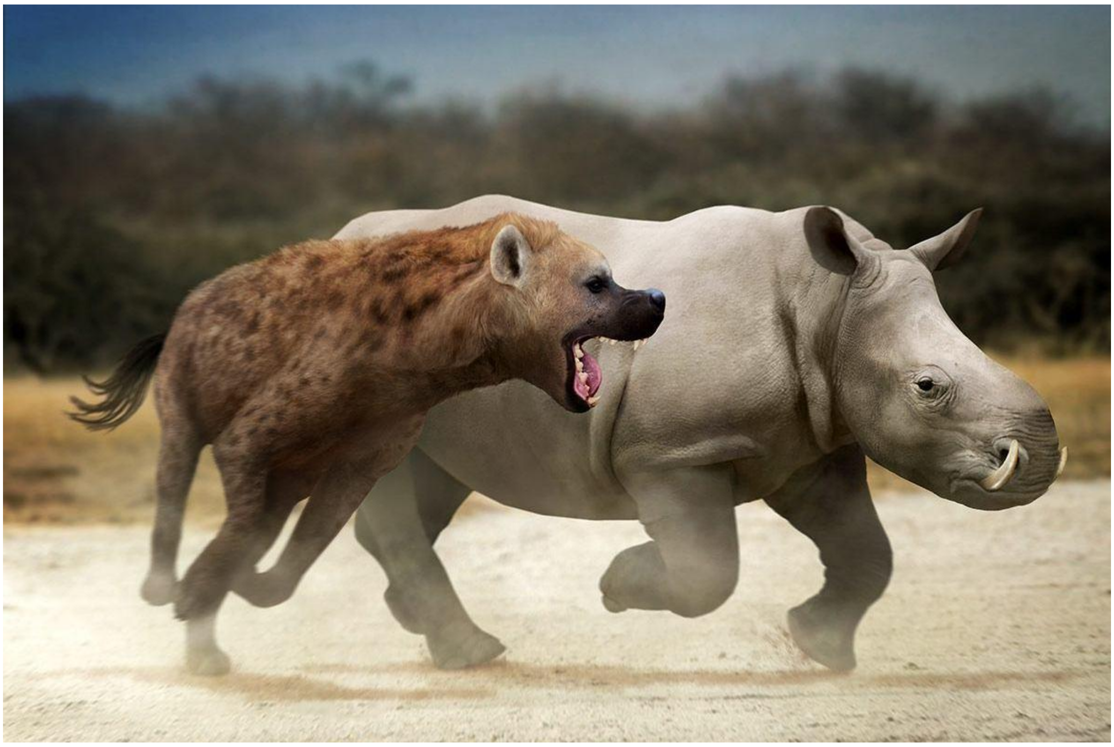


Fig. 140: *Dinocrocuta gigantea* and *Chilotherium.* Source: eartharchives.org. Artist: J. Lacerda

Fig. 141: *Dinocrocuta gigantea* from Pentalophos (LGPUT-PNT-70)

Family Percrocutidae WERDELIN & SOLOUNIAS, 1991

Genus *Dinocrocuta* SCHMIDT-KITTLER, 1976

Dinocrocuta salonicae (ANDREWS, 1918)

Stratigraphical Range: MN9-MN11?

Geographical Range: Greece

Localities: Diavata (Andrews, 1918; Koufos, 2011),

Table 33: Ecomorphological characteristics of *Dinocrocuta salonicae*
Data from Koufos (1995), Deng & Tseng (2010) and present study.

Body Mass		300+ kg
P3 W/L		71.4%
Dental Mesowear	**T**	1-3
	H	1-3

Dietary Category: 3-5

Diet: Medium-large sized ruminants (*Palaeotragus*, *Protoryx*, *Ouzocerus*), *Hipparion*, *Chilotherium*

Sociality: ?

Modern analogue: *Crocuta crocuta*

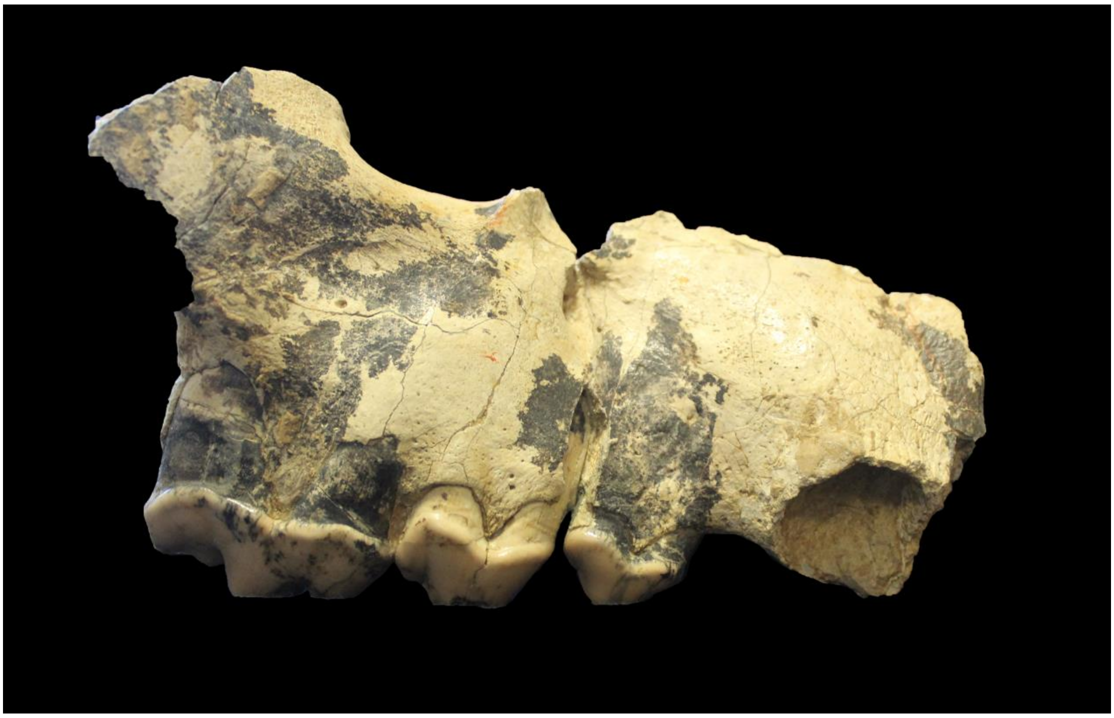


Fig. 142: *Dinocrocuta salonicae* from Diavata (MNHUK-M11413)

Family Percrocutidae WERDELIN & SOLOUNIAS, 1991
Genus *Belbus* WERDELIN & SOLOUNIAS, 1991
Belbus beaumonti (QIU, 1987)

Stratigraphical Range: MN12

Geographical Range: Greece

Localities: Samos (Koufos, 2011),

Table 34: Ecomorphological characteristics of *Belbus beaumonti*
Data from de Beaumont (1968) and present study.

Body Mass		≈40 kg
p4 W/L		52.5%
Dental Mesowear	**T**	1
	H	1

Dietary Category: 3-5

Diet: Medium sized ruminants (*Pliocervus*, *Gazella*), hipparions, *Pliohyrax*, *Amphiorycteropus*, *Hystrix*, birds.

Sociality: Solitary

Modern analogue: *Hyaena hyaena*

Fig. 143: *Belbus beaumonti* from Samos (SMNS-32)

Family Mustelidae FISHER DE WALDHEIM, 1817
Subfamily Mustelinae FISHER DE WALDHEIM, 1817
Genus *Martes* PINEL, 1792
Martes woodwardi PILGRIM, 1931

Stratigraphical Range: MN12

Geographical Range: Greece

Localities: Pikermi (Koufos, 2011)

Table 35: Ecomorphological characteristics of *Martes woodwardi*

Body Mass		4.5-5.5 kg
Dental Mesowear	**T**	1
	H	1

Dietary Category: 9

Diet: Rodents (e.g. *Parapodemus*, *Micromys*), hares (*Prolagus*, *Alilepus*), insectivores (*Schizogalerix*), birds, reptiles, fish, eggs, insects, plant material 20-40% (fruits, seeds, fungi).

Sociality: Solitary

Modern analogue: *Martes foina*

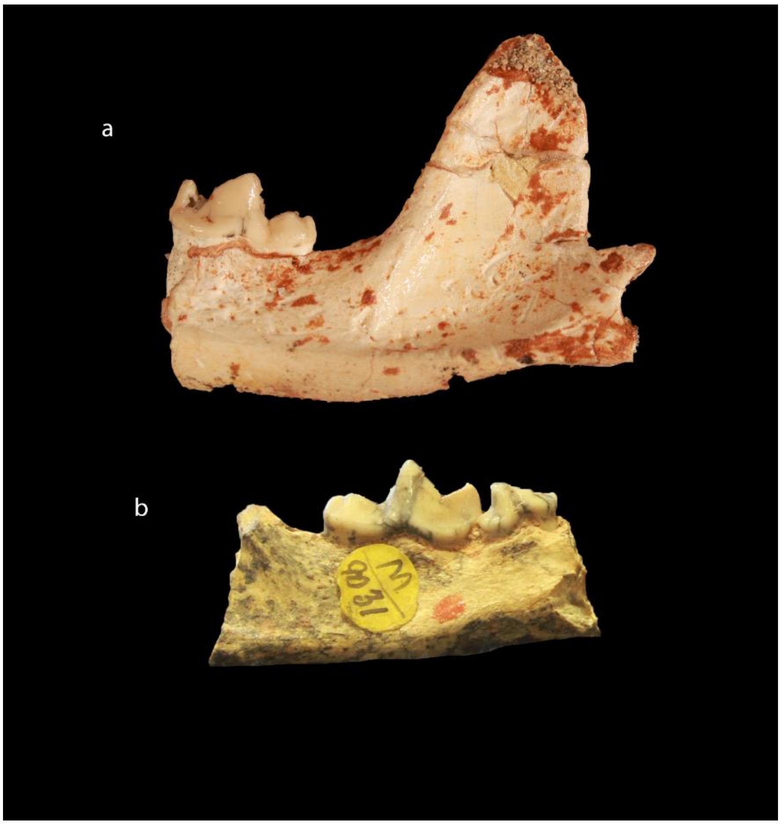


Fig. 144: *Martes woodwardi* from Pikermi (a: AMPG-PA2032/91; b: MNHUK-M9031). Not in scale.

Family Mustelidae FISHER DE WALDHEIM, 1817
Subfamily Mustelinae FISHER DE WALDHEIM, 1817
Genus *Sinictis* ZDANSKY, 1924
Sinictis pentelici (GAUDRY, 1861)

Stratigraphical Range: MN12

Geographical Range: Greece

Localities: Pikermi (Koufos, 2011)

Table 36: Ecomorphological characteristics of *Sinictis pentelici*

Body Mass		6.2 kg
M1BSZ		0.13
M2SZ		0.04
LGR		0.07
Dental Mesowear	**T**	1
	H	1

Dietary Category: 9

Diet: Rodents (e.g. *Parapodemus*, *Micromys*), hares (*Prolagus*, *Alilepus*), insectivores (*Schizogalerix*), birds, reptiles, fish, eggs, insects, plant material 20-40% (fruits, seeds, fungi).

Sociality: Solitary

Modern analogue: *Martes foina*

Fig. 145: *Sinictis pentelici* (MNHN-PIK-326). Courtesy: S. Roussiakis

Family Mustelidae FISHER DE WALDHEIM, 1817
Subfamily Mustelinae FISHER DE WALDHEIM, 1817
Genus *Baranogale* KORMOS, 1934
Baranogale* aff. *helbingi KORMOS, 1934

Stratigraphical Range: MN14-MN17

Geographical Range: Greece and Poland

Localities: Dafnero-1 (Koufos, 2014), Podlesice, Weze 1, Rebielice Krolewskie 1 (NOW, 2016)

Table 37: Ecomorphological characteristics of *Baranogale helbingi*

Body Mass		2.7
Total Intercuspid Notches		9
Dental Mesowear	**T**	2
	H	2

Dietary Category: 9

Diet: Rodents, birds, lizards, eggs, insects, plant material 20-30% (fruits, seeds, fungi).

Sociality: Solitary

Modern analogue: *Martes foina*

Fig. 146: The specimen attributed to *Baranogale* aff. *helbingi* (LGPUT-DFN-189)

Family Mustelidae FISHER DE WALDHEIM, 1817
Subfamily Mustelinae FISHER DE WALDHEIM, 1817
Genus *Plesiogulo* ZDANSKY, 1924
Plesiogulo crassa TEILHARD & LEROY, 1945

Stratigraphical Range: MN11-MN13

Geographical Range: Greece, Italy, Kazakhstan

Localities: Vathylakkos-3, Perivolaki, Pikermi?, Maramena? (Koufos, 2011), Baccinelo V3, Botamojnak, Kalmakpaj (NOW, 2016)

Table 38: Ecomorphological characteristics of *Plesiogulo crassa*

Body Mass		60-80 kg
Endocranial Volume		100 mL
Relative Rostrum Width		22%
Canine Sx/Sy		66/85
Canine Bite Force		922 N
Carnassial Bite Force		1400 N
Total Intercuspid Notches		2
M1BSZ		0.12
M2SZ		0.04
LGR		0.07
UGR		0.09
Dental Mesowear	**T**	2
	H	2

Dietary Category: 9

Diet: Young ruminants (*Gazella*, *Dorcatherium*, *Pliocervus*), rodents (e.g. *Parapodemus*, *Micromys*), hares (*Prolagus*, *Alilepus*), insectivores (*Schizogalerix*), birds, reptiles, fish, eggs, insects, plant material 20-40% (fruits, seeds, fungi).

Sociality: Solitary

Modern analogue: *Gulo gulo*

Fig. 147: *Plesiogulo crassa*. Source: dinopedia.fandom.com

Fig. 148: *Plesiogulo crassa* from Perivolaki (LGPUT-PER1239). Not in scale.

Family Mustelidae FISHER DE WALDHEIM, 1817
Subfamily Melinae BONAPARTE, 1838
Genus n. g.
Species n. sp.

Stratigraphical Range: MN12

Geographical Range: Greece

Localities: Pikermi

Table 39: Ecomorphological characteristics of Mustelidae n. sp.

Body Mass		7 kg
Relative Rostrum Width		18%
M1BSZ		0.09
UGR		0.12
Dental Mesowear	**T**	1
	H	1

Dietary Category: 9-10

Diet: Rodents (e.g. *Parapodemus*, *Micromys*), insectivores (*Schizogalerix*), birds, reptiles, insects, eggs, plant material 30-40% (fruits, seeds, fungi, grass).

Sociality: Solitary

Modern analogue: *Mellivora capensis*

Fig. 149: The skull and the two hemimandibles of Mustelidae n. sp. (PA4879/91)
in occlusal and lateral view.

Family Mustelidae Fisher de Waldheim, 1817
Subfamily Melinae Bonaparte, 1838
Genus *Promeles* Zittel, 1893
Promeles palaeattica (Weithofer, 1888)

Stratigraphical Range: MN11-MN12

Geographical Range: Greece, Germany, Moldova and Iran

Localities: Pikermi, Perivolaki, Samos? (Koufos, 2011), Dorn Dörkheim, Choburchi, Chimishlija, Maragheh (NOW, 2016)

Table 40: Ecomorphological characteristics of *Promeles palaeattica*

Body Mass		5-10 kg
Endocranial Volume		18-25 mL
Relative Rostrum Width		18-22%
Canine Sx/Sy		6-7/8-11
Canine Bite Force		320 N
Carnassial Bite Force		410 N
Total Intercuspid Notches		4-7
M1BSZ		0.10-0.14
M2SZ		0.06-0.07
LGR		0.10-0.12
UGR		0.13-0.16
Dental Mesowear	**T**	1-3
	H	1-3

Dietary Category: 9

Diet: Rodents (e.g. *Parapodemus*, *Micromys*), insectivores (*Schizogalerix*), birds, reptiles, insects, eggs, plant material 30-40% (fruits, seeds, fungi, grass).

Sociality: Solitary

Modern analogue: *Mellivora capensis*

Fig. 150: *Promeles palaeattica* from Pikermi (MNHUK-M9029). Not in scale.

Family Mustelidae FISHER DE WALDHEIM, 1817
Subfamily Mustelinae FISHER DE WALDHEIM, 1817
Genus *Parataxidea* ZDANSKY, 1924
Parataxidea maraghana (KITTL, 1887)

Stratigraphical Range: MN11-MN12

Geographical Range: Greece, Turkey, Iran and China

Localities: Samos (Koufos, 2011), Corakyerler (Eroli et al., 2016), Maragheh (NOW, 2016), Pai Jao Jaun, Kao Jung Ling, Po Viu Po (AMNH)

Table 41: Ecomorphological characteristics of *Parataxidea maraghana*

Body Mass		4 kg
Endocranial Volume		44 mL
Canine Bite Force		290 N
Carnassial Bite Force		470 N
UGR		0.17-0.19
Dental Mesowear	**T**	1-3
	H	1-2

Dietary Category: 10

Diet: Rodents (e.g. *Parapodemus*, *Micromys*), insectivores (*Schizogalerix*), birds, reptiles, insects, eggs, plant material 50-70% (fruits, seeds, fungi, grass).

Sociality: Solitary

Modern analogue: *Meles meles*

Fig. 151: *Parataxidea maraghana* from Samos (a: NHMA-MTLA-283; b: NHMA-MTLA-465). Not in scale.

Family Mustelidae FISHER DE WALDHEIM, 1817
Subfamily Melinae BONAPARTE, 1838
Genus *Meles* BODDAERT, 1785
Meles dimitrius KOUFOS, 1992

Stratigraphical Range: MN18-MN19

Geographical Range: Greece

Localities: Gerakarou, Apollonia (Koufos, 2014)

Table 42: Ecomorphological characteristics of *Meles dimitrius*

Body Mass		11-17 kg
Endocranial Volume		45 mL
Relative Rostrum Width		22%
Canine Sx/Sy		13/17
Canine Bite Force		550 N
Carnassial Bite Force		650 N
Total Intercuspid Notches		5
M1BSZ		0.10
M2SZ		0.09-0.10
LGR		0.13-0.14
UGR		0.15
Dental Mesowear	**T**	1-3
	H	1-2

Dietary Category: 9

Diet: Rodents, birds, lizards, eggs, insects, plant material 40-50% (fruits, seeds, fungi, grass).

Sociality: Solitary

Modern analogue: *Meles meles*

Fig. 152: *Meles dimitrius* from Apollonia (a: LGPUT-APL-544; b: LGPUT-APL-546). Not in scale.

Family Mephitidae BONAPARTE, 1845
Genus *Promephitis* GAUDRY, 1861
Promephitis lartetii GAUDRY, 1861

Stratigraphical Range: MN12

Geographical Range: Greece

Localities: Pikermi, Perivolaki, Samos (Koufos, 2011)

Table 43: Ecomorphological characteristics of *Promephitis lartetii*

Body Mass		2 kg
Relative Rostrum Width		29%
Canine Sx/Sy		5/6
Total Intercuspid Notches		0
M1BSZ		0.12
M2SZ		0.08
LGR		0.12
UGR		0.13
Dental Mesowear	**T**	2
	H	1

Dietary Category: 9

Diet: Insects, lizards, eggs, plant material 30-40% (fruits, seed, fungi).

Sociality: Solitary

Modern analogue: *Mephitis mephitis*

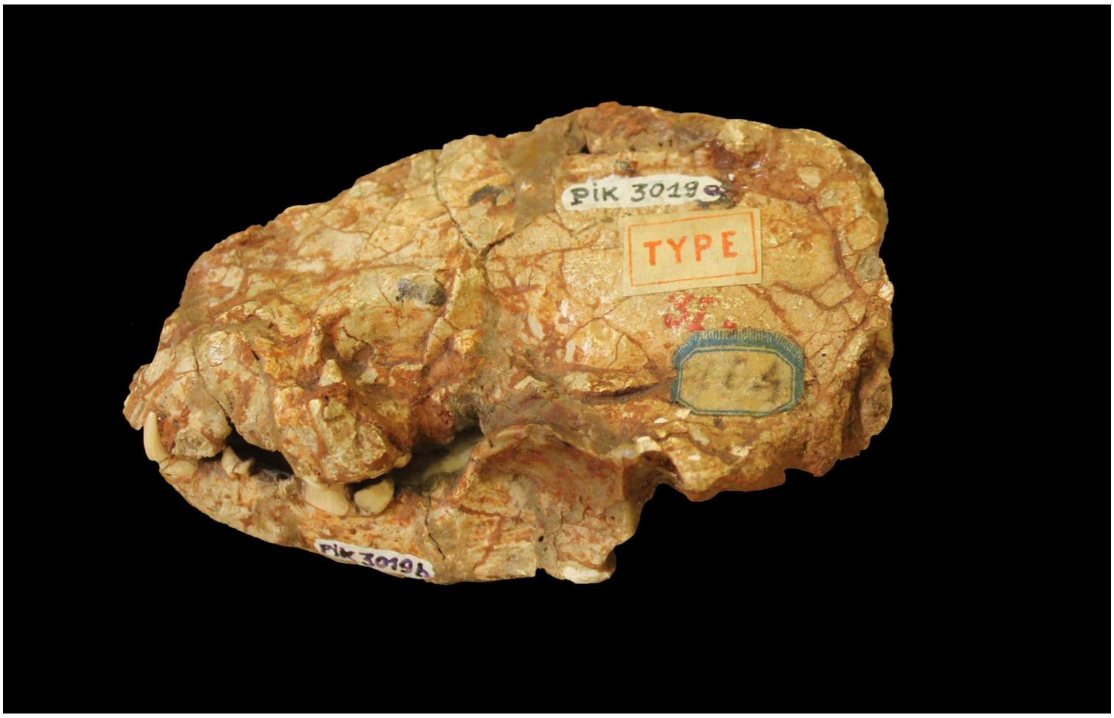


Fig. 153: *Promephitis lartetii* from Pikermi (MNHN-PIK-3019)

Family Ursidae FISHER DE WALDHEIM, 1817
Subfamily Ailuropodinae GREVÉ, 1894
Genus *Indarctos* PILGRIM, 1913
Indarctos atticus (WEITHOFER, 1888)

Stratigraphical Range: MN10-MN13

Geographical Range: Greece, Italy, Spain, France, Germany, Hungary, Libya and Iran

Localities: Pikermi, Samos (Koufos, 2011), Terassa, Crevillente 2, Puente Minero, Dorn Dörkheim, Concud, Los Mansuetos, Valdecebro 5, Cerro de la Garita, Aubignas, Baltavar, Sahabi, Maragheh (Roussiakis, 2001), Crevillente-2 (NOW, 2016)

Table 44: Ecomorphological characteristics of *Indarctos atticus*

Body Mass		≈150 kg
Canine Sx/Sy		110/200
M1BSZ		0.10
M2SZ		0.12
LGR		0.16
UGR		0.18
Dental Mesowear	**T**	1-3
	H	1

Dietary Category: 11

Diet: Mainly plant material (grass, leaves, fruits, seeds, fungi, 70-80%) completing its diet opportunistically with eggs, lizards, rodents etc.

Sociality: Solitary

Modern analogue: *Ursus thibetanus*

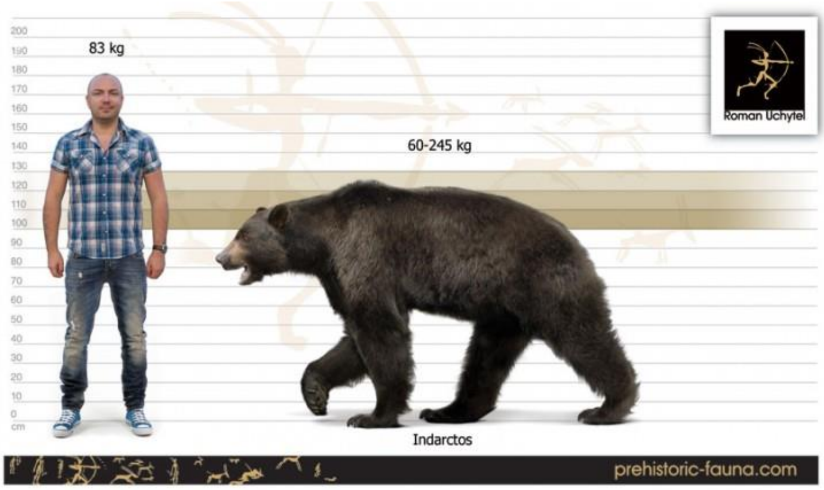


Fig. 154: *Indarctos arctoides*. Source: prehistoric-fauna.com. Artist: R. Uchytel

Fig. 155: *Indarctos atticus* from Samos (AMPG-No Nu, cast from Natural History Museum of Basel). Not in scale

Family Ursidae FISHER DE WALDHEIM, 1817
Subfamily Ursinae FISHER DE WALDHEIM, 1817
Genus *Ursavus* SCHLOSSER, 1899
Ursavus depereti SCHLOSSER, 1902

Stratigraphical Range: MN9-MN12

Geographical Range: Greece, France, Germany and China?

Localities: Perivolaki, Samos? (Koufos, 2011), Soblay, Luzinay (Qiu et al., 2011), Melchingen, Dorn Dörkheim, Lufeng? (NOW, 2016)

Table 45: Ecomorphological characteristics of *Ursavus depereti*

Body Mass		≈100 kg
M1BSZ		0.07
M2SZ		0.10
LGR		0.14
Dental Mesowear	**T**	1-3
	H	1

Dietary Category: 10

Diet: Mostly plant material (grass, leaves, fruits, seeds, fungi, 50-60%) completing its diet opportunistically with eggs, lizards, rodents etc.

Sociality: Solitary

Modern analogue: *Ursus arctos*

Fig. 156: *Ursavus depereti* from Perivolaki (LGPUT-PER-1270)

Family Ursidae FISHER DE WALDHEIM, 1817
Subfamily Ursinae FISHER DE WALDHEIM, 1817
Genus *Ursavus* SCHLOSSER, 1899
Ursavus ehrenbergi THENIUS, 1947

Stratigraphical Range: MN12

Geographical Range: Greece

Localities: Halmyropotamos (Koufos, 2011)

Table 46: Ecomorphological characteristics of *Ursavus ehrenbergi*

Body Mass		≈100 kg
Dental Mesowear	**T**	1-3
	H	1

Dietary Category: 10

Diet: Mostly plant material (grass, leaves, fruits, seeds, fungi, 50-60%) completing its diet opportunistically with eggs, lizards, rodents etc.

Sociality: Solitary

Modern analogue: *Ursus arctos*

Fig. 157: *Ursavus ehrenbergi* from Halmyropotamos (AMPG-No Nu)

Family Ursidae FISHER DE WALDHEIM, 1817
Subfamily Ursinae FISHER DE WALDHEIM, 1817
Genus *Ursus* LINNAEUS, 1758
Ursus etruscus CUVIER, 1865

Stratigraphical Range: MN16-MN19

Geographical Range: Greece, Spain, France, Netherlands, Hungary, Romania, Georgia and Tadzhikistan?

Localities: Dafnero, Vassiloudi, Apollonia, Makineia, Kastritsi, Sesklon?, Psychiko? (Koufos, 2014), Tsiotra Vryssi (Koufos et al., 2018), Villaroya, El Rincon, Casablanca, La Puebla de Valverde, St. Vallier, Vialette, Etouaires, Pardines, Chihac, Senèze, Dmanisi, Tegelen, Kislang, Graunceanu, Keklikbulak? (NOW, 2016)

Table 47: Ecomorphological characteristics of *Ursus etruscus*

Body Mass		≈150 kg
Endocranial Volume		263 mL
Relative Rostrum Width		20%
Canine Bite Force		1250 N
Carnassial Bite Force		1450 N
Canine Sx/Sy		72-81/109-112
UGR		0.19
Dental Mesowear	**T**	1-3
	H	1

Dietary Category: 10

Diet: Mostly plant material (grass, leaves, fruits, seeds, fungi, 50-60%) completing its diet opportunistically with eggs, lizards, rodents etc.

Sociality: Solitary

Modern analogue: *Ursus arctos*

Fig. 158: *Ursus etruscus*. Source: alchetron.com.

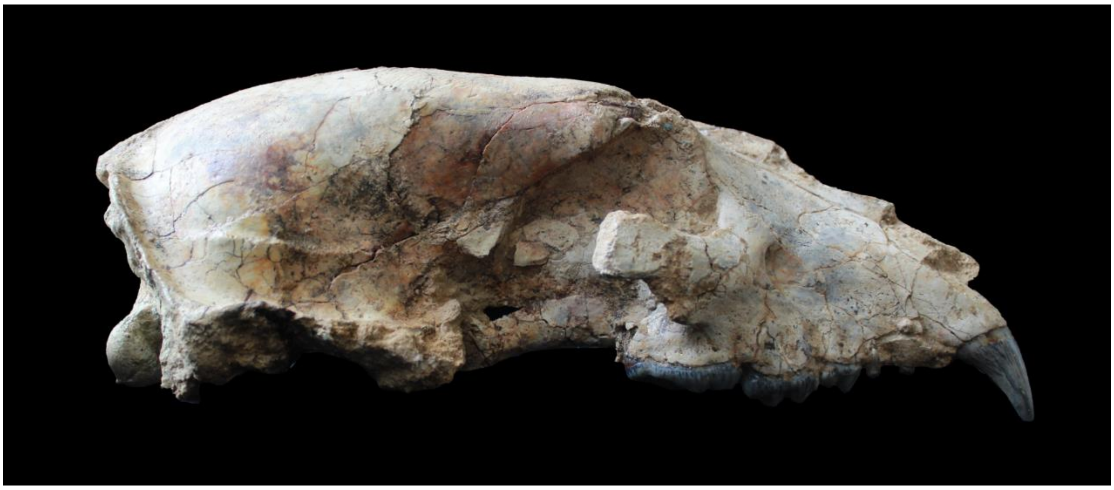


Fig. 159: *Ursus etruscus* from Tsiotra Vryssi (LGPUT-TSR-E21-50)

Family Ailuridae GRAY, 1843
Subfamily Simocyoninae DAWKINS, 1868
Genus *Simocyon* WAGNER, 1858
Simocyon primigenius (ROTH & WAGNER, 1854)

Stratigraphical Range: MN9-MN13

Geographical Range: Greece, Northern Macedonia, Spain, Germany, Hungary and Moldova

Localities: Pikermi, Halmyropotamos (Koufos, 2011), Karaslari (Spassov & Geraads, 2011), Cerro de la Garita, Eppelsheim, Chobruchi, Baltavar (NOW, 2016)

Table 48: Ecomorphological characteristics of *Simocyon primigenius*

Body Mass		≈20 kg
Endocranial Volume		85-110 mL
Relative Rostrum Width		28%
Canine Bite Force		840 N
Carnassial Bite Force		1050 N
Canine Sx/Sy		45/60
M1BSZ		0.11-0.12
M2SZ		0.08-0.09
LGR		0.10-0.12
UGR		0.14-0.15
Dental Mesowear	**T**	1-3
	H	1-2

Dietary Category: 9-5

Diet: Opportunistic scavenging, small mammals (*Gazella*, *Dorcatherium*, *Hystrix*), birds and reptiles, plant material approximately 20% (fruit, seeds).

Sociality: Solitary

Modern analogue: *Gulo gulo*

Fig. 160: *Simocyon primigenius*. Source: Spassov & Geraads (2011). Artist: V. Simeonovski

Fig. 161: *Simocyon primigenius* from Pikermi (a: MNHN-PIK-3359; MNHN-PIK-3343). Not in scale.

Family Canidae FISHER DE WALDHEIM, 1817
Genus *Canis* LINNAEUS, 1758
Canis arnensis DEL CAMPANA, 1913

Stratigraphical Range: MN18-MN19

Geographical Range: Greece, Italy and France

Localities: Gerakarou, Apollonia, Ravin of Voulgarakis, Alikes (Koufos, 2014), Valldarno (Athanassiou, 1998), Petralona (Baryshnikov & Tsoukala, 2010), Il Tasso, Poggio Rosso (Bartolini-Lucenti & Rook, 2016), Bucine (Brugal & Boudadi-Maligne, 2011)

Table 49: Ecomorphological characteristics of *Canis arnensis*

Body Mass		10-15 kg
Endocranial Volume		70 mL
Relative Rostrum Width		16%
Canine Sx/Sy		24/40
UGR		0.11
Dental Mesowear	**T**	1-3
	H	1-3

Dietary Category: 9

Diet: Small bovids (*Gazella*, *Gazellospira*), boars, small horses, insectivores (*Erinaceus*), hares (*Lagurodon*), rodents (*Borsodia*, *Hystrix*), birds, reptiles, plant material approximately 30-40% (fruits, seeds, fungi).

Sociality: Social

Modern analogue: *Canis mesomelas*

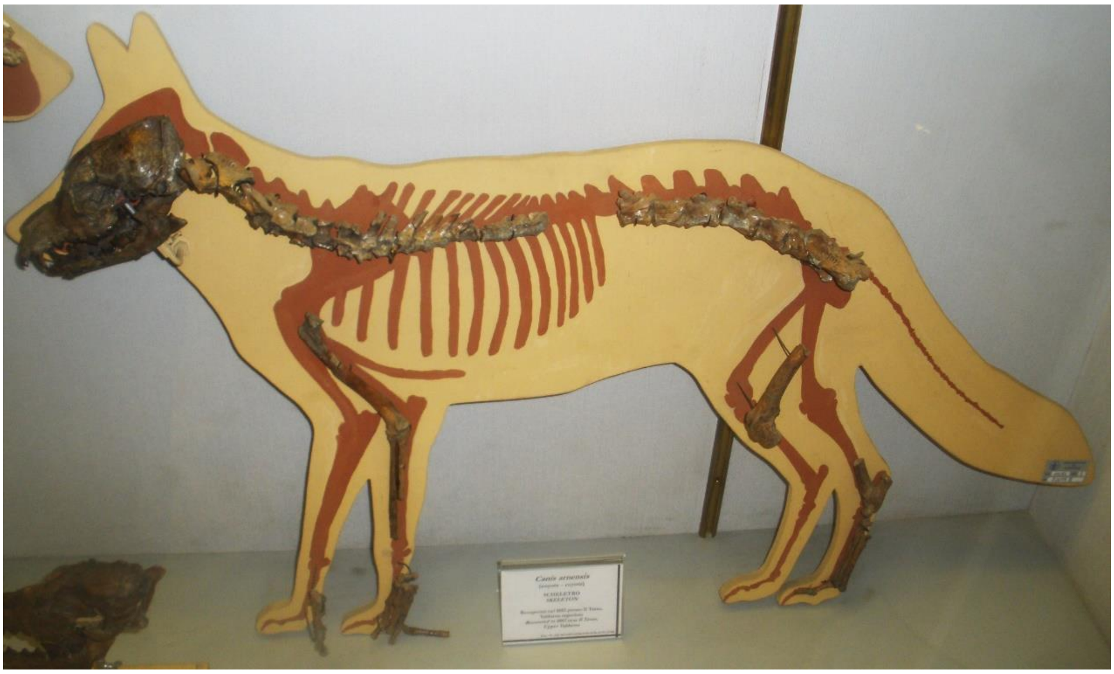


Fig. 162: *Canis arnensis*. Source: en.wikipedia.org

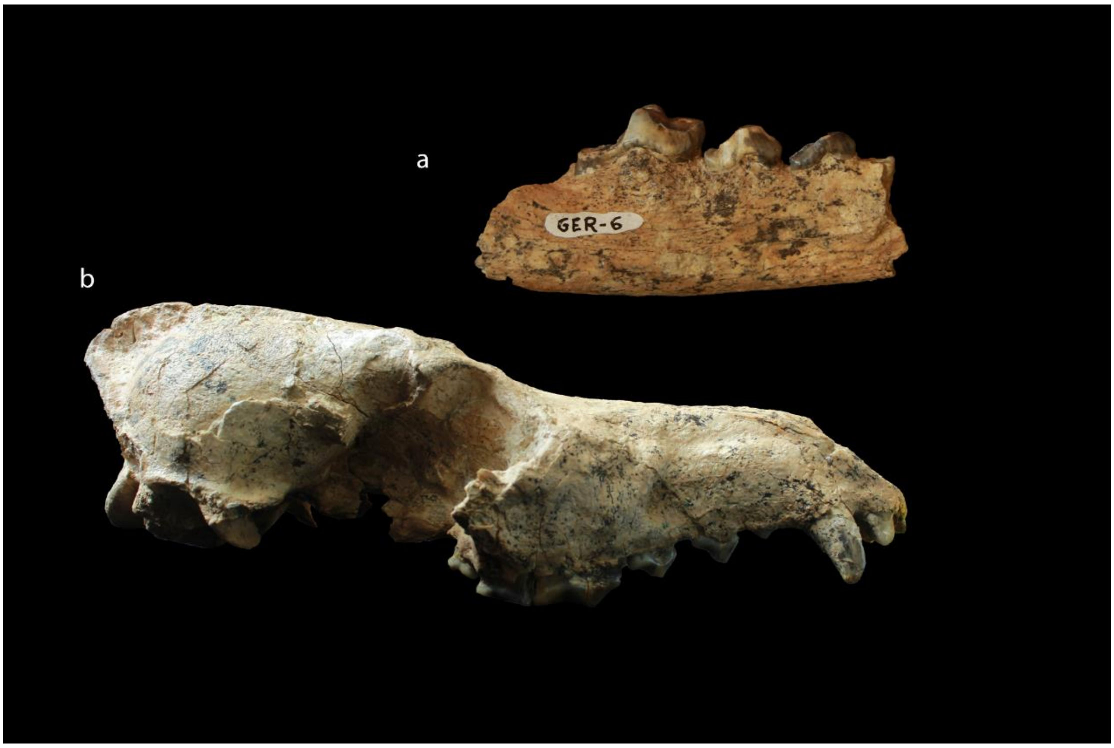


Fig. 163: *Canis arnensis* from Gerakarou (a: LGPUT-GER-6; b: LGPUT-GER-45). Not in scale

Family Canidae FISHER DE WALDHEIM, 1817

Genus *Canis* LINNAEUS, 1758

Canis apolloniensis KOUFOS & KOSTOPOULOS, 1997

Stratigraphical Range: MN19

Geographical Range: Greece

Localities: Apollonia (Koufos, 2014)

Table 50: Ecomorphological characteristics of *Canis apolloniensis*

Body Mass		15-20 kg
Canine Sx/Sy		10-15/18-27
Total Intercuspid Notches		11-12
M1BSZ		0.11-0.12
M2SZ		0.05-0.06
LGR		0.08-0.09
UGR		0.12
Dental Mesowear	**T**	1-3
	H	1-2

Dietary Category: 9

Diet: Small bovids (*Gazella*, *Gazellospira*), boars, small horses, insectivores (*Erinaceus*), hares (*Lagurodon*), rodents (*Borsodia*, *Hystrix*), birds, reptiles, plant material approximately 30% (fruits, seeds, fungi).

Sociality: Social

Modern analogue: *Canis mesomelas*

Fig. 164: *Canis apolloniensis* (a: LGPUT-APL-523; b: LGPUT-APL-17). Not in scale.

Family Canidae FISHER DE WALDHEIM, 1817
Genus *Canis* LINNAEUS, 1758
Canis etruscus FORSYTH MAJOR, 1877

Stratigraphical Range: MN16-MN19

Geographical Range: Greece, Bulgaria, Italy, France, Georgia, Tadzhikistan?, Kazakhstan? and Kirgizia?

Localities: Gerakarou, Apollonia, Alikes (Koufos, 2014), Slivnitsa, Vialette?, Etouaires?, Dmanisi, Tepke 1?, Kuruksaj?, Kopala 2? (NOW, 2016), Valdarno, Olivola, Ceyssaguet (Brugal & Boudadi-Maligne, 2011), Pantalla (Cherin & Iurino, 2014)

Table 51: Ecomorphological characteristics of *Canis etruscus*

Body Mass		20 kg
Endocranial Volume		75 mL
Relative Rostrum Width		16%
Canine Bite Force		500 N
Carnassial Bite Force		750 N
Canine Sx/Sy		25/40
Total Intercuspid Notches		12
M1BSZ		0.12
M2SZ		0.06
Dental Mesowear	**T**	1-3
	H	1-3

Dietary Category: 9

Diet: Small bovids (*Gazella*, *Gazellospira*), boars, small horses, insectivores (*Erinaceus*), hares (*Lagurodon*), rodents (*Borsodia*, *Hystrix*), birds, reptiles, plant material approximately 20% (fruits, seeds, fungi).

Sociality: Social

Modern analogue: *Canis latrans*

Fig. 165: *Canis etruscus*. Source: carnivora.net.

Fig. 166: *Canis etruscus* from Apollonia (a: LGPUT-APL-522; b: LGPUT-APL-526). Not in scale.

Family Canidae FISHER DE WALDHEIM, 1817
Genus *Lycaon* BROOKES, 1827
Lycaon lycaonoides (KRETZOI, 1938)

Stratigraphical Range: MN17-MN19

Geographical Range: Greece, Italy, Spain, Slovakia, Romania, Hungary

Localities: Apollonia (Koufos, 2018), Petralona (Baryshnikov & Tsoukala, 2010) La Puebla de Valverde, Pietris (NOW, 2016), Episcopia, Nagyharsanyhegy, Gombasek (Kurtén, 1968)

Table 52: Ecomorphological characteristics of *Lycaon lycaonoides*

Body Mass		30 kg
Canine Sx/Sy		28/40
Total Intercuspid Notches		17
M1BSZ		0.15
M2SZ		0.06
LGR		0.09
UGR		0.13
Dental Mesowear	**T**	1
	H	1

Dietary Category: 3

Diet: Large sized ruminants (*Eucladoceros*, *Praemegaceros*, *Bison*), horses.

Sociality: Social

Modern analogue: *Canis lupus*

Fig. 167: *Lycaon lycaonoides.* Source: prehistoric-fauna.com. Artist: R. Uchytel

Fig. 168: *Lycaon lycaonoides* from Apollonia (LGPUT-APL-771)

Family Canidae Fisher de Waldheim, 1817
Genus *Nyctereutes* Temminck, 1838
Nyctereutes megamastoides (Pomel, 1842)

Stratigraphical Range: MN16-MN17

Geographical Range: Greece, France, Spain, Romania, Georgia, Russia, Tadzhikistan and Mongolia

Localities: Dafnero-1, Volax, Sesklon, Vatera-F (Koufos, 2014), Villaroya, El Rincon, La Puebla de Valverde, St. Vallier, Etouaires, Roccaneyra, Pardines, Chihac, Senèze, Pietris, Graunceanu, Kvabebi, Beregovaya, Kuruksaj, Dzagso-Hairhan-3-2?, Shamar (NOW, 2016)

Table 53: Ecomorphological characteristics of *Nyctereutes megamastoides*

Body Mass		6-12 kg
Canine Sx/Sy		5-10/7-16
Endocranial Volume		38-67 mL
Relative Rostrum Width		15-18%
Total Intercuspid Notches		9-11
M1BSZ		0.09
M2SZ		0.06-0.07
LGR		0.12
UGR		0.12
Dental Mesowear	**T**	1-3
	H	1-3

Dietary Category: 10

Diet: Rodents, birds, lizards, eggs, insects, plant material 50% of its diet depending on availability (fruits, seeds, fungi).

Sociality: Solitary

Modern analogue: *Nyctereutes procyonoides*

Fig. 169: *Nyctereutes megamastoides* from Dafnero (a: LGPUT-DFN-17; b: LGPUT-DFN-20). Not in scale.

Family Canidae FISHER DE WALDHEIM, 1817
Genus *Vulpes* FRISCH, 1775
Vulpes alopecoides FORSYTH MAJOR, 1875

Stratigraphical Range: MN16-MN17

Geographical Range: Greece, Bulgaria, Italy, France, Spain, Austria, Hungary and Georgia?

Localities: Dafnero-1, Makineia, Kastritsi, Sesklon? (Koufos, 2014, 2018), Varshets, Slivnitsa?, St. Vallier, Senèze, Villaroya, La Puebla de Valverde (NOW, 2016), Val d' Arno, Beremend, Villány, Episcopia, Brassó, Hundsheim? (Kurtén, 1968), Kvabebi? (Rook et al., 2017)

Table 54: Ecomorphological characteristics of *Vulpes alopecoides*

Body Mass		6-7 kg
M1BSZ		0.10
M2SZ		0.07
Dental Mesowear	**T**	1
	H	1

Dietary Category: 9

Diet: Rodents, birds, lizards, eggs, insects, plant material 20-30% (fruits, seeds, fungi).

Sociality: Solitary

Modern analogue: *Vulpes vulpes*

Fig. 170: *Vulpes alopecoides* from (a): Kastritsi (AMPG-K987) and (b): Dafnero (LGPUT-DFN-172). Not in scale

Family Canidae FISHER DE WALDHEIM, 1817
Genus *Vulpes* FRISCH, 1775
Vulpes praeglacialis (KORMOS, 1932)

Stratigraphical Range: MN19

Geographical Range: Greece, France, Spain, Czech Republic

Localities: Apollonia (Koufos, 2018), Volos (Athanassiou, 2002), Petralona, Grotte de l' Escale, Vergranne, Stránska Skála (Baryshnikov & Tsoukala, 2010), Venta Micena, Fuente Nueva-3 (Medin et al., 2017)

Table 55: Ecomorphological characteristics of *Vulpes praeglacialis*

Body Mass		7 kg
Canine Bending Strength		4/7
Total Intercuspid Notches		8
M1BSZ		0.11
M2SZ		0.05
Dental Mesowear	**T**	1-3
	H	1-3

Dietary Category: 9

Diet: Rodents, birds, lizards, eggs, insects, plant material 20-30% (fruits, seeds, fungi).

Sociality: Solitary

Modern analogue: *Vulpes vulpes*

Fig. 171: *Vulpes praeglacialis* from Apollonia (LGPUT-APL-11)

Abstract

This Thesis deals with the palaeoecology of the fossil carnivorans of Greece and, in particular, with their diet. Carnivora don't eat exclusively meat, but they frequently are omnivores, insectivores or even herbivores. In this study extant Carnivora were divided into 12 dietary categories. The studied fossil material belongs to 47 species from 8 families, coming from two periods of geological time: the Late Miocene (11.6-5.3 Mya) and the Villafranchian (3.5.-0.8 Mya). These periods include some of the richest fossiliferous localities in Greece, providing enough material to apply the necessary methods. To test the made assumptions, a comparative sample of 75 species belonging to 13 families of extant carnivorans was used.

The main focus of this work is to calculate a number of proxies which are connected to the diet of these species. The proxies studied here were: bite force, upper canines' and incisors' bending strength, endocranial volume, relative rostrum width, mastoid musculature, dental mesowear, dental carnassial and grinding surfaces, dental intercuspid notches and dental morphology in general. All these parameters are combined, in order to extract a more accurate result.

The first chapter of the results concerns the diets of some enigmatic species. *Indarctos atticus* resulted to be an omnivore, based mostly on plant material. *Ursus etruscus*, *Ursavus ehrenbergi* and *Ursavus depereti* were found being opportunistic omnivores. *Simocyon primigenius* resulted being probably a scavenger, but also a predator of small-medium sized mammals and probably completed its diet with a small amount of plants. A similar niche, without the ability of bone-cracking, is proposed for *Plesiogulo crassa*. *Baranogale helbingi* resulted to be a meat-based omnivore, similar to extant martens.

The second chapter of the results deals with the coexistence of species that seem to have a similar ecology. The first part were the *Crocuta*-like hyenas of the Turolian (*Adcrocuta eximia*, *Lycyaena chaeretis* and *Belbus beaumonti*). It was found that *Adcrocuta* is so dominant over the other species because it was larger, more robust, better adapted to bone-cracking and probably social, resulting to lower abundances forthe other two genera. The next case were the ictitheres of Late Miocene (*Plioviverrops orbignyi, Protictitherium crassum*, *Ictitherium viverrinum* and *Hyaenotherium wongii*). The first two genera were found to be opportunistic insectivores-omnivores. However the other two genera seem to have a similar ecological niche, with *Hyaenotherium* being more carnivorous and *Ictitherium* being more opportunistic. This niche overlapping is probably the cause for their distinct biogeography, with *Ictitherium* thriving in Pikermi and *Hyaenotherium* in Samos. The third case of coexistence was the felids of Pikermi (*Pristifelis attica*, *Metailurus parvulus*, *Metailurus major*, *Paramachairodus orientalis* and *Amphimachairodus giganteus*). These species were able to coexist, because they did not have the same body size. Therefore, their prey also had a relevant body size. The only species of the same size were *Paramachairodus* and *Metailurus major*, which represent two different evolutionary stages of sabertooths. Thus, these two taxa must have been competitive with each other and maybe that's the reason for their infrequency. Another part was the small-sized mustelids of Turolian (*Martes woodwardi, Promeles palaeattica*, *Promephitis lartetii*, *Parataxidea maraghana*, *Sinictis pentelici* and a new

species of mustelid). These species seemed to cover similar niches and having similar body sizes, with the exception of the smaller *Promephitis*. Probably this is the reason for their low abundance and the distinct biogeography of *Promeles* and *Parataxidea* (present in Pikermi and Samos respectively). The fifth case was the coexistence of the sabertooths *Homotherium* and *Megantereon* in the Villafranchian. It seems that this coexistence was possible due to the size difference between the two taxa and because of their different hunting strategies, since *Homotherium* was more cursorial and probably didn't make an instant canine-shear bite as *Megantereon*. A similar case can be seen with *Chasmaporthetes lunensis* and *Pliohyaena perrieri*, with the former being a social and cursorial hunter and the latter being a solitary scavenger. The last case of coexistence were the canids of Apollonia (*Vulpes praeglacialis*, *Lycaon lycaonoides*, *Canis arnensis*, *Canis etruscus* and *Canis apolloniensis*). *Vulpes praeglacialis* occupied a niche similar to extant foxes and *Lycaon* similar to extant wolves. The other three canids probably represent a gradual transition from a form similar to jackal (*Canis arnensis*) to a form similar to a small wolf (*Canis etruscus*) with *Canis apolloniensis* being the intermediate stage. This coexistence of three species of canids probably led to interspecific competition between them.

The third chapter of results dealt with the temporal alternation (or no alternation) of some phylogenetic lines. The first case was the transition *Promeles palaeattica* → *Meles dimitrius* → *Meles meles*. This lineage seems to adapt to a more plant-based diet and an increase in size. The second line was that of *Nyctereutes*: *N. donnezani* → *N. megamastoides* → *N. procyonoides*. This line also moved to a more plant-based omnivory, but this time the body size of the species was reduced. The next two cases dealt with two lineages that had similar representatives in the fossil record of Greece from the Miocene until the Late Pleistocene. The first lineage was that of *Crocuta*-like bone-crushing hyenas: *Dinocrocuta* → *Adcrocuta* → *Pliohyaena* → *Pachycrocuta* → *Crocuta* and the second was that of large felids *Amphimachairodus* / *Paramachairodus* / *Metailurus major* → *Homotherium* / *Megantereon* / *Panthera gombaszoegensis* → *Panthera leo* / *pardus*.

Finally, the dietary category for every species was defined in a table and a suggestion for its possible prey genera (based on its already known associated faunas) was made, accompanied with the reference of a modern analogue species.

Περίληψη

Το θέμα της παρούσας Διπλωματικής εργασίας είναι η παλαιοοικολογία των απολιθωμένων σαρκοφάγων της Ελλάδας και συγκεκριμένα οι διατροφικές τους συνήθειες. Τα Σαρκοφάγα δεν τρέφονται αποκλειστικά με κρέας, αλλά συχνά έχουν παμφαγικές, εντομοφαγικές ή ακόμα και φυτοφαγικές συνήθειες. Σε αυτή την εργασία τα σημερινά σαρκοφάγα χωρίστηκαν σε 12 διατροφικές κατηγορίες. Το απολιθωμένο υλικό ανήκει σε 47 είδη σε 8 οικογένειες, που προέρχονται από δύο περιόδους του γεωλογικού χρόνου: το Ανώτερο Μειόκαινο (11,6-5,3 εκατομμύρια χρόνια πριν) και το Βιλλαφράγκιο (3,5-0,8 εκατομμύρια χρόνια πριν). Αυτές οι περίοδοι περιλαμβάνουν κάποιες από τις πιο πλούσιες απολιθωματοφόρες θέσεις της Ελλάδας, παρέχοντας αρκετό υλικό για να πραγματοποιηθούν οι απαραίτητες μέθοδοι. Τα εξαγόμενα αποτελέσματα προέκυψαν μετά από σύγκριση με 75 είδη σε 13 οικογένειες αρτίγονων Σαρκοφάγων.

Το κυρίως τμήμα αυτής της εργασίας ήταν ο υπολογισμός μίας σειράς παραμέτρων που συνδέονται με την δίαιτα των ειδών. Οι παράμετροι που υπολογίστηκαν ήταν οι εξής: δύναμη δαγκώματος, αντοχή των άνω κυνοδόντων και κοπτήρων στην κάμψη, εγκεφαλική χωρητικότητα, σχετικό πλάτος ρύγχους, μυολογία μαστοειδούς περιοχής, οδοντική μεσοτριβή, κοπτικές και αλεστικές επιφάνειες των δοντιών, διαφυματικές εντομές των δοντιών και γενικότερη οδοντική μορφολογία. Όλες αυτές οι παράμετροι χρησιμοποιήθηκαν συνδυαστικά, ώστε να εξαχθεί το ακριβέστερο δυνατό αποτέλεσμα.

Το πρώτο κεφάλαιο των αποτελεσμάτων έχει να κάνει με την δίαιτα κάποιων αινιγματικών ειδών. Η *Indarctos atticus* φαίνεται ότι ήταν παμφάγα με τα φυτά να αποτελούν το μεγαλύτερο κομμάτι της διατροφής της. Τα είδη *Ursus etruscus, Ursavus ehrenbergi* και *Ursavus depereti* ήταν οπορτουνιστικά παμφάγα. Ο *Simocyon primigenius* φαίνεται πως ήταν πτωματοφάγο, αλλά και θηρευτής μικρού-μεσαίου μεγέθους θηλαστικών και πιθανά συμπλήρωνε την δίαιτά του σε μικρό ποσοστό από φυτά. Έναν παρόμοιο ρόλο, χωρίς οστεοθραυστικές ικανότητες, φαίνεται πως είχε το είδος *Plesiogulo crassa*. Τέλος, το είδος *Baranogale helbingi* εκτιμάται ότι ήταν παμφάγο με προτίμηση στο κρέας, όπως τα σημερινά κουνάβια.

Το δεύτερο κεφάλαιο των αποτελεσμάτων ασχολείται με την συνύπαρξη ειδών που φαίνονται να έχουν παρόμοια οικολογία. Το πρώτο κομμάτι είναι οι ύαινες, που ήταν παρόμοιες με την σημερινή στικτή ύαινα, και ζούσαν στο Τουρώλιο (*Adcrocuta eximia, Lycyaena chaeretis* και *Belbus beaumonti*). Προέκυψε ότι η *Adcrocuta* επικρατεί έναντι των άλλων ειδών, επειδή ήταν μεγαλύτερη, πιο εύρωστη, καλύτερα προσαρμοσμένη στην θραύση οστών και πιθανότατα κοινωνική, οδηγώντας τις άλλες δύο ύαινες σε χαμηλές πληθυσμιακές πυκνότητες. Η επόμενη ομάδα ήταν τα ικτιθήρια του Ανώτερου Μειοκαίνου (*Plioviverrops orbignyi, Protictitherium crassum, Ictitherium viverrinum* και *Hyaenotherium wongii*). Τα πρώτα δύο γένη φαίνεται πως ήταν οπορτουνιστικά εντομοφάγα-παμφάγα. Όμως τα άλλα δύο γένη υπολογίστηκε πως είχαν παρόμοιους οικολογικούς ρόλους με το *Hyaenotherium* να είναι πιο σαρκοφάγο και το *Ictitherium* πιο οπορτουνιστικό. Αυτή η αλληλοεπικάλυψη των οικολογικών τους θώκων είναι πιθανότατα και η αιτία για την διακριτή τους βιογεωγραφία με το *Ictitherium* να κυριαρχεί στο Πικέρμι και το *Hyaenotherium* στη Σάμο. Η τρίτη περίπτωση συνύπαρξης που μελετήθηκε ήταν τα

αιλουροειδή του Πικερμίου (*Pristifelis attica, Metailurus parvulus, Metailurus major, Paramachairodus orientalis, Amphimachairodus giganteus*). Αυτά τα είδη μπορούσαν να συνυπάρχουν καθώς δεν είχαν το ίδιο σωματικό βάρος. Κατά συνέπεια και τα θηράματά τους δεν είχαν το ίδιο βάρος. Τα μόνα είδη που είχαν αντίστοιχο μέγεθος ήταν τα *Metailurus major* και *Paramachairodus orientalis*, που αποτελούν δύο διαφορετικά εξελικτικά στάδια μαχαιροδόντων. Επομένως, αυτά τα δύο είδη θα πρέπει να ήταν ανταγωνιστικά μεταξύ τους και πιθανότατα αυτός είναι ο λόγος για την σπανιότητά τους. Άλλο ένα κομμάτι ήταν τα Mustelidae του Τουρώλιου (*Martes woodwardi, Promeles palaeattica, Promephitis lartetii, Parataxidea maraghana, Sinictis pentelici* και ένα νέο είδος αυτής της οικογένειας). Αυτά τα είδη φαίνεται ότι κάλυπταν αντίστοιχους θώκους και είχαν παρόμοιο σωματικό μέγεθος, με την εξαίρεση του μικρότερου *Promephitis*. Πιθανότατα, αυτός είναι ο λόγος για την χαμηλή τους πυκνότητα και για την διακριτή βιογεωγραφία των *Promeles* και *Parataxidea* (παρόντα στο Πικέρμι και στη Σάμο αντίστοιχα). Η πέμπτη περίπτωση ήταν η συνύπαρξη των μαχαιροδόντων *Homotherium* και *Megantereon* στο Βιλλαφράγκιο. Φαίνεται ότι αυτή η συνύπαρξη ήταν δυνατή λόγω της διαφοράς των δύο ειδών στο σωματικό μέγεθος και στις κυνηγετικές στρατηγικές, με το *Homotherium* να είναι καλύτερα προσαρμοσμένο σαν δρομέας και να μην πραγματοποιεί το στιγμιαίο δάγκωμα των μαχαιροδόντων. Κάτι αντίστοιχο φαίνεται και στα είδη *Chasmaporthetes lunensis* και *Pliohyaena perrieri*. Το πρώτο είδος φαίνεται ότι ήταν ένας αγελαίος, ταχύς κυνηγός, ενώ το δεύτερο ένα μοναχικό πτωματοφάγο. Η τελευταία ομάδα ήταν τα κυνοειδή της Απολλωνίας (*Vulpes praeglacialis, Lycaon lycaonoides, Canis apolloniensis, Canis arnensis* και *Canis etruscus*). Η *Vulpes praeglacialis* κατελάμβανε έναν θώκο αντίστοιχο των σημερινών αλεπούδων και ο *Lycaon* αντίστοιχο των σημερινών λύκων. Τα άλλα τρία είδη αποτελούν μία διαδοχή από μία μορφή παρόμοια με τσακάλι (*Canis arnensis*) σε μία μορφή παρόμοια με μικρόσωμο λύκο (*Canis etruscus*) με τον *Canis apolloniensis* να αποτελεί ένα ενδιάμεσο στάδιο. Αυτή η συνύπαρξη των τριών ειδών πιθανότατα οδηγούσε σε διαειδικό ανταγωνισμό μεταξύ τους.

Το τρίτο κεφάλαιο των αποτελεσμάτων έχει να κάνει με την χρονική αλλαγή (ή μη αλλαγή) κάποιων φυλογενετικών γραμμών. Η πρώτη περίπτωση είναι η γραμμή *Promeles palaeattica* → *Meles dimitrius* → *Meles meles*. Αυτή η γραμμή φαίνεται να προσαρμόζεται σε μία διατροφή περισσότερο βασισμένη στα φυτά και σε ένα αυξανόμενο σωματικό μέγεθος. Η δεύτερη γραμμή ήταν αυτή του γένους *Nyctereutes*: *N. donnezani* → *N. megamastoides* → *N. procyonoides*. Και σε αυτήν την γραμμή παρατηρείται η επιλογή της αύξησης του ποσοστού των φυτών στην δίαιτα, αλλά αυτή τη φορά το σωματικό μέγεθος μειώνεται. Οι επόμενες δύο περιπτώσεις έχουν να κάνουν με δύο γραμμές που είχαν σταθερούς αντιπροσώπους στο απολιθωματοφόρο αρχείο της Ελλάδας από το Μειόκαινο μέχρι το Ανώτερο Πλειστόκαινο. Η πρώτη γραμμή είναι αυτή των οστεοθραυστικών υαινών αντίστοιχων της σημερινής στικτής ύαινας: *Dinocrocuta* → *Adcrocuta* → *Pliohyaena* → *Pachycrocuta* → *Crocuta* και η δεύτερη είναι αυτή των μεγαλόσωμων αιλουροειδών: *Amphimachairodus*/*Paramachairodus*/*Metailurus major* → *Homotherium*/*Megantereon*/*Panthera gombaszoegensis* → *Panthera leo*/*pardus*.

Τελικά, για κάθε είδος ορίζεται η διατροφική του κατηγορία σε έναν πίνακα, προτείνονται πιθανές του λείες σε επίπεδο γένους (με βάση τις ήδη γνωστές σχετικές του πανίδες) και αναφέρεται ένα αντίστοιχο είδος ως ανάλογο.

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Appendix

Table 56. Material of specimens of extant species used in this study.

Family	Species	Museum	Code
Felidae	*Lynx lynx*	ZMUA	5108
Felidae	*Lynx lynx*	MNHN	1994-2443
Felidae	*Lynx lynx*	MNHN	1941-79
Felidae	*Lynx lynx*	NMNHS	280
Felidae	*Lynx lynx*	NMNHS	270
Felidae	*Leptailurus serval*	MNHN	1995-450
Felidae	*Leptailurus serval*	SMNS	18904
Felidae	*Leptailurus serval*	SMNS	18903
Felidae	*Leptailurus serval*	SMNS	18899
Felidae	*Leptailurus serval*	SMNS	18897
Felidae	*Leptailurus serval*	SMNS	42429
Felidae	*Felis silvestris*	NMNHC	80.5.65.9
Felidae	*Felis silvestris*	NMNHC	80.5.65.25
Felidae	*Felis silvestris*	NMNHC	80.5.65.7
Felidae	*Felis silvestris*	NMNHC	80.5.65.22
Felidae	*Felis silvestris*	NMNHC	80.5.65.29
Felidae	*Felis silvestris*	NMNHC	80.5.65.36
Felidae	*Felis silvestris*	NMNHS	304
Felidae	*Felis silvestris*	NMNHC	80.5.65.11
Felidae	*Felis silvestris x Felis catus*	NMNHC	80.5.65.10
Felidae	*Felis catus*	AMPG	EV62
Felidae	*Felis catus*	AMPG	EV74
Felidae	*Felis catus*	AMPG	EV75
Felidae	*Felis catus*	AMPG	EV76
Felidae	*Felis catus*	AMPG	EV77
Felidae	*Felis catus*	AMPG	EV78
Felidae	*Felis catus*	AMPG	EV92
Felidae	*Felis catus*	AMPG	EV93
Felidae	*Felis catus*	AMPG	EV262
Felidae	*Felis catus*	AMPG	EV265
Felidae	*Felis catus*	AMPG	EV266
Felidae	*Felis catus*	AMPG	EV267
Felidae	*Leopardus tigrinus*	AMPG	EV63
Felidae	*Leopardus wiedii*	SMNS	18917
Felidae	*Leopardus wiedii*	SMNS	18916
Felidae	*Leopardus pardalis*	AMPG	EV64
Felidae	*Leopardus pardalis*	SMNS	45532
Felidae	*Leopardus pardalis*	SMNS	26674
Felidae	*Leopardus pardalis*	SMNS	447
Felidae	*Prionailurus viverrinus*	AMPG	EV82
Felidae	*Prionailurus viverrinus*	SMNS	18912
Felidae	*Profelis aurata*	AMPG	EV65

Felidae	*Caracal caracal*	MNHN	2006-529
Felidae	*Caracal caracal*	SMNS	5763
Felidae	*Caracal caracal*	SMNS	5742
Felidae	*Caracal caracal*	SMNS	6955
Felidae	*Caracal caracal*	SMNS	6956
Felidae	*Puma concolor*	MNHN	2016-1669
Felidae	*Puma concolor*	AMPG	EV60
Felidae	*Puma concolor*	AMPG	EV61
Felidae	*Puma concolor*	AMPG	EV81
Felidae	*Acinonyx jubatus*	MNHN	1960-3664
Felidae	*Acinonyx jubatus*	AMPG	EV89
Felidae	*Acinonyx jubatus*	AMPG	EV90
Felidae	*Acinonyx jubatus*	AMPG	EV91
Felidae	*Acinonyx jubatus*	SMNS	18941
Felidae	*Acinonyx jubatus*	SMNS	42997
Felidae	*Acinonyx jubatus*	SMNS	857
Felidae	*Acinonyx jubatus*	NMNHS	1036
Felidae	*Neofelis nebulosa*	MNHN	2006-431
Felidae	*Panthera onca*	MNHN	A7929
Felidae	*Panthera onca*	SMNS	18942
Felidae	*Panthera onca*	SMNS	18944
Felidae	*Panthera onca*	SMNS	5762
Felidae	*Panthera pardus*	AMPG	EV88
Felidae	*Panthera pardus*	MNHN	1905-49
Felidae	*Panthera pardus*	AMPG	EV83
Felidae	*Panthera pardus*	AMPG	EV84
Felidae	*Panthera pardus*	AMPG	EV87
Felidae	*Panthera pardus*	SMNS	18955
Felidae	*Panthera pardus*	SMNS	5760
Felidae	*Panthera pardus*	SMNS	18959
Felidae	*Panthera pardus*	SMNS	31915
Felidae	*Panthera pardus*	SMNS	31914
Felidae	*Panthera pardus*	SMNS	18960
Felidae	*Panthera pardus*	SMNS	18961
Felidae	*Panthera tigris*	MNHN	1952-161
Felidae	*Panthera leo*	ZMUA	5270
Felidae	*Panthera leo*	MNHN	1962-2872
Felidae	*Panthera leo*	AMPG	EV4
Felidae	*Panthera leo*	AMPG	EV5
Felidae	*Panthera leo*	AMPG	EV53
Felidae	*Panthera leo*	AMPG	EV66
Felidae	*Panthera leo*	AMPG	EV80
Felidae	*Panthera leo*	AMPG	EV85
Felidae	*Panthera leo*	AMPG	EV86
Felidae	*Panthera leo*	SMNS	2055
Felidae	*Panthera leo*	SMNS	31902

Felidae	*Panthera leo*	SMNS	50920
Felidae	*Panthera leo*	SMNS	50919
Felidae	*Panthera leo*	SMNS	31903
Felidae	*Panthera leo*	SMNS	49240
Felidae	*Panthera sp.*	ZMUA	5269
Felidae	*Panthera sp.*	ZMUA	5268
Felidae	*Panthera sp.*	ZMUA	5176
Hyaenidae	*Crocuta crocuta*	ZMUA	5112
Hyaenidae	*Crocuta crocuta*	ZMUA	5312
Hyaenidae	*Crocuta crocuta*	ZMUA	5048
Hyaenidae	*Crocuta crocuta*	MNHN	1936-656
Hyaenidae	*Crocuta crocuta*	AMPG	EV3
Hyaenidae	*Crocuta crocuta*	AMPG	EV67
Hyaenidae	*Crocuta crocuta*	AMPG	EV98
Hyaenidae	*Crocuta crocuta*	AMPG	EV344
Hyaenidae	*Crocuta crocuta*	SMNS	18982
Hyaenidae	*Crocuta crocuta*	SMNS	18981
Hyaenidae	*Crocuta crocuta*	SMNS	8058
Hyaenidae	*Crocuta crocuta*	SMNS	4458
Hyaenidae	*Crocuta crocuta*	SMNS	2655
Hyaenidae	*Crocuta crocuta*	SMNS	18983
Hyaenidae	*Parahyaena brunnea*	SMNS	379
Hyaenidae	*Hyaena hyaena*	MNHN	2006-635
Hyaenidae	*Hyaena hyaena*	SMNS	18979
Hyaenidae	*Hyaena hyaena*	SMNS	18978
Hyaenidae	*Hyaena hyaena*	SMNS	18977
Hyaenidae	*Hyaena hyaena*	SMNS	18976
Hyaenidae	*Hyaena hyaena*	SMNS	18975
Hyaenidae	*Hyaena hyaena*	SMNS	31843
Hyaenidae	*Hyaena hyaena*	MNHN	1934-318
Hyaenidae	*Proteles cristatus*	SMNS	24103
Hyaenidae	*Proteles cristatus*	SMNS	1897
Viverridae	*Genetta genetta*	MNHN	1967-222
Viverridae	*Genetta genetta*	AMPG	EV58
Viverridae	*Genetta tigrina*	NMNHS	721
Viverridae	*Genetta tigrina?*	NMNHS	No Nu
Viverridae	*Civettictis civetta*	AMPG	EV59
Viverridae	*Civettictis civetta*	SMNS	30159
Viverridae	*Civettictis civetta*	SMNS	6352
Viverridae	*Civettictis civetta*	SMNS	21596
Viverridae	*Civettictis civetta*	SMNS	30160
Viverridae	*Poiana richardosni*	SMNS	20638
Viverridae	*Poiana richardosni*	SMNS	20363
Viverridae	*Paradoxurs hermaprhoditus*	SMNS	35159
Viverridae	*Paradoxurs hermaprhoditus*	SMNS	21603
Viverridae	*Paradoxurs hermaprhoditus*	SMNS	7206

Viverridae	*Paradoxurs hermaprhoditus*	SMNS	20640
Viverridae	*Paradoxurs hermaprhoditus*	SMNS	20642
Viverridae	*Paradoxurs hermaprhoditus*	SMNS	20641
Viverridae	*Arctictis binturong*	SMNS	4968
Viverridae	*Arctictis binturong*	SMNS	474
Viverridae	*Arctictis binturong*	SMNS	9478
Viverridae	*Arctictis binturong*	SMNS	37896
Herpestidae	*Mungos mungo*	AMPG	EV109
Herpestidae	*Mungos mungo*	SMNS	50403
Herpestidae	*Mungos mungo*	SMNS	7312
Herpestidae	*Mungos mungo*	SMNS	21608
Herpestidae	*Mungos mungo*	SMNS	21607
Herpestidae	*Suricatta suricata*	SMNS	1319
Herpestidae	*Suricatta suricata*	SMNS	21612
Herpestidae	*Herpestes ichneumon*	AMPG	EV110
Herpestidae	*Herpestes ichneumon*	AMPG	EV56
Herpestidae	*Herpestes ichneumon*	SMNS	1873
Herpestidae	*Herpestes edwardsi*	SMNS	7620
Herpestidae	*Herpestes edwardsi*	SMNS	7621
Herpestidae	*Ichneumia albicauda*	SMNS	24107
Herpestidae	*Ichneumia albicauda*	SMNS	21606
Herpestidae	*Ichneumia albicauda*	SMNS	24108
Herpestidae	*Ichneumia albicauda*	SMNS	21044
Herpestidae	*Bdeogale crassicauda*	NMNHS	732
Herpestidae	*Bdeogale crassicauda*	NMNHS	736
Eupleridae	*Galidia elegans*	SMNS	1397
Nandiniidae	*Nandinia binotata*	SMNS	1930
Nandiniidae	*Nandinia binotata*	SMNS	6395
Nandiniidae	*Nandinia binotata*	SMNS	30154
Nandiniidae	*Nandinia binotata*	SMNS	6393
Canidae	*Otocyon megalotis*	MNHN	1992-392
Canidae	*Otocyon megalotis*	AMPG	EV132
Canidae	*Otocyon megalotis*	SMNS	4967
Canidae	*Otocyon megalotis*	SMNS	24102
Canidae	*Otocyon megalotis*	SMNS	1398
Canidae	*Urocyon cinereoargenteus*	MNHN	1980-509
Canidae	*Vulpes vulpes*	AMPG	EV70
Canidae	*Vulpes vulpes*	AMPG	EV117
Canidae	*Vulpes vulpes*	AMPG	EV118
Canidae	*Vulpes vulpes*	AMPG	EV119
Canidae	*Vulpes vulpes*	AMPG	EV120
Canidae	*Vulpes vulpes*	AMPG	EV121
Canidae	*Vulpes vulpes*	AMPG	EV253
Canidae	*Vulpes vulpes*	AMPG	EV254
Canidae	*Vulpes vulpes*	AMPG	EV268
Canidae	*Vulpes vulpes*	NMNHC	80.5.67.21

Canidae	*Vulpes vulpes*	NMNHC	80.5.67.6
Canidae	*Vulpes vulpes*	NMNHC	80.5.67.5
Canidae	*Vulpes vulpes*	NMNHS	No Nu
Canidae	*Nyctereutes procyonoides*	MNHN	1888-665
Canidae	*Nyctereutes procyonoides*	NMNHS	No Nu
Canidae	*Nyctereutes procyonoides*	NMNHS	549
Canidae	*Cuon alpinus*	SMNS	2191
Canidae	*Speothos venaticus*	SMNS	19136
Canidae	*Lycaon pictus*	SMNS	5747
Canidae	*Lycaon pictus*	SMNS	4460
Canidae	*Lycaon pictus*	SMNS	4461
Canidae	*Lycaon pictus*	SMNS	6097
Canidae	*Canis adustus*	MNHN	1969-478
Canidae	*Canis adustus*	SMNS	24100
Canidae	*Canis adustus*	SMNS	19005
Canidae	*Canis adustus*	SMNS	7503
Canidae	*Canis adustus*	SMNS	19002
Canidae	*Canis mesomelas*	SMNS	4409
Canidae	*Canis mesomelas*	SMNS	7182
Canidae	*Canis mesomelas*	SMNS	19007
Canidae	*Canis mesomelas*	SMNS	19008
Canidae	*Canis latrans*	SMNS	51589
Canidae	*Canis latrans*	SMNS	51588
Canidae	*Canis latrans*	SMNS	18944
Canidae	*Canis latrans*	SMNS	7580
Canidae	*Canis latrans*	MNHN	1962-967
Canidae	*Canis aureus*	ZMUP	4011
Canidae	*Canis aureus*	AMPG	EV71
Canidae	*Canis aureus*	NMNHS	567
Canidae	*Canis aureus*	NMNHS	572
Canidae	*Canis aureus*	NMNHS	522
Canidae	*Canis lupus*	MNHN	-
Canidae	*Canis lupus*	ZMUP	5546
Canidae	*Canis lupus*	ZMUP	5949
Canidae	*Canis lupus*	ZMUP	2832
Canidae	*Canis lupus*	ZMUP	5749
Canidae	*Canis lupus*	ZMUP	2830
Canidae	*Canis lupus*	ZMUP	5954
Canidae	*Canis lupus*	ZMUP	5948
Canidae	*Canis lupus*	ZMUP	5953
Canidae	*Canis lupus*	ZMUP	5750
Canidae	*Canis lupus*	ZMUP	5749
Canidae	*Canis lupus*	ZMUP	5545
Canidae	*Canis lupus*	ZMUP	5544
Canidae	*Canis lupus*	ZMUP	5543
Canidae	*Canis lupus*	ZMUP	6065

Canidae	*Canis lupus*	ZMUP	6166
Canidae	*Canis lupus*	AMPG	EV115
Canidae	*Canis lupus*	AMPG	EV343
Canidae	*Canis lupus*	NMNHS	No Nu
Canidae	*Canis lupus*	NMNHS	530
Canidae	*Canis lupus*	NMNHS	23/198
Canidae	*Canis lupus*	NMNHS	635
Canidae	*Canis lupus*	NMNHS	629
Canidae	*Canis lupus*	NMNHS	16/1980
Canidae	*Canis lupus*	NMNHS	58/1980
Canidae	*Canis lupus*	NMNHS	568
Canidae	*Canis lupus*	NMNHS	913
Canidae	*Canis lupus*	NMNHS	460
Canidae	*Canis lupus*	NMNHS	55/1980
Canidae	*Canis lupus*	NMNHS	450
Canidae	*Canis lupus*	NMNHS	50/1980
Canidae	*Canis familiaris*	ZMUA	5139
Canidae	*Canis familiaris*	ZMUA	5113
Canidae	*Canis familiaris*	AMPG	EV69
Canidae	*Canis familiaris*	AMPG	EV113
Canidae	*Canis familiaris*	AMPG	EV114
Canidae	*Canis familiaris*	AMPG	EV116
Canidae	*Canis familiaris*	AMPG	EV122
Canidae	*Canis familiaris*	AMPG	EV123
Canidae	*Canis familiaris*	AMPG	EV124
Canidae	*Canis familiaris*	AMPG	EV125
Canidae	*Canis familiaris*	AMPG	EV126
Canidae	*Canis familiaris*	AMPG	EV127
Canidae	*Canis familiaris*	AMPG	EV128
Canidae	*Canis familiaris*	AMPG	EV129
Canidae	*Canis familiaris*	AMPG	EV130
Canidae	*Canis familiaris*	AMPG	EV131
Canidae	*Canis familiaris*	AMPG	EV133
Canidae	*Canis familiaris*	AMPG	EV134
Canidae	*Canis familiaris*	AMPG	EV135
Canidae	*Canis familiaris*	AMPG	EV136
Canidae	*Canis familiaris*	AMPG	EV137
Canidae	*Canis familiaris*	AMPG	EV138
Canidae	*Canis familiaris*	AMPG	EV233
Procyonidae	*Nasua nasua*	AMPG	EV72
Procyonidae	*Nasua nasua*	AMPG	EV107
Procyonidae	*Nasua nasua*	AMPG	EV108
Procyonidae	*Nasua nasua*	SMNS	21766
Procyonidae	*Nasua nasua*	SMNS	2768
Procyonidae	*Nasua nasua*	SMNS	5797
Procyonidae	*Nasua nasua*	SMNS	7957

Procyonidae	*Nasua narica*	SMNS	1497
Procyonidae	*Procyon lotor*	AMPG	EV73
Procyonidae	*Potos flavus*	SMNS	51580
Procyonidae	*Potos flavus*	SMNS	40179
Procyonidae	*Potos flavus*	SMNS	43238
Procyonidae	*Potos flavus*	SMNS	41954
Procyonidae	*Potos flavus*	SMNS	1643
Ailuridae	*Ailurus fulgens*	SMNS	791
Ailuridae	*Ailurus fulgens*	SMNS	4971
Ailuridae	*Ailurus fulgens*	SMNS	26079
Ailuridae	*Ailurus fulgens*	SMNS	15287
Ailuridae	*Ailurus fulgens*	SMNS	9475
Ailuridae	*Ailurus fulgens*	SMNS	26676
Ailuridae	*Ailuropoda melanoleuca*	SMNS	2298
Ursidae	*Tremarctos ornatus*	MNHN	1992-1469
Ursidae	*Tremarctos ornatus*	SMNS	26250
Ursidae	*Tremarctos ornatus*	SMNS	573b
Ursidae	*Helarctos malayanus*	MNHN	1936-398
Ursidae	*Helarctos malayanus*	SMNS	2129
Ursidae	*Ursus thibetanus*	SMNS	15286
Ursidae	*Ursus thibetanus*	SMNS	31853
Ursidae	*Ursus thibetanus*	SMNS	51598
Ursidae	*Ursus thibetanus*	SMNS	21749
Ursidae	*Ursus thibetanus*	SMNS	21759
Ursidae	*Ursus thibetanus*	SMNS	21756
Ursidae	*Ursus americanus*	MNHN	1990-460
Ursidae	*Ursus americanus*	SMNS	51597
Ursidae	*Ursus americanus*	SMNS	21743
Ursidae	*Ursus americanus*	SMNS	21742
Ursidae	*Ursus americanus*	SMNS	7263
Ursidae	*Ursus maritimus*	MNHN	1928-303
Ursidae	*Ursus maritimus*	SMNS	21751
Ursidae	*Ursus maritimus*	SMNS	31849
Ursidae	*Ursus maritimus*	SMNS	43704
Ursidae	*Ursus maritimus*	SMNS	325
Ursidae	*Ursus maritimus*	SMNS	21760
Ursidae	*Ursus maritimus*	NMNHS	No Nu
Ursidae	*Ursus arctos*	MNHN	1988-131
Ursidae	*Ursus arctos*	ZMUP	-
Ursidae	*Ursus arctos*	AMPG	EV68
Ursidae	*Ursus arctos*	AMPG	EV97
Ursidae	*Ursus arctos*	AMPG	EV257
Ursidae	*Ursus arctos*	NMNHS	No Nu
Ursidae	*Ursus arctos*	NMNHS	1024
Ursidae	*Ursus arctos*	NMNHS	1023
Ursidae	*Ursus arctos*	NMNHS	1463

Ursidae	*Ursus arctos*	NMNHS	1032
Ursidae	*Ursus arctos*	NMNHS	1017
Ursidae	*Ursus arctos*	NMNHS	1020
Ursidae	*Ursus sp.*	ZMUA	5132
Mustelidae	*Meles meles*	ZMUA	5300
Mustelidae	*Meles meles*	AMPG	EV54
Mustelidae	*Meles meles*	AMPG	EV99
Mustelidae	*Meles meles*	AMPG	EV100
Mustelidae	*Meles meles*	AMPG	EV101
Mustelidae	*Meles meles*	AMPG	EV102
Mustelidae	*Meles meles*	AMPG	EV103
Mustelidae	*Meles meles*	AMPG	EV105
Mustelidae	*Meles meles*	NMNHC	80.5.63.14
Mustelidae	*Meles meles*	NMNHC	80.5.63.26
Mustelidae	*Meles meles*	NMNHC	80.5.63.47
Mustelidae	*Meles meles*	NMNHC	80.5.63.15
Mustelidae	*Meles meles*	NMNHC	80.5.63.25
Mustelidae	*Meles meles*	NMNHC	80.5.63.27
Mustelidae	*Meles meles*	NMNHC	80.5.63.9
Mustelidae	*Eira barbara*	AMPG	EV55
Mustelidae	*Gulo gulo*	MNHN	1936-190
Mustelidae	*Gulo gulo*	SMNS	6833
Mustelidae	*Gulo gulo*	SMNS	51682
Mustelidae	*Mustela nivalis*	MNHN	1955-283
Mustelidae	*Mustela nivalis*	ZMUP	-
Mustelidae	*Mustela nivalis*	AMPG	EV106
Mustelidae	*Mustela putorius*	MNHN	A3392
Mustelidae	*Mustela putorius*	ZMUP	4022
Mustelidae	*Mustela putorius*	NMNHS	21/1980
Mustelidae	*Mustela putorius*	NMNHS	2_1980
Mustelidae	*Mustela putorius*	NMNHS	32/1980
Mustelidae	*Mustela putorius*	NMNHS	99/1980
Mustelidae	*Mustela putorius*	NMNHS	20/1980
Mustelidae	*Mustela putorius*	NMNHS	5_1980
Mustelidae	*Mustela putorius*	NMNHS	10_1980
Mustelidae	*Mustela putorius*	NMNHS	13/1980
Mustelidae	*Vormela peregusna*	NMNHS	23/1980
Mustelidae	*Vormela peregusna*	NMNHS	105/1980
Mustelidae	*Vormela peregusna*	NMNHS	9_1980
Mustelidae	*Vormela peregusna*	NMNHS	4_1980
Mustelidae	*Vormela peregusna*	NMNHS	10_1980
Mustelidae	*Vormela peregusna*	NMNHS	6_1980
Mustelidae	*Vormela peregusna*	NMNHS	33/1980
Mustelidae	*Vormela peregusna*	NMNHS	3_1980
Mustelidae	*Martes martes*	MNHN	1912-69
Mustelidae	*Martes martes*	NMNHS	17/1980

Mustelidae	*Martes martes*	NMNHS	20/1980
Mustelidae	*Martes martes*	NMNHS	16/1980
Mustelidae	*Martes martes*	NMNHS	15/1980
Mustelidae	*Martes martes*	NMNHS	23/1980
Mustelidae	*Martes martes*	NMNHS	12_1980
Mustelidae	*Martes martes*	NMNHS	13/1980
Mustelidae	*Martes martes*	NMNHS	19/1980
Mustelidae	*Martes martes*	NMNHS	21/1980
Mustelidae	*Martes martes*	NMNHS	22/1980
Mustelidae	*Martes foina*	NMNHC	80.5.61.43
Mustelidae	*Martes foina*	NMNHC	80.5.61.32
Mustelidae	*Martes foina*	NMNHC	80.5.61.27
Mustelidae	*Martes foina*	NMNHC	80.5.61.29
Mustelidae	*Martes foina*	NMNHC	80.5.61.6
Mustelidae	*Martes foina*	NMNHC	80.5.31.80
Mustelidae	*Martes foina*	NMNHC	80.5.61.26
Mustelidae	*Martes foina*	NMNHC	80.5.61.28
Mustelidae	*Martes foina*	MNHN	1911-181
Mustelidae	*Martes foina*	AMPG	EV57
Mustelidae	*Martes foina*	AMPG	EV104
Mustelidae	*Martes foina*	AMPG	EV232
Mustelidae	*Martes foina*	AMPG	EV345
Mustelidae	*Lutra lutra*	MNHN	1929-24
Mustelidae	*Lutra lutra*	NMNHS	21/1980
Mustelidae	*Lutra lutra*	NMNHS	10_1980
Mustelidae	*Lutra lutra*	NMNHS	15/1980
Mustelidae	*Lutra lutra*	NMNHS	14/1980
Mustelidae	*Lutra lutra*	NMNHS	6_1980
Mustelidae	*Lutra lutra*	NMNHS	33/1980
Mustelidae	*Lutra lutra*	NMNHS	8_1980
Mustelidae	*Lutra lutra*	NMNHS	32/1980
Mustelidae	*Lutra lutra*	NMNHS	25/1980
Mustelidae	*Lutra lutra*	NMNHS	27/1980
Mustelidae	*Lutra lutra*	NMNHS	23/1980
Mustelidae	*Enhydra lutris*	MNHN	1935-123
Mustelidae	*Enhydra lutris*	SMNS	26359
Mustelidae	*Pteronura brasiliensis*	SMNS	2771
Mustelidae	*Amblonyx cinereus*	SMNS	13741
Mustelidae	*Amblonyx cinereus*	SMNS	13742
Mephitidae	*Mephitis mephitis*	SMNS	35189
Mephitidae	*Mephitis mephitis*	SMNS	21881
Mephitidae	*Mephitis mephitis*	SMNS	702
Mephitidae	*Mephitis mephitis*	SMNS	1023
Mephitidae	*Conepatus chinga*	SMNS	21875
Mephitidae	*Conepatus chinga*	SMNS	21873
Mephitidae	*Conepatus chinga*	SMNS	26335

Mephitidae	*Conepatus humboldtii*	SMNS	39681
Mephitidae	*Conepatus humboldtii*	SMNS	522
Mephitidae	*Conepatus humboldtii*	SMNS	21873
Phocidae	*Monachus monachus*	GMNH	No Nu

Table 57. Material of specimens of fossil species used in this study.

Family	**Species**	**Museum**	**Code**	**Locality**
Felidae	*Amphimachairodus giganteus*	MNHUK	37356	Pikermi
Felidae	*Amphimachairodus giganteus*	MNHUK	49674	Pikermi
Felidae	*Amphimachairodus giganteus*	MNHUK	M8968	Pikermi
Felidae	*Amphimachairodus giganteus*	MNHN	PIK-418	Pikermi
Felidae	*Amphimachairodus giganteus*	MNHN	PIK-3387	Pikermi
Felidae	*Amphimachairodus giganteus*	AMPG	HAL-1967/5	Halmyropotamos
Felidae	*Amphimachairodus giganteus*	AMPG	PG01/100	Pikermi
Felidae	*Amphimachairodus giganteus*	AMPG	PIK1967/7	Pikermi
Felidae	*Amphimachairodus giganteus*	AMPG	No Nu	Choirostasion
Felidae	*Amphimachairodus giganteus*	AMPG	PG01/101	Pikermi
Felidae	*Amphimachairodus giganteus*	NHMA	PMMS-69	Samos
Felidae	*Amphimachairodus giganteus*	MNHN	SLQ-93B	Salonica
Felidae	*Machairodus aphanistus*	MNHN	KTD-63	Kemiklitepe
Felidae	*Paramachairodus orientalis*	MNHUK	M8959	Pikermi
Felidae	*Metailurus major*	AMPG	HAL-1967/1	Halmyropotamos
Felidae	*Metailurus major*	AMPG	PA1257/91	Pikermi
Felidae	*Metailurus major*	AMPG	HAL1967/3	Halmyropotamos
Felidae	*Metailurus major*	AMPG	HAL1967/2	Halmyropotamos
Felidae	*Metailurus major*	AMPG	No Nu	Pikermi
Felidae	*Metailurus major*	AMPG	PG95/1532	Pikermi
Felidae	*Metailurus parvulus*	AMPG	No Nu	Kisdari
Felidae	*Metailurus parvulus*	AMPG	No Nu	Kisdari
Felidae	*Metailurus parvulus*	AMPG	PG01/103	Pikermi
Felidae	*Metailurus parvulus*	AMPG	No Nu	Pikermi
Felidae	*Metailurus parvulus*	AMPG	HAL1967/5	Halmyropotamos
Felidae	*Metailurus parvulus*	NHMA	MTLA-234	Samos
Felidae	*Metailurus parvulus*	NHMA	MTLA-235	Samos
Felidae	*Pristifelis attica*	MNHN	PIK-3034	Pikermi
Felidae	*Pristifelis attica*	MNHN	PIK-3232	Pikermi
Felidae	*Pristifelis attica*	MNHN	SLQ-935	Salonica
Felidae	*Pristifelis attica*	AMPG	PG01/106	Pikermi
Felidae	*Pristifelis attica*	AMPG	PG01/107	Pikermi
Felidae	*Pristifelis attica*	AMPG	PG01/108	Pikermi
Hyaenidae	*Adcrocuta eximia*	LGPUT	RPl-14	Ravin de la Pluie
Hyaenidae	*Adcrocuta eximia*	LGPUT	RZO-425	Ravin de Zouaves
Hyaenidae	*Adcrocuta eximia*	LGPUT	NIK-1550	Nikiti
Hyaenidae	*Adcrocuta eximia*	LGPUT	PER-1240	Perivolaki
Hyaenidae	*Adcrocuta eximia*	MNHUK	37357	Pikermi
Hyaenidae	*Adcrocuta eximia*	MNHUK	49673	Pikermi
Hyaenidae	*Adcrocuta eximia*	MNHUK	M4162	Samos
Hyaenidae	*Adcrocuta eximia*	MNHUK	M4163	Samos
Hyaenidae	*Adcrocuta eximia*	MNHUK	M4164	Samos
Hyaenidae	*Adcrocuta eximia*	MNHUK	M8966	Pikermi
Hyaenidae	*Adcrocuta eximia*	MNHUK	M8967	Pikermi

Hyaenidae	*Adcrocuta eximia*	MNHUK	M8968	Pikermi
Hyaenidae	*Adcrocuta eximia*	MNHUK	M8969	Pikermi
Hyaenidae	*Adcrocuta eximia*	MNHUK	M8970	Pikermi
Hyaenidae	*Adcrocuta eximia*	MNHUK	M8971	Pikermi
Hyaenidae	*Adcrocuta eximia*	MNHUK	M8972	Pikermi
Hyaenidae	*Adcrocuta eximia*	MNHUK	M8973	Pikermi
Hyaenidae	*Adcrocuta eximia*	MNHUK	M8974	Pikermi
Hyaenidae	*Adcrocuta eximia*	MNHUK	M8980	Pikermi
Hyaenidae	*Adcrocuta eximia*	MNHUK	M9041	Pikermi
Hyaenidae	*Adcrocuta eximia*	MNHN	SLQ-934	Salonica
Hyaenidae	*Adcrocuta eximia*	MNHN	MAR-3371	Maraghah
Hyaenidae	*Adcrocuta eximia*	MNHN	MAR-3373	Maraghah
Hyaenidae	*Adcrocuta eximia*	MNHN	MAR-3364	Maraghah
Hyaenidae	*Adcrocuta eximia*	MNHN	MAR-3363	Maraghah
Hyaenidae	*Adcrocuta eximia*	MNHN	MAR-3362	Maraghah
Hyaenidae	*Adcrocuta eximia*	AMPG	PG95/1507	Pikermi
Hyaenidae	*Adcrocuta eximia*	AMPG	PG95/1506	Pikermi
Hyaenidae	*Adcrocuta eximia*	AMPG	1890	Samos
Hyaenidae	*Adcrocuta eximia*	AMPG	No Nu	Pikermi
Hyaenidae	*Adcrocuta eximia*	AMPG	PA57/1991	Pikermi
Hyaenidae	*Adcrocuta eximia*	AMPG	PA490/1991	Pikermi
Hyaenidae	*Adcrocuta eximia*	AMPG	PA1296/91	Pikermi
Hyaenidae	*Adcrocuta eximia*	AMPG	PA445/91	Pikermi
Hyaenidae	*Adcrocuta eximia*	NHMA	PMMS-70	Samos
Hyaenidae	*Adcrocuta eximia*	NHMA	PMMS-70a	Samos
Hyaenidae	*Adcrocuta eximia*	NHMA	PMMS-71	Samos
Hyaenidae	*Adcrocuta eximia*	NHMA	MTLA-6	Samos
Hyaenidae	*Adcrocuta eximia*	AMPG	PG01/110	Pikermi
Hyaenidae	*Adcrocuta eximia*	AMPG	PA15/91	Pikermi
Hyaenidae	*Adcrocuta eximia*	AMPG	PG01/111	Pikermi
Hyaenidae	*Adcrocuta eximia*	AMPG	PG01/109	Pikermi
Hyaenidae	*Adcrocuta eximia*	AMPG	No Nu	Pikermi
Hyaenidae	*Lycyaena chaeretis*	MNHUK	M8978	Pikermi
Hyaenidae	*Lycyaena chaeretis*	MNHUK	M8979	Pikermi
Hyaenidae	*Lycyaena chaeretis*	MNHN	PIK-3383	Pikermi
Hyaenidae	*Lycyaena chaeretis*	MNHN	PIK-3384	Pikermi
Hyaenidae	*Lycyaena chaeretis*	MNHN	SMS-4	Samos
Hyaenidae	*Lycyaena chaeretis*	AMPG	PG95/1531	Pikermi
Hyaenidae	*Lycyaena chaeretis*	AMPG	PA31/91	Pikermi
Hyaenidae	*Lycyaena chaeretis*	SMNS	41654	Samos
Hyaenidae	*Hyaenotherium wongii*	MNHUK	M4161	Samos
Hyaenidae	*Hyaenotherium wongii*	MNHN	PIK-3709	Pikermi
Hyaenidae	*Hyaenotherium wongii*	MNHN	SMS-5	Samos
Hyaenidae	*Hyaenotherium wongii*	MNHN	SLQ-929	Salonica
Hyaenidae	*Hyaenotherium wongii*	MNHN	MAR-3353	Maraghah
Hyaenidae	*Hyaenotherium wongii*	MNHN	MAR-3354	Maraghah

Hyaenidae	*Hyaenotherium wongii*	AMPG	No Nu	Samos
Hyaenidae	*Hyaenotherium wongii*	AMPG	KE-124	Kerassia
Hyaenidae	*Hyaenotherium wongii*	AMPG	KE99/53	Kerassia
Hyaenidae	*Hyaenotherium wongii*	NHMA	MTLA-200	Samos
Hyaenidae	*Hyaenotherium wongii*	NHMA	MTLA-1	Samos
Hyaenidae	*Hyaenotherium wongii*	NHMA	MTLB-171	Samos
Hyaenidae	*Hyaenotherium wongii*	NHMA	MTLA-2	Samos
Hyaenidae	*Hyaenotherium wongii*	NHMA	MTLB-1	Samos
Hyaenidae	*Hyaenotherium wongii*	NHMA	MTLA-237	Samos
Hyaenidae	*Hyaenotherium wongii*	NHMA	MTLA-266	Samos
Hyaenidae	*Hyaenotherium wongii*	NHMA	MTLB-100	Samos
Hyaenidae	*Hyaenotherium wongii*	NHMA	MTLC-18	Samos
Hyaenidae	*Hyaenotherium wongii*	NHMA	MTLA-468	Samos
Hyaenidae	*Ictitherium viverrinum*	MNHUK	49676	Pikermi
Hyaenidae	*Ictitherium viverrinum*	MNHUK	M8981	Pikermi
Hyaenidae	*Ictitherium viverrinum*	MNHUK	M8982	Pikermi
Hyaenidae	*Ictitherium viverrinum*	MNHUK	M8983	Pikermi
Hyaenidae	*Ictitherium viverrinum*	MNHUK	M8984	Pikermi
Hyaenidae	*Ictitherium viverrinum*	MNHUK	M8986	Pikermi
Hyaenidae	*Ictitherium viverrinum*	MNHUK	M8987	Pikermi
Hyaenidae	*Ictitherium viverrinum*	MNHUK	M8988	Pikermi
Hyaenidae	*Ictitherium viverrinum*	MNHUK	M8989	Pikermi
Hyaenidae	*Ictitherium viverrinum*	MNHN	PIK-3009	Pikermi
Hyaenidae	*Ictitherium viverrinum*	MNHN	PIK-3010	Pikermi
Hyaenidae	*Ictitherium viverrinum*	MNHN	PIK-3011	Pikermi
Hyaenidae	*Ictitherium viverrinum*	MNHN	PIK-3004	Pikermi
Hyaenidae	*Ictitherium viverrinum*	MNHN	PIK-3341	Pikermi
Hyaenidae	*Ictitherium viverrinum*	MNHN	PIK-3030	Pikermi
Hyaenidae	*Ictitherium viverrinum*	MNHN	SLQ-927	Salonica
Hyaenidae	*Ictitherium viverrinum*	MNHN	SLQ-926	Salonica
Hyaenidae	*Ictitherium viverrinum*	AMPG	PG01/119	Pikermi
Hyaenidae	*Ictitherium viverrinum*	AMPG	PA59/1991	Pikermi
Hyaenidae	*Ictitherium viverrinum*	AMPG	PG01/115	Pikermi
Hyaenidae	*Ictitherium viverrinum*	AMPG	PG01/121	Pikermi
Hyaenidae	*Ictitherium viverrinum*	AMPG	No Nu	Pikermi
Hyaenidae	*Ictitherium viverrinum*	AMPG	PG01/122	Pikermi
Hyaenidae	*Protictitherium gaillardi*	MNHN	SML-1194	Malartic
Hyaenidae	*Protictitherium gaillardi*	MNHN	SML-453	Malartic
Hyaenidae	*Protictitherium crassum*	NHMA	MLN-26	Samos
Hyaenidae	*Plioviverrops orbignyi*	MNHN	PIK-3016	Pikermi
Hyaenidae	*Plioviverrops orbignyi*	LGPUT	PER-1	Perivolaki
Hyaenidae	*Plioviverrops orbignyi*	LPUT	PER-1295	Perivolaki
Hyaenidae	*Plioviverrops orbignyi*	NHMA	MTLB-170	Samos
Hyaenidae	*Plioviverrops orbignyi*	AMPG	PG95/1515	Pikermi
Hyaenidae	*Plioviverrops orbignyi*	AMPG	PG95/1516	Pikermi
Hyaenidae	*Belbus beaumonti*	SMNS	32	Samos

Percrocutidae	*Dinocrocuta gigantea*	LGPUT	PNT-70	Pentalophos
Percrocutidae	*Dinocrocuta salonicae*	MNHUK	M11413	Salonica
Herpestidae	*Herpestes sp.*	MNHUK	M13072	Pikermi
Ursidae	*Ursavus depereti*	LGPUT	PER-1270	Perivolaki
Ursidae	*Ursavus ehrenbergi*	AMPG	1898	Halmyropotamos
Ursidae	*Indarctos atticus*	MNHUK	M13997	Pikermi
Ursidae	*Indarctos atticus*	AMPG	No Nu	Samos
Ursidae	*Indarctos atticus*	SMNS	No Nu	Samos
Ailuridae	*Simocyon primigenius*	MNHUK	37355	Pikermi
Ailuridae	*Simocyon primigenius*	MNHUK	49675	Pikermi
Ailuridae	*Simocyon primigenius*	MNHUK	M9032	Pikermi
Ailuridae	*Simocyon primigenius*	MNHUK	M9033	Pikermi
Ailuridae	*Simocyon primigenius*	MNHUK	M9034	Pikermi
Ailuridae	*Simocyon primigenius*	MNHN	PIK-3342	Pikermi
Ailuridae	*Simocyon primigenius*	MNHN	PIK-3343	Pikermi
Ailuridae	*Simocyon primigenius*	MNHN	PIK-3359	Pikermi
Ailuridae	*Simocyon primigenius*	AMPG	No Nu	Pikermi
Ailuridae	*Simocyon primigenius*	AMPG	HAL1967/8	Halmyropotamos
Ailuridae	*Simocyon primigenius*	AMPG	PG01/104	Pikermi
Hemicyonidae	*Hemicyon sansaniensis*	MNHN	SEP-54	En Pejouan
Mustelidae	*Promephitis lartetii*	MNHN	PIK-3019	Pikermi
Mustelidae	*Promephitis lartetii*	LGPUT	PER-1278	Perivolaki
Mustelidae	*Sinictis pentelici*	MNHN	PIK-3260	Pikermi
Mustelidae	*Sinictis pentelici*	MNHN	PIK-3821	Pikermi
Mustelidae	*Martes woodwardi*	MNHUK	M9031	Pikermi
Mustelidae	*Martes woodwardi*	AMPG	PA2032/91	Pikermi
Mustelidae	Mustelidae n. sp.	AMPG	PA4879/91	Pikermi
Mustelidae	*Parataxidea maraghana*	NHMA	MTLA-283	Samos
Mustelidae	*Parataxidea maraghana*	NHMA	MTLA-465	Samos
Mustelidae	*Parataxidea maraghana*	NHMA	MTLA-7	Samos
Mustelidae	*Promeles palaeattica*	MNHUK	M9028	Pikermi
Mustelidae	*Promeles palaeattica*	MNHUK	M9029	Pikermi
Mustelidae	*Promeles palaeattica*	MNHUK	M9030	Pikermi
Mustelidae	*Promeles palaeattica*	MNHN	PIK-3454	Pikermi
Mustelidae	*Promeles palaeattica*	LGPUT	PER-1280	Perivolaki
Mustelidae	*Promeles palaeattica*	AMPG	No Nu	Pikermi
Mustelidae	*Promeles palaeattica*	AMPG	PG01/105	Pikermi
Mustelidae	*Promeles palaeattica*	AMPG	PA3501/91	Pikermi
Mustelidae	*Plesiogulo crassa*	LGPUT	PER-1239	Perivolaki
Felidae	*Megantereon cultridens*	LGPUT	APL-12	Apollonia
Felidae	*Megantereon cultridens*	LGPUT	APL-13	Apollonia
Felidae	*Megantereon megantereon*	AMPG	984	Makineia
Felidae	*Homotherium latidens*	LGPUT	APL-684	Apollonia
Felidae	*Homotherium latidens*	LGPUT	APL-710	Apollonia
Felidae	*Lynx issiodorensis*	LGPUT	APL-14	Apollonia
Felidae	*Lynx issiodorensis*	LGPUT	APL-543	Apollonia

Felidae	*Lynx issiodorensis*	MNHN	ACA-388	Calta
Felidae	*Lynx issiodorensis*	MNHN	ACA-351	Calta
Felidae	*Lynx issiodorensis*	AMPG	960	Tourkovounia 3-5
Felidae	*Panthera gombaszoegensis*	LGPUT	APL-758	Apollonia
Felidae	*Panthera gombaszoegensis*	LGPUT	APL-767	Apollonia
Felidae	*Panthera gombaszoegensis*	LGPUT	GER-165	Gerakarou
Felidae	*Panthera gombaszoegensis*	AMPG	Al200	Alikes
Felidae	*Panthera gombaszoegensis*	AMPG	Al7	Alikes
Hyaenidae	*Pliohyaena perrieri*	LGPUT	GER-150	Gerakarou
Hyaenidae	*Pliohyaena perrieri*	AMPG	S82	Sesklon
Hyaenidae	*Pliohyaena perrieri*	AMPG	S87	Sesklon
Hyaenidae	*Pachycrocuta brevirostris*	LGPUT	APL-541	Apollonia
Hyaenidae	*Pachycrocuta brevirostris*	LGPUT	APL-542	Apollonia
Hyaenidae	*Pachycrocuta brevirostris*	LGPUT	APL-700	Apollonia
Hyaenidae	*Pachycrocuta brevirostris*	LGPUT	APL-757	Apollonia
Hyaenidae	*Pachycrocuta brevirostris*	LGPUT	GER-156	Gerakarou
Hyaenidae	*Pachycrocuta brevirostris*	LGPUT	GER-157	Gerakarou
Hyaenidae	*Pachycrocuta brevirostris*	LGPUT	LIB-232	Livakos
Hyaenidae	*Pachycrocuta brevirostris*	LGPUT	KRZ-158	Karnezeika
Hyaenidae	*Chasmaporthetes lunensis*	LGPUT	DFN-75	Dafnero
Hyaenidae	*Chasmaporthetes lunensis*	LGPUT	DFN-109	Dafnero
Hyaenidae	*Chasmaporthetes lunensis*	LGPUT	DFN-111	Dafnero
Hyaenidae	*Chasmaporthetes lunensis*	LGPUT	DFN-117	Dafnero
Hyaenidae	*Chasmaporthetes lunensis*	LGPUT	DFN-194	Dafnero
Canidae	*Canis apolloniensis*	LGPUT	APL-1	Apollonia
Canidae	*Canis apolloniensis*	LGPUT	APL-16	Apollonia
Canidae	*Canis apolloniensis*	LGPUT	APL-17	Apollonia
Canidae	*Canis apolloniensis*	LGPUT	APL-523	Apollonia
Canidae	*Canis apolloniensis*	LGPUT	APL-524	Apollonia
Canidae	*Canis apolloniensis*	LGPUT	APL-527	Apollonia
Canidae	*Canis apolloniensis*	LGPUT	APL-528	Apollonia
Canidae	*Canis apolloniensis*	LGPUT	APL-530	Apollonia
Canidae	*Canis apolloniensis*	LGPUT	APL-690	Apollonia
Canidae	*Canis apolloniensis*	LGPUT	APL-703	Apollonia
Canidae	*Canis apolloniensis*	LGPUT	APL-711	Apollonia
Canidae	*Canis apolloniensis*	LGPUT	APL-715	Apollonia
Canidae	*Canis arnensis*	LGPUT	GER-6	Gerakarou
Canidae	*Canis arnensis*	LGPUT	GER-45	Gerakarou
Canidae	*Canis arnensis*	AMPG	Al19	Alikes
Canidae	*Canis etruscus*	LGPUT	APL-522	Apollonia
Canidae	*Canis etruscus*	LGPUT	APL-526	Apollonia
Canidae	*Canis etruscus*	LGPUT	APL-569	Apollonia
Canidae	*Canis etruscus*	LGPUT	APL-689	Apollonia
Canidae	*Canis etruscus*	LGPUT	GER-166	Gerakarou
Canidae	*Canis etruscus*	LGPUT	GER-167	Gerakarou
Canidae	*Canis etruscus*	LGPUT	GER-168	Gerakarou

Canidae	*Canis etruscus*	LGPUT	GER-169	Gerakarou
Canidae	*Canis etruscus*	AMPG	Al60	Alikes
Canidae	*Canis etruscus*	AMPG	Al59	Alikes
Canidae	*Canis etruscus*	AMPG	Al250	Alikes
Canidae	*Lycaon lycaonoides*	LGPUT	APL-525	Apollonia
Canidae	*Lycaon lycaonoides*	LGPUT	APL-771	Apollonia
Canidae	*Nyctereutes megamastoides*	LGPUT	DFN-17	Dafnero
Canidae	*Nyctereutes megamastoides*	LGPUT	DFN-20	Dafnero
Canidae	*Nyctereutes megamastoides*	LGPUT	DFN-23	Dafnero
Canidae	*Nyctereutes megamastoides*	LGPUT	DFN-173	Dafnero
Canidae	*Nyctereutes megamastoides*	AMPG	PSY-1	Psychiko
Canidae	*Nyctereutes megamastoides*	AMPG	Σ-73	Sesklon
Canidae	*Nyctereutes megamastoides*	AMPG	Σ-440	Sesklon
Canidae	*Nyctereutes megamastoides*	AMPG	Σ-483	Sesklon
Canidae	*Nyctereutes megamastoides*	AMPG	Σ-437	Sesklon
Canidae	*Nyctereutes megamastoides*	AMPG	Σ-454	Sesklon
Canidae	*Nyctereutes megamastoides*	AMPG	Σ-492	Sesklon
Canidae	*Nyctereutes megamastoides*	AMPG	Σ-442	Sesklon
Canidae	*Nyctereutes megamastoides*	AMPG	Σ-438	Sesklon
Canidae	*Nyctereutes megamastoides*	AMPG	Σ-384	Sesklon
Canidae	*Nyctereutes megamastoides*	AMPG	Σ-1100	Sesklon
Canidae	*Nyctereutes megamastoides*	NHCV	PO-060	Vatera-F
Canidae	*Nyctereutes megamastoides*	NHCV	PO-004	Vatera-E
Canidae	*Nyctereutes donnezani*	MNHN	ACA-291	Calta
Canidae	*Nyctereutes donnezani*	MNHN	ACA-292	Calta
Canidae	*Nyctereutes donnezani*	MNHN	ACA-293	Calta
Canidae	*Nyctereutes donnezani*	MNHN	ACA-549	Calta
Canidae	*Vulpes alopecoides*	LGPUT	DFN-22	Dafnero
Canidae	*Vulpes alopecoides*	LGPUT	DFN-172	Dafnero
Canidae	*Vulpes alopecoides*	LGPUT	DFN-190	Dafnero
Canidae	*Vulpes alopecoides*	AMPG	987	Kastritsi
Canidae	*Vulpes alopecoides*	AMPG	983	Makineia
Canidae	*Vulpes alopecoides*	AMPG	S493	Sesklon
Canidae	*Vulpes alopecoides*	AMPG	S229	Sesklon
Canidae	*Vulpes praeglacialis*	LGPUT	APL-11	Apollonia
Ursidae	*Ursus etruscus*	LGPUT	DFN-195	Dafnero
Ursidae	*Ursus etruscus*	LGPUT	TSR-E16-18	Tsiotra Vryssi
Ursidae	*Ursus etruscus*	LGPUT	TSR-E21-50	Tsiotra Vryssi
Ursidae	*Ursus etruscus*	AMPG	986	Kastritsi
Ursidae	*Ursus etruscus*	AMPG	S88	Sesklon
Mustelidae	*Meles dimitrius*	LGPUT	APL-15	Apollonia
Mustelidae	*Meles dimitrius*	LGPUT	APL-544	Apollonia
Mustelidae	*Meles dimitrius*	LGPUT	APL-546	Apollonia
Mustelidae	*Meles dimitrius*	LGPUT	APL-772	Apollonia
Mustelidae	*Baranogale helbingi*	LGPUT	DFN-189	Dafnero