MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

Food preferences of the Mustelids from Göriach (Early to Middle Miocene, Styria, Austria)

verfasst von / submitted by

Julius Lindenbauer, BSc

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien, 2020 / Vienna 2020

Studienkennzahl lt. Studienblatt / degree programme code as it appears on the student record sheet:	UA 066 815
Studienrichtung lt. Studienblatt / degree programme as it appears on the student record sheet:	Masterstudium Erdwissenschaften
Betreut von / Supervisor:	ao. Univ.-Prof. Mag. Dr. Doris Nagel

Contents

Abstract

Mustelids have a high diversity in food preferences and locomotion. They range from carnivorous members, like *Mustela*, to more omnivorous badgers and mollusk-crushing otters. The aim of this work is to differentiate the modern European Mustelidae on the base of their food preference. To classify the feeding types a more detailed database of extant European Mustelidae was created. We combine traditional tooth measurements, which we correlate with a newly developed dental mesowear analysis, based on the carnassial dentition. For the mesowear study, landmark analysis of the carnassials was executed. Principal component analysis was performed for the interpretation of the results. We further use these results to determine the dietary preferences of the Early to Middle Miocene mustelid fossil remains from Göriach near Turnau (Styria, Austria). The following fossil taxa were included in our analysis: *Potamotherium miocenicum, Lartetictis dubia, Trocharion albanense, Trochictis depereti* and *Taxodon sansaniensis*.

To clarify the result, outgroups were taken for each feeding type. Felids (*Panthera leo, Lynx lynx, Felis silvestris* and the fossil *Megantereon cultridens*) are typically known to be hypercarnivores. The crushing feeding type is represented by the sea otter (*Enhydra lutris*) and the omnivorous type by the badger (*Meles meles*).

The smaller *Mustela*, as well as the bigger *Gulo* are a carnivore group. On the contrary the group of *Martes* are more omnivore, closer to the badgers. The European otter plots more to the sea otter.

Based on the results of this study it is possible to differentiate the three feeding types (carnivorous, omnivorous and crushing/hard object feeding) between the European mustelids. The Miocene mustelids from Göriach plot clearly in the omnivorous to crushing niche, close to the otters, badgers and the martins.

Zusammenfassung

Die Familie der Mustelidae ist bekannt für ihre Vielfalt, ihre Anpassungsfähigkeit an unterschiedlichste Nahrungsspektren, sowie für ihre diverse Arten der Fortbewegung. Einzelne Vertreter der Familie gelten als strikte Fleischfresser, wie zum Beispiel die Gattung *Mustela*, andere sind eindeutige Allesfresser wie der Dachs, bis zu den Muschel- und Schnecken knackenden Ottern.

Das Ziel dieser Arbeit ist es rezent, in Europa vorkommende Musteliden aufgrund ihrer Nahrungspräferenz einzuteilen. Basierend auf metrischen Zahnvermessungen wurde eine Datenbank erstellt. Zusätzlich wurde versucht diese metrischen Werte mit den Daten der neu etablierten Mesowear Analyse zu kombinieren. Die Daten der Mesowear Analyse wurde an der Brechschere (Unterkiefer m1, Oberkiefer P4) mit Hilfe der Landmark Analyse erhoben. Um die Daten auszuwerten, wurden Principle Component Analysen, Non-Metric-Multidimnesional-Scaling und einfache X/Y-Graphiken durchgeführt, die wiederum für die weiterführenden Interpretationen dienten. Des Weiteren wird die Datenbank verwendet um die Nahrungspräferenzen der fossilen Musteliden aus dem frühen bis mittleren Miozän aus Göriach (Steiermark) zu bestimmen. Folgende Arten sind aus Göriach bekannt und wurden etabliert: *Potamotherium miocenicum, Larteictis dubia, Trocharion albanense, Trochicits depereti und Taxodon sansaniensis.*

Um die Ergebnisse klarerer definieren zu können wurden Outgroups in der Auswertung mit ein bezogen. Felidae wie *Panthera leo*, *Lynx lynx* sowie der fossile *Megantereon cultridens* sind als reine Fleischfresser bekannt. *Enhydra lutris*, der Seeotter hat sich an das Knacken von Muschel- und Schneckenschalen angepasst, währenddessen *Meles meles*, der Dachs, ein typischer Allesfresser ist. Basierend auf diesen Studien ist es möglich die europäischen Musteliden aufgrund ihrer Nahrungspräferenz einzuteilen. Drei Gruppen konnten definiert werden: Fleischfresser, Allesfresser und Schalenknacker

Die Auswertung der Daten zeigt, dass sowohl die Gattung *Mustela* als auch die Gattung *Gulo* klar als überwiegende Fleischfresser eingestuft werden können, während *Martes* mehr dem Dachs gleich und einen Allesfresser Typus aufweist. Der Europäische Fischotter hingegen tendiert in Richtung der Schalenknacker, dem Seeotter.

Die miozänen Musteliden aus Göriach fallen in die Gruppe der Allesfresser und die Gruppe der Schalenknacker.

Introduction

The aim of this work is to differentiate the food preference of extant mustelids through a metric as well as mesowear approach and through this to evaluate the Early to Middle Miocene fossil mustelids from Göriach (Styria). So far, the following mustelids were found in the Styrian site: *Potamotherium miocenicum* Peters, 1868, *Lartetictis dubia* Blainville, 1841, *Trocharion albanense* Forsyth-Major 1903 and *Trochictis depereti* Pilgrim, 1932 (Hoernes 1882, Hoffman 1893, Toula, 1884, Thenius, 1949).

Identification of food preferences is important to understand the ecology and the resource management of communities and the resource limitation of species in a community (Litvaitis 2000, Salas & Fuller 1996). Competitive interactions between sympatric species can be clarified as well (Jaksic et al. 1993). For more detailed information it is possible to evaluate specific orders, families or genera from communities. With this knowledge a reconstruction of ecological niche of each species is possible (Litvaitis 2000) and based on that the reconstruction of the palaeoenvironment (Mörs et al. 2000) and creating a meaningful morphospace (Friscia et al. 2007).

To define the carnivore ecology are three important aspects: locomotion style, feeding habits and the body mass. The way of locomotion mirrors the environment where the carnivore is living. The locomotion type is indicated by the limb length, proportions and postcranials in carnivore skeleton (Taylor 1989, Viranta & Andrews 1995).

The body mass of mammals can be calculated by the length and the area of the lower carnassial (Roth 1989, Viranta & Andrews 1995)

The third ecological character, the food prefernce reflected by the dentition. The connection between dentary shape and diet has been well established within in mammals (Kay 1975; Friscia et al. 2007). Crusafont-Pairo & Truyols-Santonja performed such studies the first time in carnivores with simple statistics in 1956. Over time, similar studies have been conducted within various vertebrate taxa, from early tetrapods and rodents to dinosaurs and marine reptiles (Maas, Kraus & Strait, 1988; Carrano, Janis & Sepkoski, 1999; Popowics, 2003; Sacco & Van Valkenbourgh, 2004; Semprebon, Janis & Solounias, 2004; Friscia et al. 2007). The fossil carnivores of Göriach mainly consists of cranial and single tooth remains. For this reason, the study is concentrating on the diet-based tooth structures.

Another method to study palaeodiet proxies are dental microwear analysis. The first attempts to visualise microwear structure on a dental surface was by Rensberger 1978 and Walker et al. 1978. Dental microwear represents the abrasion of tooth enamel by food particles and mirror the dietary before its death (Xafis, Nagel & Bastl, 2017). Microwear analysis are quite solid, but damaged teeth-surfaces limits the usability for such studies. To fill these gaps of information new methods are tried and developed.

Traditional measurements modified after Frisca et al. (2007) are used as basement of the investigation. The authors included carnivorous material from around the world to distinguish the main food intake of carnivores below 10 kg world-wide. They acknowledged a carnivore, insectivore and omnivore/crushing hard objects feeding type. No such studies have been performed on the family of Mustelidae in particular, especially the fossil mustelids.

To differentiate more in detail, the focus herein is on European associations only. Observation and its stomach contents of extant mustelids, the feeding types cluster them in three dietary type: omnivorous, carnivorous and piscivorous. (Stubbe & Krapp 1993, MacDonalds 2006, Morlo, Gunnel & Nagel 2010). The information of extant mustelid plus data aquiered through calculations following Frisca et al. (2007) resulted in a database of extant European mustelids as well as outgroups.

The carnivorous feeding types are represented by outgroups. The Felidae (*Panthera leo, Lynx lynx, Felis silvestris*) and the Hyaenidae (*Hyaena striata*) are typically described as hypercarnivores (Morlo, Gunnel & Nagel 2010, Stubbe & Krapp 1993a & 1993b). The omnivorous type is characterized by the badgers (*Meles meles)* (Stubbe & Krapp, 1993). The sea otter (*Enhydra lutris)* characterizes the third, the crushing feeding type (Tinker et al. 2018, Rheingantz & Ruiz-Olmo 2018).

First task of this study was to evaluate smaller Mustelinae (*Mustela nivalis, M. erminea, M. eversmanni, Putorius putorius* and *Neovison vison*), as well as the larger member of the Martinae, *Gulo gulo,* and the Martinae, represented by *Martes martes* and *M. foina*.

Due to the fragmentary status of fossil material not all measurements can be taken. Often only single teeth are preserved on which a mesowear study can be performed. Therefore, a combination of traditional tooth measurements with a new developed dental mesowear

analysis (through landmark analysis) based on the carnassial dentition should improve the results. Principle component analysis (PCA), non-metric-multidimensional-scaling (NMDS) as well as simple x/y graphs are performed for interpretation of the results.

Abbreviations

Institutional abbreviations

PIUW   Paläontologisches Institut Universität Wien

NHMW   Natural History Museum Vienna

UMJGP   Universal Museum Joanneum Geology and Palaeontology

BMNH   British Museum of Nature History

Abbreviations of taken measurements

<u>MANDIBLE:</u>

Lp2L   … Length of lower second premolar: anteroposterior length of p2.

MWp2   … Maximum width of lower second premolar: buccal-lingual width of p2.

Lp3L   … Length of lower third premolar: anteroposterior length of p3

MWp3   … Maximum width of the lower third molar: buccal-lingual width of p3.

Lp4L   … Length of lower fourth premolar: anteroposterior length of p4.

Lp4W   … Width of lower fourth premolar: buccal-lingual width of p4.

LMLP   … Maximum length of lower premolars: summed length of p4 + p3 + p2.

LGA   … Lower grinding area: summed length of the m1 talonid + length of m2 and m3 if present.

LGAMW   … Lower grinding area maximum width: the maximum width of the lower grinding area (LGA).

LBL   … Lower blade length: trigonid length of the lower m1.

Lm1L   … Length of lower first molar: anteroposterior length of lower m1 (carnassial).

MaL   … Mandibular length: measured distance between the posterior margin of the mandibular condyle and the anterior margin of the canine.

Lm2L   … Length of lower second molar: anteroposterior length of m2.

MWm2   … Width of lower second molar: buccal-lingual width of m2.

Lm2A   … Area of lower second molar: maximum length of m2 multiplied by maximum width of m2.

Lm3L   … Length of lower third molar: anteroposterior length of m3.

MWm3   … Width of lower third molar: buccal-lingual width of m3.

MAXILLAR:

UP1L	…	Length of upper first premolar: anteroposterior length of P1.
UP1MW	…	Maximum width of upper first premolar: buccal-lingual width of P1
UP2L	…	Length of upper second premolar: anteroposterior length of P2.
UP2MW	…	Maximum width of upper second premolar: buccal-lingual width of P2.
UP3L	…	Length of upper third premolar: anteroposterior length of P3.
UP3MW	**…**	Maximum width of the third upper premolar: buccal-lingual width of P3
UMLP	…	Maximum length of upper premolars: summed length of P4 + P3 + P2.
UP4MW	…	Maximum width of upper fourth premolar: buccal-lingual width of P4.
UGA	…	Upper grinding area: summed length of m1 + if present m2 + m3.
UGMW	…	Upper grinding area maximum width: the maximum width of the upper grinding area (UGA).
UBL	…	Upper blade length: anteroposterior length of P4 (carnassial).
UM1L	…	Maximum length of upper first molar: anteroposterior length of M1.
UM1MW	…	Maximum width of upper first molar: buccal-lingual width of M1.
UM1A	…	Area of upper first molar: length of M1 multiplied by maximum width of M1.
UM2L	…	Maximum length of upper second molar: anteroposterior length of M2.
UM2MW	…	Maximum width of upper second molar: buccal-lingual width of M2

Material

The majority of the mustelid used for the database are housed in the Natural History Museum Vienna (Mammal section), others are from the Department Palaeontology, University of Vienna.

The fossil remains from Göriach (*Potamotherium miocenicum* Peters, 1868, *Lartetictis dubia* Blainville, 1841, *Trocharion albanense* Forsyth-Major 1903 and *Trochictis depereti* Pilgrim, 1932) are located in Joanneum Graz and Natural History Museum Vienna (Geological-Palaeontological section).

Methods

Teeth constitute important elements for the identification of many mammalian species, while they also reflect their different food preferences. Herein, traditional tooth measurements, are combined with a newly developed dental mesowear analysis, based on the carnassial dentition. The traditional measurements used in this study follow the ones proposed by Friscia et al. (2007). All measurements are presented in abbreviations and depicted in Fig. 1 and 2. In the latter study, the authors made a detailed attempt to distinguish the main food intake of carnivores below 10 kg worldwide. Their results revealed three distinct feeding types: carnivorous, insectivorous and omnivorous/hard-object-crushing.

The carnivores, especially the Mustelidae are known for their wide range of food sources. Basally the molars are used for grinding and the premolars for cutting, except the lower first molar (m1), which has a grinding (talonid) and a cutting area (trigonid). The opponent is the upper fourth premolar (P4). The proportion of grinding and cutting area is defined by the adaptation to feeding habitat. Fresh meat consumption requires cutting abilities, while the dietary of fruits or vegetables forces more the grinding area (Viranta & Andrews 1995). Similar is the adaptation on crushing/hard object feeding only with stronger dentition which is able to resist high stress (Van Valkenburgh, 1989; Van Valkenburgh & Koepfli, 1993; Friscia et al., 2007).

Insectivorous taxa are somewhere between the carnivorous and the omnivorous extremes because of shorter blade lengths than the carnivores and weaker jaws. Their dentition is adapted to pray manly hard and soft invertebrates (>50%) like insects, chelicerates and worms (Friscia et al., 2007). The variation in dentation and feeding methods between the insectivorous depends on hardness of insect exoskeletons (Strait, 1993b; Strait & Vincent, 1999).
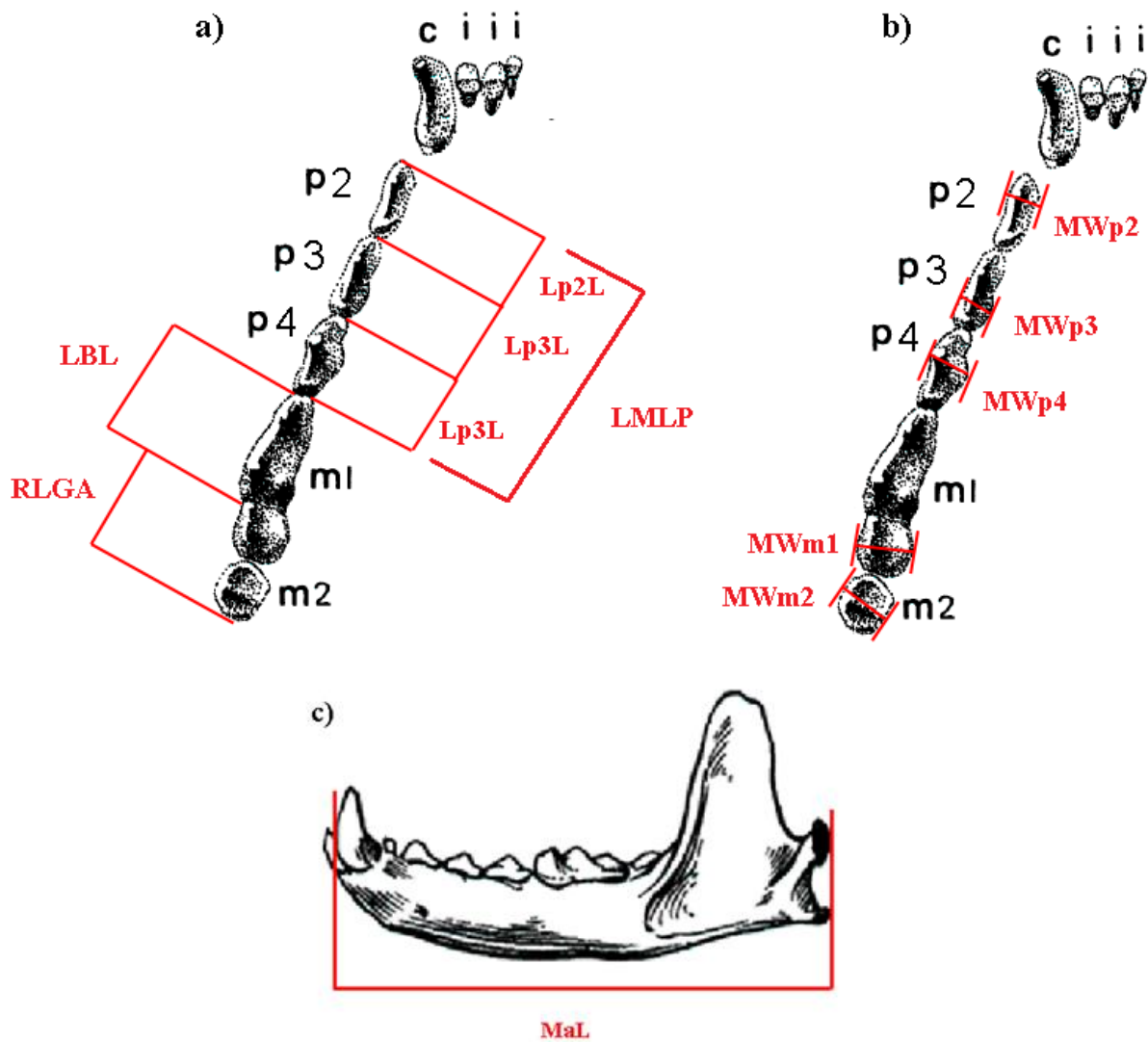
Figure 1: Measurements in the lower jaw after Friscia et al. 2007, modified. 1a: Length of the lower teeth; 1b: Width of the lower teeth; 1c: Mandibular length.
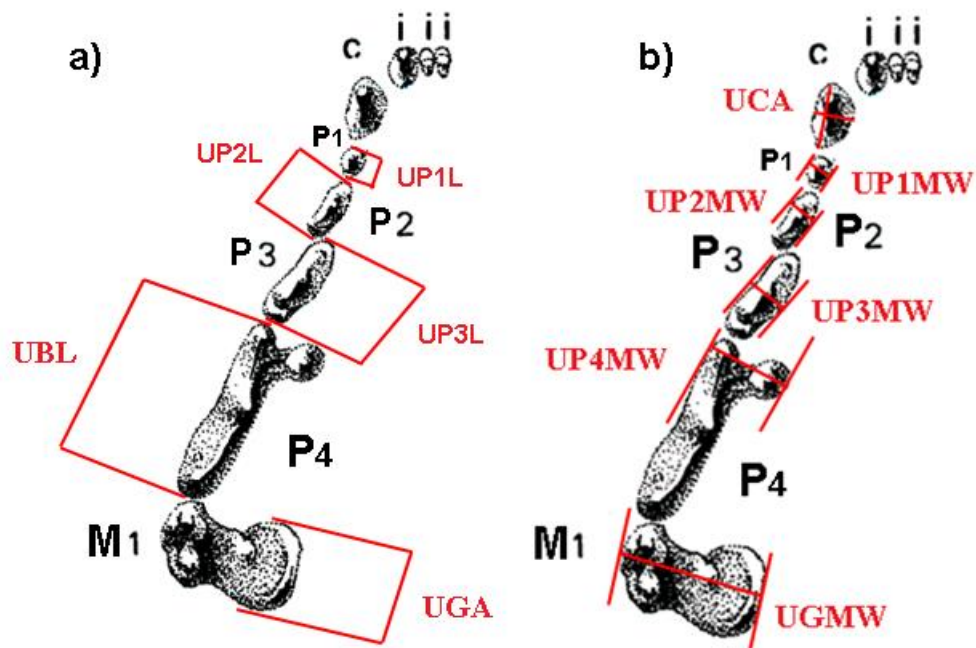
Figure 2: Measurements of the upper jaw after Friscia et al. 2007, modified. a) lenght upper teeth, b) width upper teeth.

The raw measurements are used for the following formula after Frisca et al. (2007). The chosen variables, which are presented below, have been found to be functionally significant in carnivore taxa by Jones (2003), Sacco & Van Valkenburgh (2004), Van Valkenburgh & Koepfli (2004), Friscia et al. (2007).

Formula

$$RBL = \frac{LBL}{MaL}$$ ... Relative blade length

$$RLGA = \frac{\sqrt{LGA * LGMW}}{LBL}$$ ... Relative lower grinding area
.

$$RUGA = \frac{\sqrt{UGA * UGMW}}{UBL}$$ ... Relative upper grinding area

$$m1BS = \frac{LBL}{MaL}$$ ... m1 blade size relative to mandibular length

$$m2S = \frac{\sqrt{Lm2L * Lm2W}}{MaL}$$ ... m2 size relative to mandibular length

$$P4P = \frac{UP4MW}{UBL}$$ ... Relative size of the protocone of the upper fourth premolar

$$p4S = \frac{Lp4W}{Lp4L}$$ ... Lower fourth premolar shape

$$PMZ = \frac{LMLP}{MaL}$$ ... Relative total length of premolars

$$RLCS = \frac{LMLP + LBL}{MaL}$$ ... Relative lower cutting size

$$p4Z = \frac{Lp4L}{MaL}$$ ... Relative length of fourth lower premolar

The extant comparative database was collected on 192 extant carnivore taxa from nearly (Tab. 1); sample size from one to 18. The focus of the database is on mustelids. Data from other groups like the ursids (*Ursus arctos, Ailuropoda melanoleuca*), procyonids (*Bassaricyon gabbii, B. sumichrasti, B. astutus, Nasua narica, N. nasua* & *Potos flavus*), nandiniids (*Nandinia binotata*), viverrids (*Genetta* sp.), hyaenids (*Hyaena striata*) and felids (*Panthera leo, Lynx lynx, Felis domestica, Felis silvestris*) are outgroups to emphasize the largest difference in food preferences.

Table 1: Extant and fossil taxa and their common names used in this work and sample size (n).

__Family__	__Taxon__	__Common name__	__n__
__Felidae__	*Felis silvestris*	Wildcat	2
	Lynx lynx	Eurasian lynx	2
	Panthera leo	Lion	1
	Megantereon cultridens	Saber-toothed cat	1
__Procyonidae__			
	Bassaricyon gabbii	Northern olingo	1
	Bassariscus sumichrasti	Cacomistle	1
	Bassariscus astutus	Ringtail	2
	Nasua narica	White-nosed coati	6
	Nasua nasua	South American coati/ Ring-tailed coati	6
	Nasua nasua rufa	Red-nosed coati	3
	Potos flavos		7
__Hyaenidae__			
	Plioviverrops sp.		1
	Hyaena striata	Striped hyena	1
__Ursidae__			
	Ailuropoda melanoleuca	Giant panda	1
	Ursus arctos	Brown bear	1
__Nandiniidae__			
	Nandinia binotata	African palm civet/ Two-spotted palm civet	1
__Viverridae__			
	Paradoxurus hermaphroditus	Asian palm civet	1
	Genetta sp.	Geneta	2
__Canidae__			
	Vulpes vulpes	Red fox	2
__Mustelidae__			
	Meles meles	European badger	4
	Martes martes	European pine marten	18

.	*Martes foina*	Stone marten	17
.	*Putorius putorius*	Ferret	31
.	*Neovison vison*	American mink	9
.	*Mustela eversmanni*	Steppe polecat	13
.	*Mustela nivalis*	Weasel	12
.	*Mustela erminea*	Stoat	13
.	*Mustela lutreola*	Eurasian mink	3
.	*Enhydra lutris*	Sea otter	3
.	*Lutra lutra*	Eurasian otter	6
.	*Gulo gulo*	Wolverin	7
.	*Ictonyx striatus*	Zorilla	1
.	*Mellivora* sp.	Honey badger	1
.	*Potamotherium miocenicum*		3
.	*Trochictis taxodon*		1
.	*Trochictis depereti*		3
.	*Trocharion albanense*		1
.	*Lartetictis dubia*		4
.	*Ischyritis anatolicus*		1
.			
Total number:			192

Procyonidae are of interest because phylogenetically they represent the closest related family to the Mustelidae (Sato et al. 2012, Yonezawa et al. 2007). I follow Frisca et al (2007) and classify: 1) carnivore 2) omnivore 3) crushing/hard feeding. These three categories define the entire ecological adaptation of mustelids (Rheingantz & Ruiz-Olmo 2018).

These types are classified by percentage of food. Carnivorous taxa have diets composed of >50% vertebrate flesh, including mammals, birds, reptiles and amphibians, regardless of size. Diet of hypercarnivores consists of >90% of meat (Van Valkenburgh, 1991 zitate). The food spectrum of the omnivorous category needs to be chewed up. The spectrum includes carrion as well as plants. The true omnivores have no dominant food type. The food range of the crushing/hard-object-feeder, also best seen in *Enhydra* and includes i.e. molluscs or large crustaceans (Tinker et al. 2018, Rheingantz & Ruiz-Olmo 2018). *Enhydra lutris* is known as a full aquatic Lutrinae that feeds mostly on invertebrates (60%). *Lutra lutra,* the Eurasian otter, is more specialized on fish (Medina-Vogel et al. 2004, Krook 2006).

The chosen measurements characterise the typical features in dentition, which mirrors the diet. The dental measurements on extant specimen were taken with a manual calliper.

Geometric morphometrics (GM) were used to visualize deviations of the shape of the carnassials. Geometric morphometrics is a quantitative representation and analysis of the morphology through geometric coordinates. The coordinates are defined by manual placed homologous points (landmarks) which define the morphology of biological objects as a XY matrix. The matrix can be analysed in 2D or 3D (Dryden & Mardia 2016, Polly 2018).

There are three different types of landmarks: 1) Type I Landmark: anatomical landmarks, homologues positions like openings of foramens or junctions between bones; 2) Typ II Landmark: mathematical landmarks, defined by local properties (geometric landmarks), for example the maximum depth of the mandibular ramus; 3) Type III Landmark: pseudo landmarks, e.g. centre of eye representing positions of particular structure. Landmarks type I cannot be found in buccal teeth shape. The third type is very problematic because the landmarks depends on landmark type I and II and is not a position of a particular structure (Polly 2018, Dryden & Mardia 2016). Therefore, only landmarks type II can be found on buccal teeth morphology and used in following analyses.

Curves can be recorded by contentiously set semilandmarks, which trace the outline of the shape and covers the surface by a three-dimensional grid. Semilandmarks can be optimate by sliding them to minimize the shape between objects. It is also known as "sliding smilandmarks" (Polly 2018, Dryden & Mardia 2016).

For visualizing the food preference, the shapes of the most ecological significant and stressed teeth are taken, the carnassial (Butler 1946, Roth 1988, Viranta & Andrews 1995, Szuma & Germonpré 2020). For the analysis, digital pictures were taken from the buccal side of the scaled carnassial. The picture format "-jpg" were formed into "-.tps" files with the freeware tpsutil (Rohlf 2015 & 2015). Landmarks are placed using the freeware tpsDig2 (Rohlf 2005 & 2015). These values were converted to "-.nts" files by tpsutil. Statistical analyses are performed by the freeware's MorphoJ (Klingenberg, 2011) and PAST3 (Hammer, Harper & Ryan, 2001).

In total seven landmarks type II were used to define the shape of the lower m1. The shape of the upper P4 is defined through five type II landmarks in total (Fig. 3).
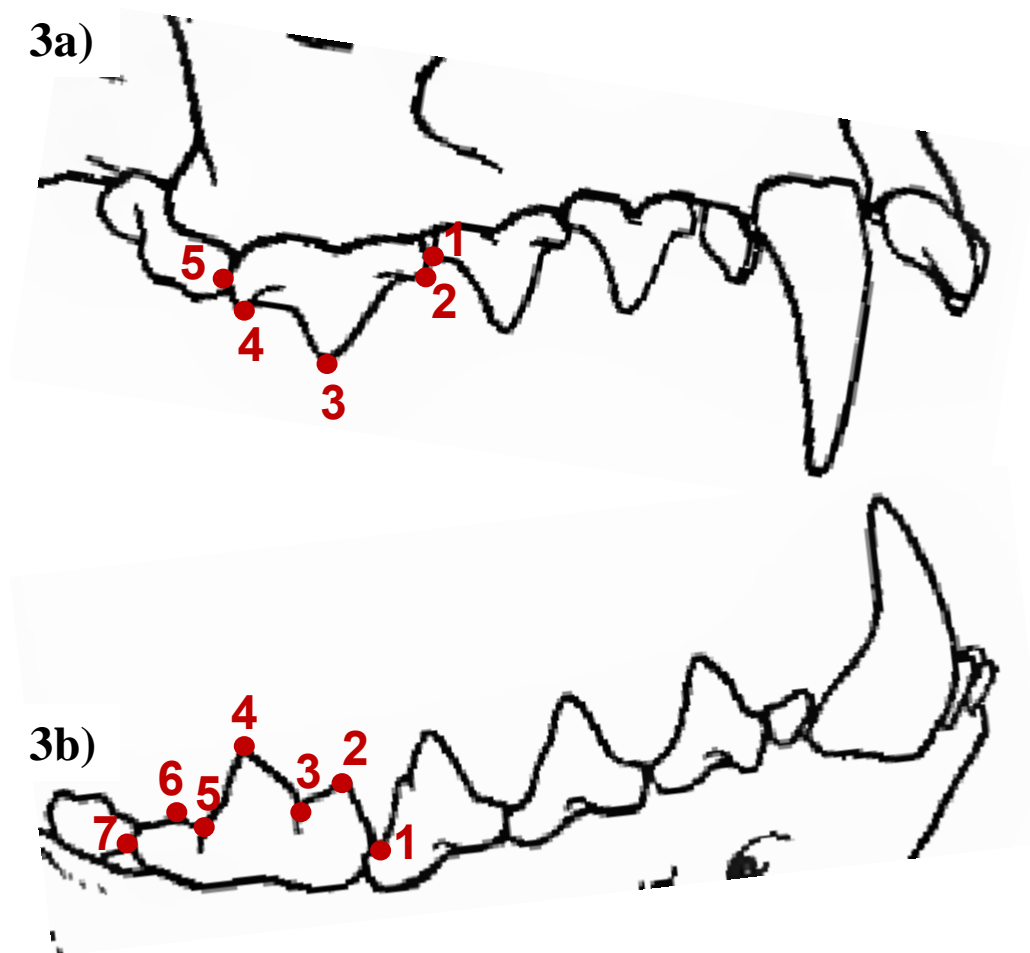
Figure 3: Carnassial of *Martes martes* modified by Lindenbauer after Miller (1912) with strict ordered positions of the Landmarks:.3a: positioning of the landmarks 1-5 on the upper P4; 3b: positioning of the landmarks 1-7 on the lower m1.

Landmark 1 and 5 describe the length of the P4 and are located on the anterior and the posterior margin of the P4. The third landmark marks the highest point of the P4, the peak of the paracone. Landmark 2 is located on the top of the parastyle if present as in *Gulo gulo*. Otherwise the highest point of the anterior cingulum is used. The fourth landmark is placed on the highest peak of the metastyl blade (Fig. 3).

The length of the m1 is described by landmark 1 and 7. They are positioned on the anterior and posterior margin. The trigonid is defined by landmark 2, 3 and 4. Landmark 2 and 4 are on the highest points of the trigonid, the paraconid and the protoconid. The landmark 3 describes the lowest point of the trigonid which is found between the para- and protoconid. Landmark 6 is located on the hypoconid. The lowest point of the talonid immediately after the trigonid is defined by landmark 5. The placement of the landmarks must be in a strict order,

one after the other as shown in Fig. 3. If a landmark was missing, the landmark was classified as missing landmark.

To get a cleaner evaluation a 2D Procrustes transformation was performed. A Generalized Procrustes transformation has three steps: 1) Translation: each LM is defined by XY coordinates. In this step the configurations will be centred. 2) Rotation: the centred configuration will be orientated. 3) Scaling: the size of the configuration will be removed (Rohlf & Slice 1990, Mardia & Dryden 1989 & 2016, Hammer 2001, Dryden & Mardia 2016, Polly 2018). The transformed data were used for the Principle Component Analysis (PCA). Principle component analyses finds hypothetical components, announcing for the most possible variance in the multivariate data (Davis 1986, Harper 1999). The principal component space is often described as morpho space (Polly 2018). This analyse is used to reduce the data set to only two new variables, which are linear combinations of the original variables. The new most important two components are for plotting (Hammer 2001). It is one of the most used multivariate statistical method for investigating biological patterns.

Another used method in this work is non-metric multidimensional scaling (NMDS). Non-metric multidimensional scaling is used to combine metric data with coordinate system of taken landmarks. This statistical method is based on a distance matrix. The algorithm attempts to plot the data points in a two- or three-dimensional (in this work in a 2D) coordinate system. The ranked differences between the data points in the graph are preserved. In each run the program combine on a different solution, depending on the initial state. The sequence with the smallest stress is chosen and is automatically rotated to the major axes in each run. In this analysis it is possible to implicate different environmental variables, which are not included in the ordination. Vectors from the origin presenting the correlation coefficients between each environmental variable and the NMDS. The length of the vectors are arbitrarily scaled to make the biplot readable. Simple X/Y graphs where established to clearer depict the PCA and NMDS results (Hammer 2001, Taguchi & Oono 2005).

Systematic Paleontology

Class: Mammalia Linneaus, 1758

Order: Carnivora Bowdich, 1821

Suborder: Caniformia Kretzoi, 1943

Infraorder: Arctoidea Flower, 1869

Arctoidea incertae sedis

Genus: *Potamotherium* Geoffroy Saint-Hilaire, 1833

Type Species: *Potamotherium valletoni* Geoffroy Saint-Hilaire, 1833, MP28-MN6

Holotyp: lost maxillar fragment figured by Von de Blainville 1842

Included Species: *Potamotherium miocenicum* Peters, 1868

Type Locality: St. Gérand-le-Puy

Other Locality: Elgg, Switzerland, Allier-Basin (MP30; MN 2a); Mainz Basin (MN1 – MN 2a) Germany

Remarks: The classification of *Potamotherium* spp. has been debated in the past multiple times. They have been included within the Pinnipedia (Tedford, 1976; Wolsan, 1993; Morlo, 1996 Rybczynski et al., 2009), the Musteloidea (Ginsburg, 1999; Wang et al., 2005a), and the Lutrinae (Pohle, 1919; Savage, 1957; Wank, 1977; Koretsky & Domning, 2014). Most recent attempts to make a phylogenetical classification failed to provide a consensual hypothesis (Wang et al., 2005a; Rybczynski et al., 2009). I follow Rabi et al., (2017) and leave the taxonomic position within Arctoidea.

Potamotherium miocenicum Peters, 1868

1859 *Stephanodon mosbachiensis* (H. v. Meyer. p. 427) p. p.1868 *Viverra miocenica* (Peters, p. 6, Taf. III, Fig. 8— 10).

1887 *Lutra valetoni* (Hofmann, p. 212, Taf. XI, Fig. 1— 4, Taf. XII, Fig. 5. 6).

1888 *Lutra valetoni* (Hofmann. p. 78, Taf. I, Fig. 1).1888 *Viverra miocenica* (Vacek, p. 312).

1889 *Lutra lorteti* (Schlosser, p. 347, Taf. VIII, Fig. 29, 36, 39, 40) p. p.

1889 *Lutra dubia* (Schlosser, p. 349, Taf. VIII, Fig. 64) p. p.

1890 *Viverra miocenica* (Hofmann, p. 525).

1891 *Viverra miocenica* (Schlosser , p. 396).

1902 *Lutra valetoni* (Dreger 1902, p. 92).

1902 *Viverra miocenica* (Dreger1902, p. 92).

1905 *Trochictis* cfr. *hydrocyon* (Hofmann, p. 27, Taf. II, Fig. 1— 5).

1907 *Trochictis hydrocyon* (Zdarsky, p. 437, Taf. IX, Fig. 1— 7).

1908 *Trochictis hydrocyon* (Bach, p. 100).

1908 *Lutra valetoni* (Bach, p. 101).

1908 *Viverra miocenica* (Bach, p. 102).

1908 *Viverra* sp. (Bach, p. 103).

1914 *Potamotherium* n. sp. (Steh1in. p. 150).

1919 *Potamotherium lorteti* (Pohle, p. 21) p. p.

1929 *Potamotherium* (Viret, p. 141).

1933 *Potamotherium* sp. (Viret, p. 25).

1934 *Trochictis hydrocyon* (Pia & Sickenberg. Nr. 88, 89. 101, 102. 117, 126).

1934 *Potamotherium valetoni* (Pia & Sickenberg. Nr. 86, 112— 116. 119, 120, 124, 136).

1934 *Trochictis* cfr. *hydrocyon* (Pia & Sickenberg, Nr. 87, 100).

1934 (?) *Lutra* sp. (Pia & Sickenberg, Nr. 106).

1934 *Lutra* sp. (Pia & Sickenberg, Nr. 123).

1934 *„V iverra miocenica"* (Pia & Sickenberg, Nr. 145, 146).

1934 *„V iverra"*sp. (Pia & Sickenberg, Nr. 148).

1934 Felide indet. (Pia & Sickenber, Nr. 153).

1934 Carniv. fissip. indet. Pia & Sickenberg, Nr. 162).

1936 *Potamotherium* sp. (He1bing, p. 17).

1949 *Potamotherium miocenicum* (Thenius. p. 163).

Holotype: right mandible fragment with Cinf, p2 and 3, (Peters 1868, Thenius 1949, fig. 2)

Type locality: Eibiswald (Austria)

Other localities**:** Göriach, Austria, MN4-5; Günzburg, MN4-5; Reichenstetten, Nordrhein-Westfahlen Germany, MN5; Neudorf Sandberg, Elgg, Switzerland, MN6; Artenay, Baigneaux, MN4; Tavers, Anjou France MN5;

Material: mandible dex. with c, p2-4, m1 (UMJGP 1443); mandible dex. with i2-3, c, p2-3, p4 alveoli, m1-2 (UMJGP 4007); mandible dex. with p2-4, m1 (UMJGP 4009)

Description: The specimen UMJGP 1443 represents a right mandible with the canine, p2-4, a m1 while only the alveoli of the m2 is present. The cusp of the protoconid of m1, as well as

the cusp of the canine are broken. The premolars are well preserved. The presence of a p1 is not detectable in this specimen because the mandible is broken before p1.

The mandibular fragment (UMJGP 4007) preserves most of the dental elements, except the i1, p1 and the p4. The p1 is one rooted due to the preserved alveoli.

The premolars are morphologically very similar. The anterior margin of the premolars is steeper than the posterior margin, which has the effect, that the protoconid is located more anterioriliy. The posterior part of the p4 has an accesory cusp. The teeth are surrounded by a cingulum, especially on the base of the p4 (UMJGP 4007).

The specimen UMJGP 4009 preserves the p3-4 and the m1, that are partly covered by sediments. In the case of specimen UMJGP 4009 the consequence of the enlargement of the anterior margin of the premolars, is a S shaped toothrow sitting like specimen UMJGP 1443.

Family: Mustelidae Fischer von Waldheim, 1817

Subfamily? Ictonychinae Pocock, 1921

Genus: *Trochictis* Meyer, 1842

Type Species: *Trochictis carbonaria* Meyer, 1842:584 from MN5 of Käpfnach, Swiss; left fragmented mandible with p1-m1

Included Species: *T. artenensis* Ginsburg, 1968 from MN4 of Artenay; *T. depereti* Major, 1903 from MN7/8 of La-Grive-Saint-Alban*; T. narcisoi* Petter, 1963 from MN 9 of Can Llobatereas; cf. *Trochictis* sp. From MN9 of Rudabánya Werdlin, 2005; *T. peignet* sp. Nov.

Other localities: Pontigne 2 (les Buissonneaux), MN 3-4; Pelecahus (Romieu), MN4; Contres, Loir-et-Cher, France, MN 5-6; Rudabánya, Hungary, MN 9; Pasalar, Turkey, MN 5.

Remarks: The Eurasian *Trochictis* was often taxonomically positioned within the order Melinae (Petter, 1971; Ginsburg & Morales, 2000), variously in Gulolinae Ginsburg (1999), in Mustelinae by Bernor, Kordos & Rook (2004) and most recently in Galictinae by Baskin (2011*). Trochictis depereti* possesses some similar characteristics to *Negodiaetictis* like an m1 talonid with a lager basin ward-sloping expansion of the hypoconid. Furthermore, it is rimmed by a posterior cingulid (Thenius, 1949a; Smith, Czaplewski & Cifelli, 2016). Smith, Czaplewski & Cifelli (2016) mentioned also a grooving of the entoconid on m1 in Eurasian species *Trochictis*? *pusilla* Major, 1903 and *T. taxodon* Gervais, 1852 after Pilgrim (1932). However, *Negodiaetictis* gen. nov. differs in lacking p1, crowded p2-p4, the m1 protoconid is

taller than the metaconid, the m1 is lacking a distinct entoconid and the base of the m1 talonid is higher than the trigonid base (Smith, Czaplewski & Cifelli, 2016).

More recently *Trochictis* has been positioned into the Galictinae (Ogino & Otsuka, 2009; Baskin 2011). The exact position of *Trochictis* is still under debate. I follow the most recent phylogenetically status of Baskin (2011) and classifying *Trochictis* as Galictinae.

Trochictis depereti Major, 1903

Mustela taxodon Lartet In Gervais Z. et P. fr., 1859, pl. XXIII, Fig. 1.

Trochictis depereti F. Major, pars in Pilgrim (P.Z.S. Part 4, 1932, p. 845, pl. I, Fig. 1, non Fig. 2).

Trochictis aff. *carbonaria* Meyer in Viret. 1933, p.24, pl. II, Fig. 8-11

Holotype:

Type locality: La-Grive-Saint-Alban (Isère, France) MN 7/8

Other locality: Göriach

Material: mandible sin. with c, p2-4, m1 (UMJGP 4024)

Description: Left fragmented mandible (UMJGP 4024) with the canine to the lower first molar. The canine is broken. The premolars are very well preserved. Due to the absence of any traces of an alveolus, it is assumed that the specimen lacks a p1. The main cusp of the second premolar is leaning anteriorily and has an anterior accessory cusp. The third premolar is larger in length and width than the p2. The main cusp is located centrally and is as high as the p2. A very small secondary cusp lies on the medial tooth slop. The secondary cusp is clearly detectable on the forth premolar. The p4 is twice the size of the p2. The premolars are positioned very closely to each other.

The trigonid of the m1 is higher than the talonid. Additionally, the talonid is very worn.

<div align="center">Genus: Taxodon Lartet, 1851</div>

Type species: Taxodon sansaniensis Lartet 1851

Includes species: T. cf. sansaniensis Rudabánya

Type locality: Sansan, France, MN6

<div align="center">Taxodon sansaniensis</div>

Material: mandible sin. with c, p3-4, m1 (UMJGP 1435)

Description: The eroded canine is attached to the mandible fragment. The p3 is damaged on the anterior lingual side. The p4 is well preserved, as well as the m1. The p4 is positioned closely to the anterior margin of the m1, while p3 and p4 are slightly spaced.

<div align="center">Subfamily: Leptarctinae Gazin, 1936</div>

<div align="center">Genus: Trocharion Major, 1903</div>

Type Species: Trocharion albanense Major, 1903.

Type locality: La-Grive-Saint Alban,

Other localities: Steinheim, Castell de Barberà, Can Llobateres, Sant Quirze, Vallès-Penedés Basin, Middle to Late Miocene (Robles et al. 2010)

Remarks: The phylogenetic relationship of Trocharion has been recently discussed. The most current hypothesis after Wang, Qiu & Wang 2004 and Robles et al. (2009 & 2010) places Trocharion to the basal-most members of the Leptarctinae. Their modified cladistic analysis is based on the matrix of Wang et al. (2004), which includes outgroups like procyonids, putative stem mustelids and few Leptarctinae. Robles et al. (2010) included the fossil Trocharion and excluded Gaillardina and Trochotherium because they are no longer considered as leptarctines. Additionally, they included more dental characters than described by Wolsan (1993).

<center>*Trocharion albanense* Major, 1903</center>

1833 *Lutra* (*Potamotherium*) *valetoni* Geoffroy Saint-Hilaire: Fraas, 1870:165, plate IV: Fig. 18.

1902 *Promiphitis gaudryi* Schlosser: Schlosser, tab. II/14, 16).

1903 *Trocharion albanense* Major: (Forsyth Major, pp. 536).

1932 *Trocharion albanense* Major: (Pilgrim, tab. II, Fig. 3).

1936 *Trocharion albanense* Major: (Helbing, tab. II, Fig. 8-9, text-Fig. 11-13).

1944 *Trocharion albanense* Major: (Villalta-Comella & Crusafront-Pairò, tab. I, Fig. 4, text-Fig. 8).

1946 *Trocharion albanense* Major: (Viret, text-Fig.).

1949 b *Trocharion albanense* Major: (Thenius).

1949 *Trocharion albanense* Major: (Zapfe, pp. 176-177).

1950 *Trocharion albanense* Major: (Zapfe, pp. 110-118, Fig. 1-6).

Trocharion fraasi Helbing: 1936:51 (conditional proposal)

Holotype: Right mandible with p4-m2 (BMNH 5307). This specimen was first described by Major (1903) but was not figured until Pilgrim (1933).

Type Locality: La Grive-Saint-Alban (Isère, France). MN 7/8

Other localities: Sant Wuirze, Castll de Barberà, MN8; Can Llobrateres 1 MN9; Vieuc-Collonges, Baigneaux-en- Beauce, Lasse, Noyant-sous-le-Lude, Savigné-sur-Lathan, Hommes and Pont Boutard à Saint Michel-sur-Loire, France, MN5; Edelbeuren-Maurerkopf, Germany, MN5; Hambach 6C, MN6; Steinheim, MN7-8; Melchingen, Germany, MN9; Neudorf-Spalte, Slovakia, MN6;

Material: right mandible with p2, p3-4 roots posterior, m1 (UMJGP 4015)

Description: the mandible is fragile and fragmented with p2 to m1 (UMJGP 4015). Additionally, the posterior roots of the p2 and a small fragment of the p3 and p4 cusps are maintained. Only the alveoli of the two rooted p2 is preserved. Based on the dimension of the p2 alveoli it can be assume that the p2 is well developed. The premolars are all in line no space between them. The m1 is strongly worn. Only the anterior alveolus of the m2 is still present.

Subfamily: Lutrinae Bonaparte, 1838

Genus: *Lartetictis* Ginsburg and Morales, 1996

Type species: *Lartetictis dubia* (Blainville, 1842).

Type locality: Sansan, France, MN6.

Other localities: Mala Miliva, Serbia, MN5; Faluns Anjou, France, MN5; Paşalar, Turkey, late MN5; Göriach, Austria, MN5-MN6; Goldberg, Germany, MN6; Rosenthal bei Köpflach, Austria, MN6; Devinska Nova Ves, Slovakia, MN6; Mörgen, Germany, MN8.

Remarks: The phylogenetic position of the genus *Lartetictis* is within the Mustelidae. Ginsburg and Morales described it as a Melinae form in 1996, next to the European badgers. Heimann and Morlo (1998) assumed the taxon is a semiaquatic "musteline", but the dentition is more reminiscent of lutrines. Recently it has been included within the Lutrinae by Ginsburg (1999), Salesa et al. (2013) and Valenciano et al. (2019). It is already noted by Wang et al. (2017) and mentioned in Valenciano et al. (2019), that from some Miocene lineages of otters, especially the American genus *Mionictis*, the European genus *Lartetictis* and the Asian genus *Siamogale* possess dentition similar to badgers. These species exhibit a special combination of an enlarged talon (M1), like the Old World badgers a crested protocone (P4) and a broadened talonid on the lower m1 characteristic for most living otters. Valenciano et al. (2019) considered even similarities between the dentition of the fossil *Larteticts* and the living otters like *Lutra* Brisson, 1762, *Aonyx*, Lesson, 1827, *Lontra* Gray, 1843. The M1 talon with a hypocone and an arched disto-lingual platform are similar to the living genera. The most recent cladistics were carried out by Salesa et al. (2013) to solve the taxonomy of the new lutrinae genus *Teruelictis riparius* based on the dentition and postcranial remains of extinct and extant musteloids, including *Lartetictis*. Their results suggest a closer phylogenetic relationship with Lutrinae than to the other possible subfamilies like gulonines, mustelines and melines. To clarify the phylogeny of *Lartetictis* more cranial and postcranial remains are necessary to supplement the work of Salesa et al. (2013).

<div align="center">Lartetictis dubia (Blainville, 1842)</div>

1842 *Lutra dubia* n. sp. Blainville: 59, pl. 14.

pars   1851 *Hydrocyon sansaniensis* Lartet: 17.

pars   1920 *Potamotherium dubia* (Blainv.). - Pohle: 24.

1949b *Mionictis dubia* (Blainville). – Thenius: 164.

1949 *Mionictis dubia* Thenius: 698.

1961 *Mionictis dubia* Ginsburg: 123, pl.11, Fig. 12.

1986 *Mionictis*. – Dietze: 213.

1996 *Lartetictis dubia* (Blainville, 1841). – Ginsburg & Morales: 665, pl. 1A, 2B.

1996 *Mionictis* [sic!] *dubia*. – Loncarevic & Navala: 54.

Holotype: Muséum national d´Histoire naturelle de Paris Sa 801, right hemimandible with partly damaged p2-m2.

Type locality: Sansan, France, MN6.

Other localities**:** Mala Miliva, Serbia, MN5; Faluns Anjou, France, MN5; Göriach, Austria, MN5-MN6; Goldberg, Germany, MN6; Rosenthal bei Köpflach, Austria, MN6; Devinska Nova Ves, Slovakia, MN6; Mörgen, Germany, MN8.

Material: mandible dex. with p4, m1 (UMJGP 2088); mandible dex. with m1, p4 root posterior (UMJGP 3992); posterior mandible sin. with fragmented m1-2, p4 root posterior (UMJGP 3996);

Description: The p4 is heavily fragmented and only the tip is preserved and is fused to the mandible and to the m1. The specimen UMJGP 3992 preserves a heavily worn m1. In addition, only the posterior root of the p4 is retained.

The posterior part of the left mandible (UMJGP 3996) has the posterior root and the m1-m2 included. The m1 and the m2 is split in half and only the buccal side is preserved,

Results

Multivariate analyses, PCA and NMDS as well as simple XY graphs are used to construct the interpretation. Further description will be done for the group of mustelids including specific selected outgroups (see also Tab. 1).

Legend

Mustela
✕ Mustela erminea
✕ Mustela lutreola
✕ Mustela nivalis
✕ Mustela eversmanni
✕ Putorius putorius

Gulo
▽ Gulo gulo

Neovison
✳ Neovison vison

Martes
✛ Martes foina
✛ Martes martes

Lutra
○ Lutra lutra

Meles
▬ Meles meles

Enhydra
▮ Enhydra lutris

Non Mustelids
⬭ Vulpes vulpes
△ Hyaena hyaena
◼ Panthera leo
◆ Lynx lynx
▲ Felis silvestris
⬮ Meganthereon cultridens

Fossil Mustelids
● Lartetictis dubia
◆ Taxodon sansaniensis
▲ Trochictis depereti
▼ Trocharion albanense
◼ Potamotherium miocenicum
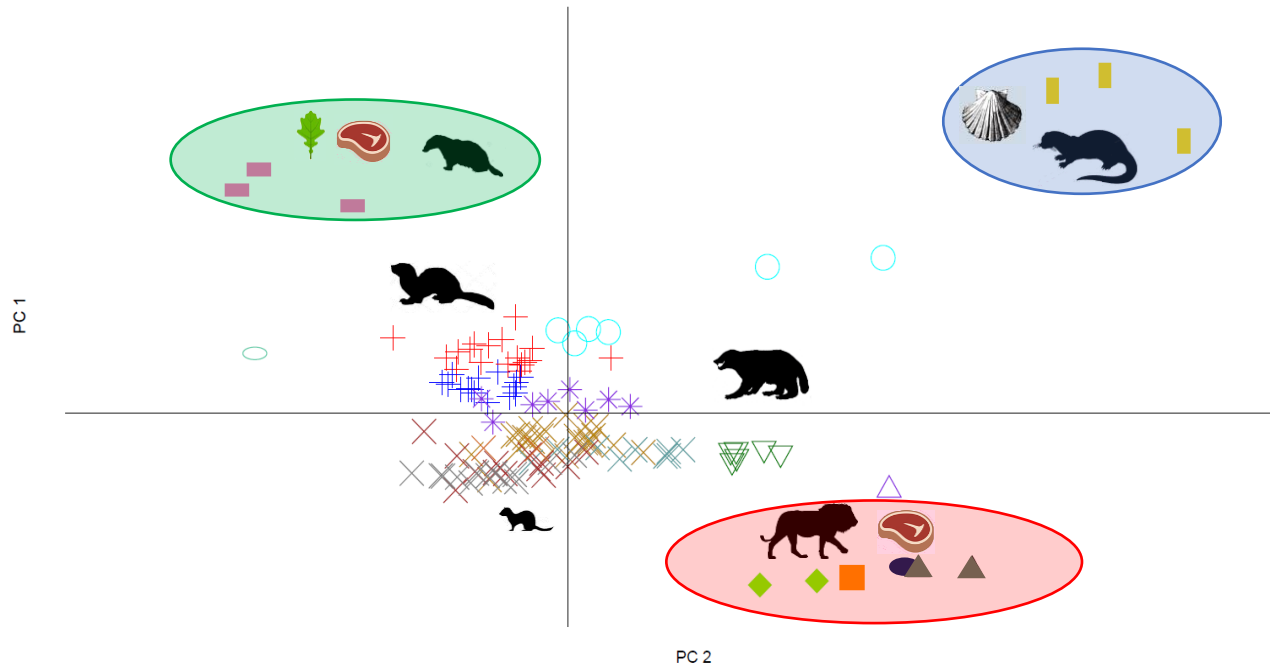
Figure 4: The PCA considering the food preferences of European mustelids including the outgroups, explained by the values RLGA, RUPGA, m1BS, m2S, RTalS, UP4P, Lp4S, PMZ, p4Z, RLCS and RUPMZ (abbreviations see chapter "Methods").

Principle component analysis in Fig. 4 includes mainly European mustelids, and for comparison felids (*Panthera leo, Lynx lynx*, *Felis silvestris* and *Megantereon cultridens*), striped hyena (*Hyaena hyaena*), a canid (*Vulpes vulpes*) and the sea otter *Enhydra lutris.*

To define and differentiate the food preference of mustelids in PCA 1 the most expressive values are chosen. The factor loadings for the first principal components explains 86,977% and the second principle component 6,4757% of variance. Included in the analyses are twelve values: the relative blade length (RBL), relative lower grinding area (RLGA), relative upper grinding (RUPGA), m1 blade shape (m1BS), relative size of the lower second molar (m2S), relative talonid shape (RTalS), relative size of the protocone of the upper fourth premolar (UP4P), relative length of the lower fourth premolar (Lp4S), relative total length of premolars (PMZ), relative length of fourth lower premolar (p4Z), relative lower cusping size (RLCS) and the relative total length of upper premolars (RUPMZ).

The PCA in Fig. 4 presents three different segregated groups. The felids and the hyena in the right lower corner, the sea otter in the right upper corner and the badger in the left upper corner. Most mustelids are more centred and closer together. The European pine marten and the stone marten are slightly separated from the mustelins and plotting in the direction of the

badgers as well as the red fox. Also, slightly separated from the main group is the European otter. In contrast to the marten and the fox, their dentition shows a trend like the sea otter. The American mink is closer to the centred group, but they also tend to hard crushing-group.

The other mustelids (stoat, ferret, steppe polecat, weasel and the Eurasian mink) are grouped in the centre of PCA 1. The wolverine plots segregated but very close on the lower right side of this large, on species level mixed, group. The wolverine as well as the steppe polecat tend slightly more to the carnivorous group.
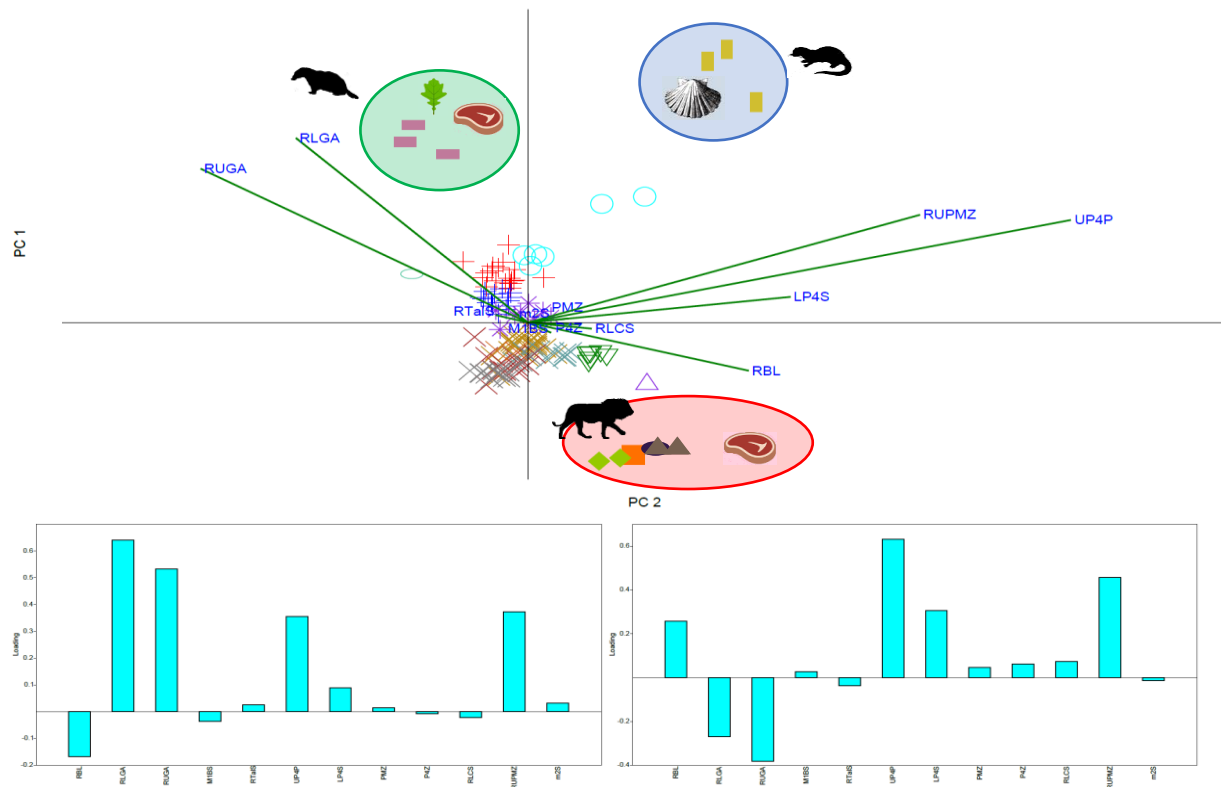
Figure 5: Principle component analysis including biplot, considering the three types of feeding. The vectors explain which measurements are decisive for the results. The factor loadings for the first principal components explains 86,977% and the second principle component 6,4757% of variance.

Principle component analysis in Fig. 5 is identical to Fig 4 with an included biplot, through which values vectors are indicate. Principle component 1 (y-axis) mainly explains the negative influence of the RBL, while RLGA, RUGA, UP4P and RUPMZ have a positive influence. Relative blade length, UP4P, UP4S and RUPMZ have a positive influence on PC 2 (x-axis), while RUPG and RLGA have a negative correlation.
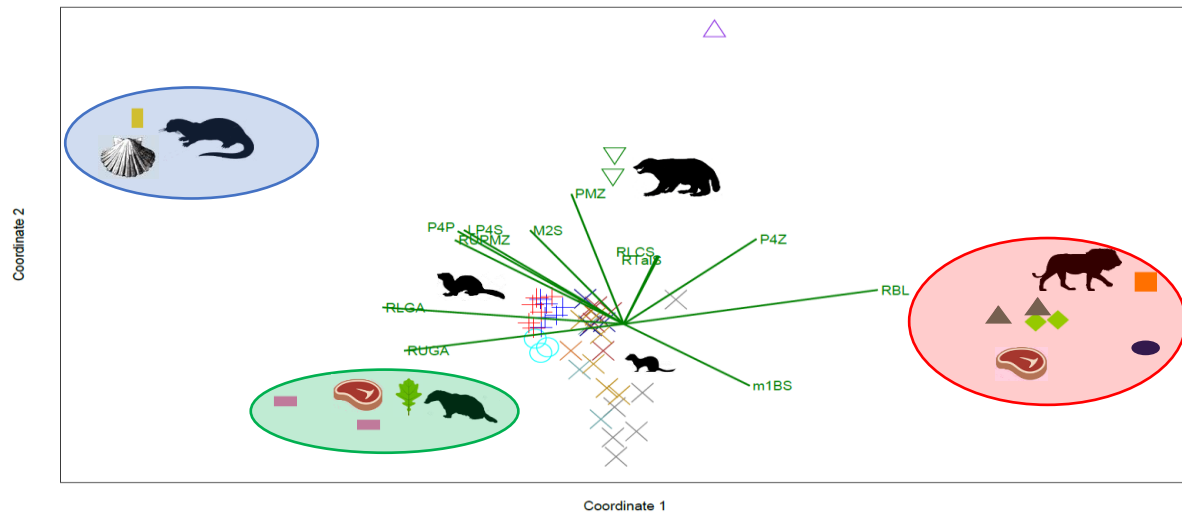
Figure 6: Nonmetric multidimensional scaling includes the same 12 values (environmental factors) as in PCA in Fig 4 additionally the procrusted coordinates of the carnassials. The vectors are built by environmental factors explaining the calculated matrix.

In NMDS (shown in Fig. 6) are the same taxa involved as in Fig. 4. Additional to the twelve values, which were already used in PCA 1, the landmark analysis, the procrusted coordinates of the first lower molar as well as the procrusted coordinates of the fourth upper premolar are used. The landmark dates are used to construct a multidimensional matrix. The twelve calculated values are defined as environmental factors, which explain the calculated matrix.

In NMDS (Fig.6) are five different groups visible. Separated on the right side the carnivorous forms are grouped. On the other side are the badger and the sea otter (omnivorous to hard crushing) separated from each other and disassociated from the centered main group. The hyena is on the top of the graph. Only the wolverine is tending to the hyena. Slightly separated from the centered mustelids are the martens, the stone marten is closer to the center as the European pine marten. The European otter is also brief outside of the mixed centred group of ferrets, American mink, steppe polecat, weasel, stoat and the Eurasian mink.
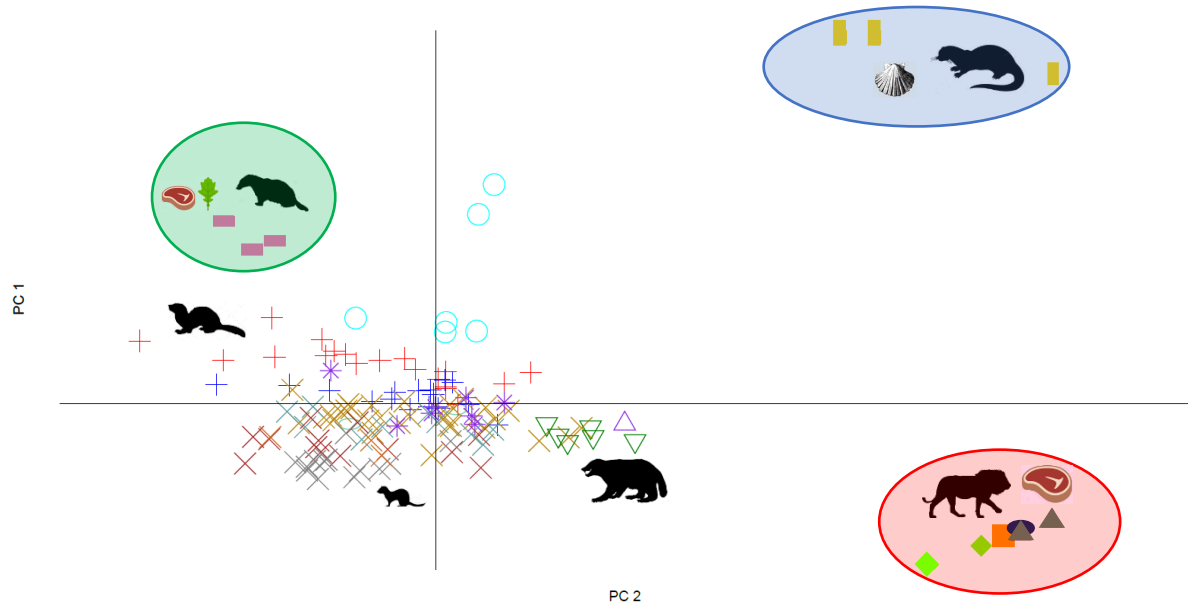
Figure 7: The PCA considering the food preferences of European mustelids including the outgroups, explained by five values of the carnassial: RBL, m1BS, RTalS, UP4P and RTalL (abbreviations see chapter "Methods").

Figure 7 includes a PCA with five metric values: RBL, m1BS, RTalS, RTalL and UP4P. The results are very similar to the PCA in Fig. 4. It includes also three different groups. The felids are plotted in the right lower corner, the sea otter in the right upper corner and the badger on the left upper side, closer to the other mustelids than the other two mentioned groups. The European otter is centered between the mustelids, the badger and the sea otter with slightly tendency to the sea otter. Next, below to the European otter are the European pine marten and the stone marten. Below plotting the mustelins as well as the American mink and the red fox. On the right side of the mustelins are the wolverine and the hyena grouped with tendency to the felids.
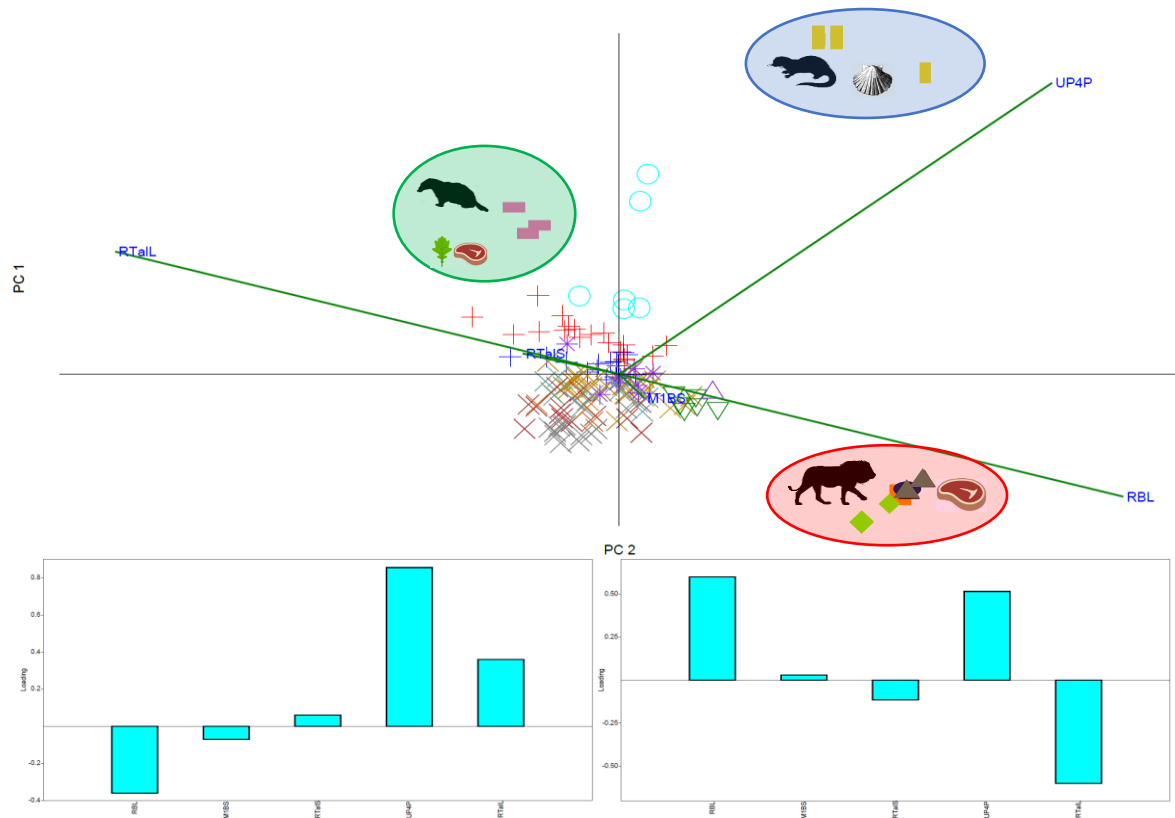
Figure 8: Principle component analysis including biplot, considering the three types of feeding. The vectors explain which measurements are decisive for the results. The factor loadings for the first principal components explains 80,76% and the second principle component 18,51% of variance.

Principle component analysis in Fig. 8 is identical to Fig. 7 with an included biplot, through which values vectors are indicate. Principle component 1 (y-axis) is negative influenced by RBL, while the UP4P and the RTalL have a positive influence. In PC 2 (x-axis) the RBL has a positive influence as well as UP4P, while RTalL has a negative correlation.
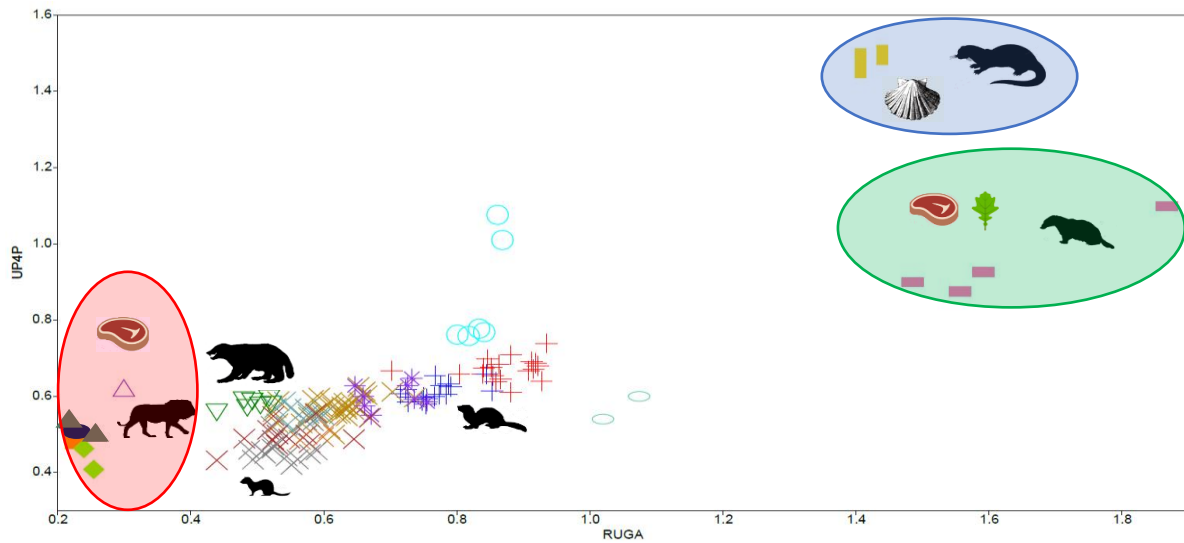
Figure 9: Relative upper grinding area (x-axis) is plotted against the relative size of the protocon of the upper fourth premolar (y-axis) in a simple x/y graph.

Figure 9 is a simple x/y graph, the relative upper grinding area (RUGA) on the x-axis versus the upper protocone of the P4 (UP4P) on the y-axis. *Meles meles* and *Enhydra lutris* already disassociated from each other, what is clarified by different UP4P values, on the right side of the graph with a similar RUGA values, far away from the other taxa. On the left side, disassociated from the major group are the felids and the hyena. In the middle section are the European mustelids scatterd to left (*Gulo gulo, Mustela nivalis, Putorius putorius,M. lutreola, Neovison vison*) and to the right (*Martes foina, M. martes, Vulpes vulpes, Lutra lutra*). *Lutra lutra* has higher UP4P values than other musteldis. *V. vulpes* on the other hand is more defined by a higher RUGA.

Relative upper grinding area (x-axis) is plotted vs the relative length of upper premolars (y-axis) in Appendix 1. The taxa and the legend are the same as in Fig.4 The constellation of the taxa is comparable to the results of Fig.9.
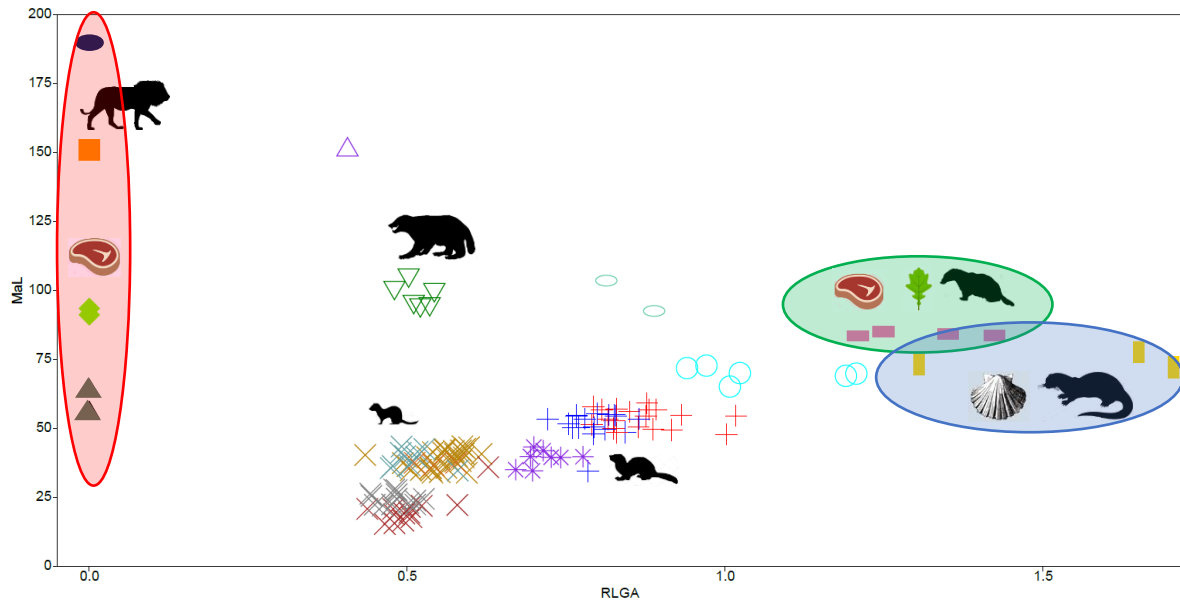
Figure 10: In x/y graph is the mandibular length (y-axis) is plotted against the relative lower grinding area (x-axis) and presents the dispersion if the size has a mainly influence.

The plotted mandibular length (y-axis) versus relative lower grinding area (x-axis) in Fig, 10 demonstrates the scattering of the taxa if the size is included. On the left site with an RLGA value of 0 are the Felidae spread over the hole y-axis. In contrast to the other graphs *Vulpes vulpes* and especially *Gulo gulo* are plotting far away from the other mustelids. *Mustela nivalis* and *M. erminea* are close together. Next but disjoined are *P. putorius*, *M. eversmanni* and *M. lutreola*. *Neovison vison* is located between the just mentioned groups and the martens grouped to the right (*M. foina* and *M. martes*). *Lutra lutra, E. lutris* and *M. meles* are slightly separated from each other with a higher RLGA value.
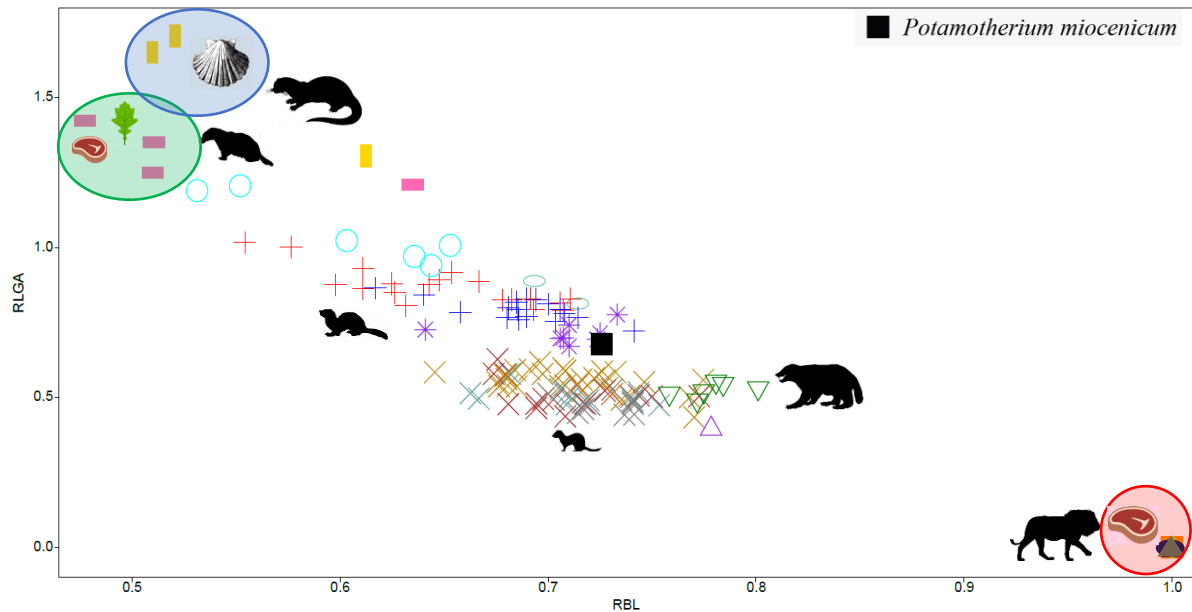
Figure 11: The RLGA (y-axis) is plotted against RBL (x-axis) and shows a clear difference between a carnivorous and a omnivorous/crushing feeding type. Within this x/y graph *Potamotherium miocenicum* is plotted close to the martens and the American mink.

In Fig. 11 the RLGA (y-axis) is plotted against the RBL (x-axis). *Potamotherium miocenicum*, a fossil taxon is included in the graph. With non-existent RLGA but the highest RBL value the felids are narrowly grouped. With a low RBL and high RLGA the sea otters and the badgers are very close together, followed by the European otter, the pine and stone marten as well as the red fox and the American mink. *Potamotherium. miocenicum* is at the right end setteled, with the lowest RLGA of the group of martens and the American mink. In the last group with an even lesser RLGA value are mainly the smaller mustelins (ferret, stoat, European mink, steppe polecat, and the weasel). Next to the group of the smaller mustelins are the wolverine and the hyena, which lean to the felids.

In Appendix 2 *Enhydra lutris* and *M. meles* have the highest RLGA value (y-axis), only the different in RLCS (x-axis) segregates them clearly. Slightly lower RLGA has *L. lutra*, followed by *M. martes*, *M. foina*, *V. vulpes* and *N. vison*. The RLCS value of these five taxa are between the values of *M. meles* and *E. lutris, Lutra lutra* has still a slightly higher RLCS then *M. martes, M. foina, N. vison* and *V. vulpes*. The group of mustelins (*P. putorius, M. eversmanni, M. nivalis, M. lutreolo* and *M. erminea*) as well as *G. gulo* have nearly the same RLGA. The RLCS scatter them from left to the right. The felids (*P. leo, M. cultridense, F.*

silvestris and *L. lynx*) have no RLGA. Also, the RLCS splits them in two groups. *Panthera leo* with *M. cultridense* and *L. lynx*, while *F. silvestris* is spread in this two groups.
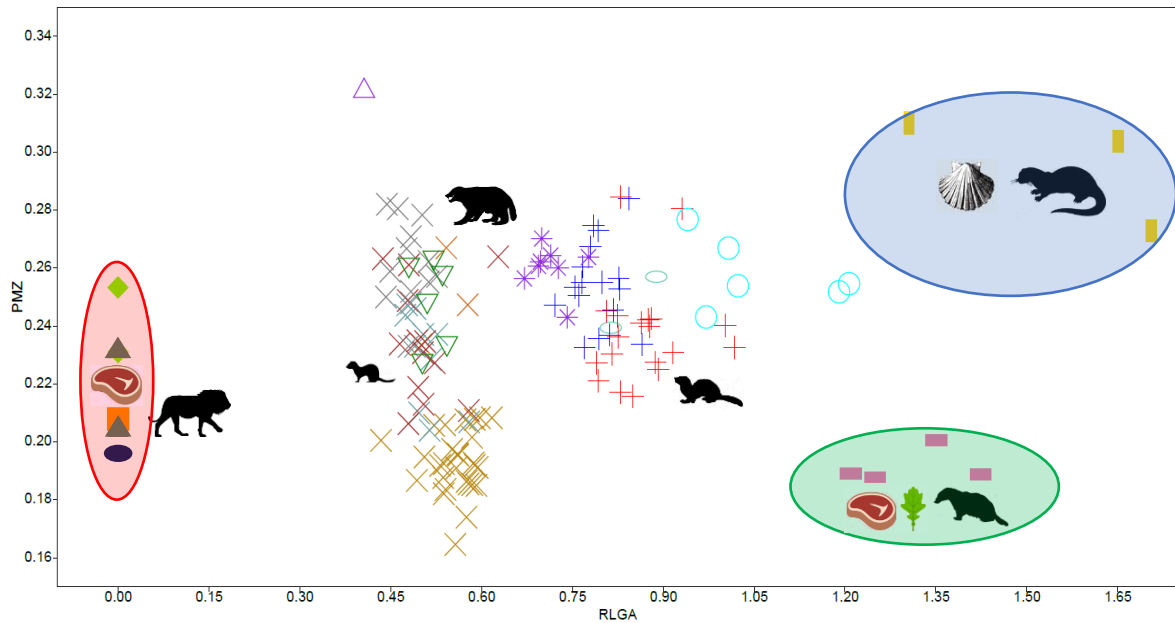
Figure 12: In x/y graph PMZ is plotted against RLGA. The taxa plotting similar to Appendix 2, where RLGA is compared to RLCS.

The RLGA is plotted against the PMZ in Fig. 12 and displays us similar results as in Appendix 2 (RLGA versus RLCS). The felids are grouped on the left margin of the graph without an RLGA rate. The group to the right consists of genera of the smaller mustelins (*M. lutreola, M. nivalis, M. eversmanni, M. erminea*) and the bigger *Gulo gulo*. A higher PMZ value separates *Hyaena hyaena* from the grouped mustelins. The taxa, right to the mustelin group, are *N. vison*, *M. foina, M. martes, L. lutra* and *V. vulpes* (left to right). These taxa are separated from each other because of different RLGA values. *Enhydra lutris* and *M. meles* are the taxa with the highest RLGA values. Different PMZ values explain the segregation between these two taxa.

Appendix 3 displays the plot of RLCS (x-axis) vs the MaL (y-axis). The results are comparable to the plot MaL vs PMZ (Appendix 4). Single taxa as well as few single individuals are more scattered. Especially the red fox is segregated from wolverine and lynx. The sea otter is more spread through the x-axis.

In Appendix 4 is PMZ (x-axis) plotted against the MaL (y-axis). The results are like in Appendix 3 With a similar high LD value and separated from the other taxa, *Hyaena hyaena. Megantereon cultridense* and *Panthera leo* are located in the upper part of the graph with

different PMZ. *Gulo gulo, Felis silvestris* and *Vulpes vulpes* are in the middle of the graph, followed, with a lower LD value, by *Meles meles, Lutra lutra* and *Enhydra lutris* from the left with a lower PMZ value, to the right with a high PMZ value. *Martes martes* and *Martes foina* have a slightly lower LD value than the before mentioned group, open the assembly of the most Mustelids. The following taxa are spread over the x-axis from left to right: *Putorius putorius*, *Mustela eversmanni*, *Mustela nivalis*, *Mustela erminea*, *Neovison vison* and *Mustela lutreola*.

In Appendix 5… P4Z (x-axis) is plotted against LD (y-axis). The highest LD rate has the hyena followed by the lion and the sabretooth cat (*Megantereon*), which also have a similar P4Z rate. The badger, red fox, wolverine and the wild cat have mainly different P4Z values and are scattered from left to the right. A slightly lower LD rate have the otters and the lynx, which are also scattered over the x-axis. Pine marten and stone marten have similar rates only slightly differences in the P4Z rates. Below the two taxa the smaller carnivores are scattered from left to the right with similar LD values: the ferret, steppe polecat, weasel, American mink and the Eurasian mink.
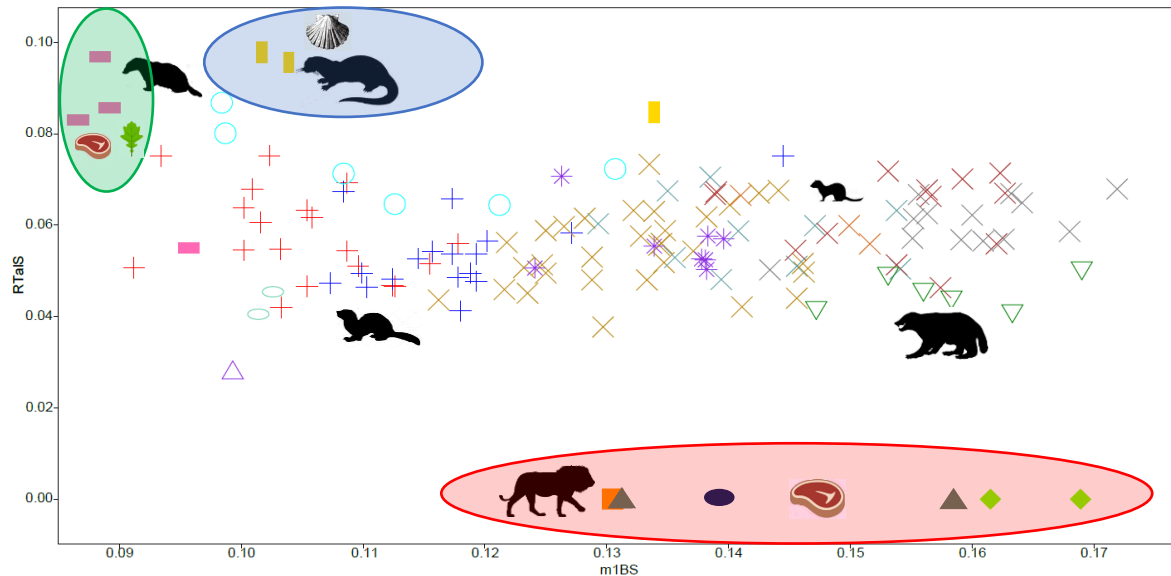
Figure 13: Values of lower carnassial is are plotted in a simple x/y-graph. Relative talonid shape is placed on the y-axis, while the blade shape of the lower m1 is on the x-axis.

In Appendix 6 (m1BS versus LD) the felids are not grouped. The lion and the sabretooth cat plot together., with the highest LD value (y-axis). The hyena has similar LD but a less m1BS (x-axis). The lynx plots in the middle of the wolverine values. The LD of the wolverine and lynx are similar to the otters, red fox, and the badger, but they differ through a higher m1BS value. The last group includes the martens and the mustelins. The martens have slightly higher LD values than the mustelins, but they are mainly scattered through m1BS. The mustelins have higher m1BS values than the martens. The wild cat plots between the mustelins and the group of wolverine and lynx.
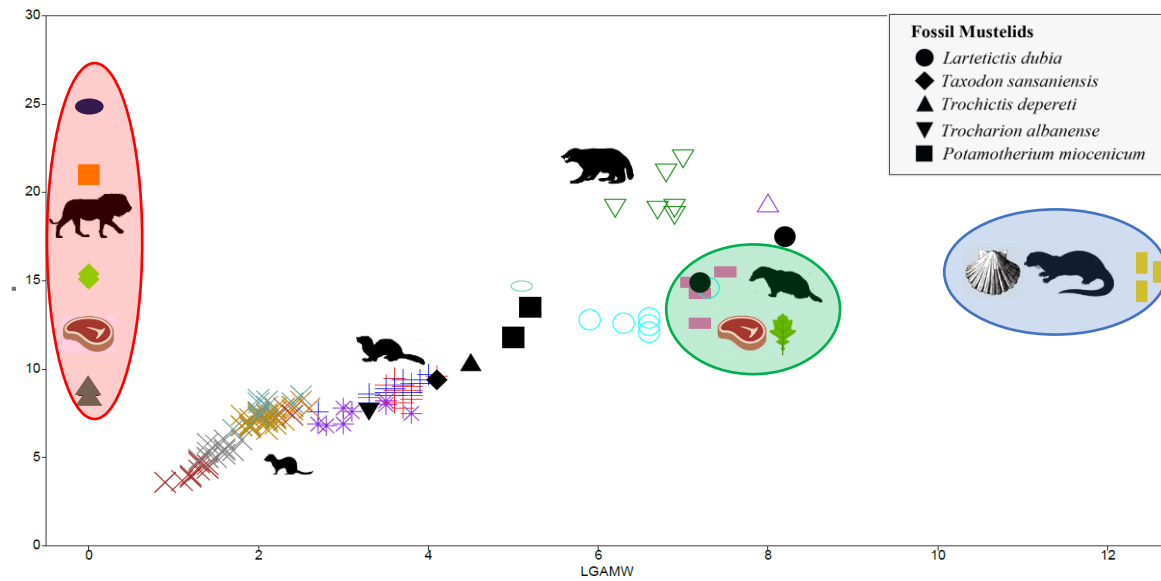
Figure 14: Length of the lower first molar is plotted against the lower grinding area maximum width. Hypercarnivores are scattered on left side over the y-axis, while the omnivores and the crushing feeding type plotting on the right side over the x-axis.

In Fig. 14 LGMW (x-axis) is plotted against Lm1L (y-axis). The felids do not have a grinding area, so they are all on the left side of the graph. On the opposite side the sea otter is segregated and has the highest width of the lower grinding area, followed by a fossil taxon, *Lartetictis dubia*, the badger and the European otter. The wolverine and the hyena are close them but have a longer m1. Close to the red fox and between the European otter and the martens plot three other fossil taxa: *P. miocenicum*, *T. deperetsi*. and *Taxodon* sp. (from right to left). *Taxodon* is closer to the martens, as well as *T. albanense*. The following group is built by the mustelins and are distinguishable by the LGMW and the Lm1L: *M. nivalis, M. erminea, P. Putorius, M. eversmanni* and *N. vison*, from left to right.
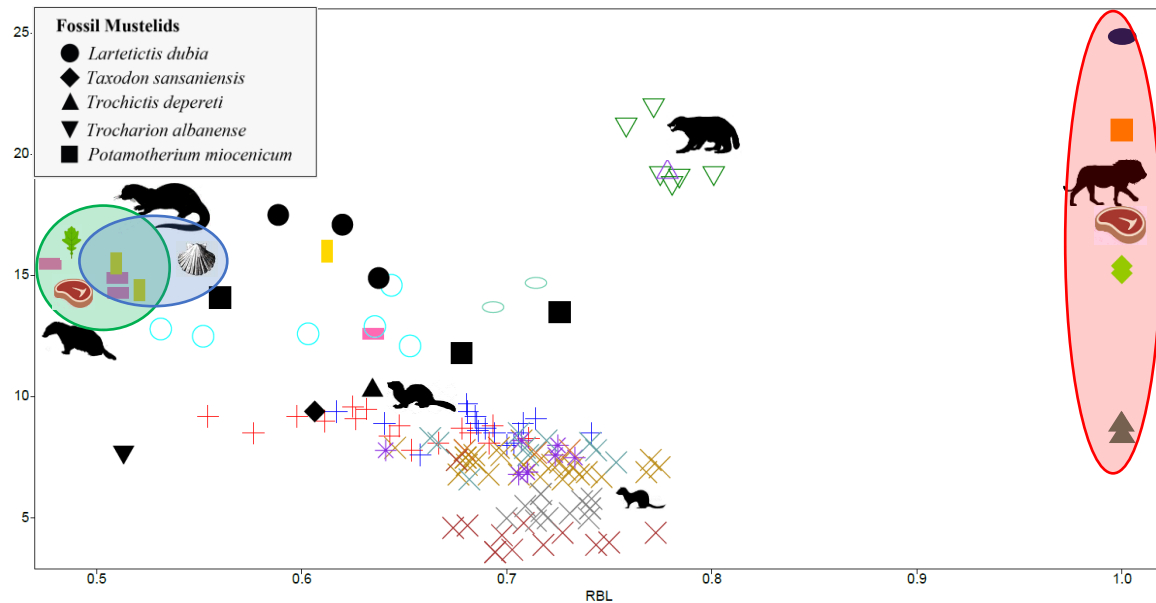
Figure 15: Length of the first molar (y-axis) is plotted against relative blade length (x-axis). The carnivorous feeding typ, represented by the felids, are located on the right side, far away from the other mustelids, while the crushing and the omnivorous feeding type, represented by the sea otter and the badger, are not segregated from each other on the left side.

Figure 15 is a simple x/y graph, in which the length of the lower first molar (y-axis) is plotted against the relative blade length (x-axis). The members of the felids, which representing the carnivorous feeding type, plotting far up on the right side from the remaining taxa. Within they scattered over the y-axis because of the size different from each taxon. The opposite, on the left side, are the sea otter and the badger, the crushing and the omnivorous feeding typ. Those taxa are followed by the European otter to the right, which are followed by the red fox. Only the RBL separates these four taxa from each other Below plotting the martens. The European pine marten plotting slightly more to the left than the stone marten, which have a RBL value. Close below are the mustelins and the American mink. The y-axis groups each taxon very well, while the x-axis spreads them more.

With the lowest Lm1L value the mouse weasel is the smallest one followed by the stoat, ferret, step polecat and the European mink. Within the plot are the fossil taxa. While *P. miocenicum* and *L. dubia* plotting between the otters and the badgers with similar Lm1L, *T. sansaniensis, T. depereti* and *T. albanense* plotting between the martens. Only *Trocharion albanense* is separated by lower RBL from the other fossils.
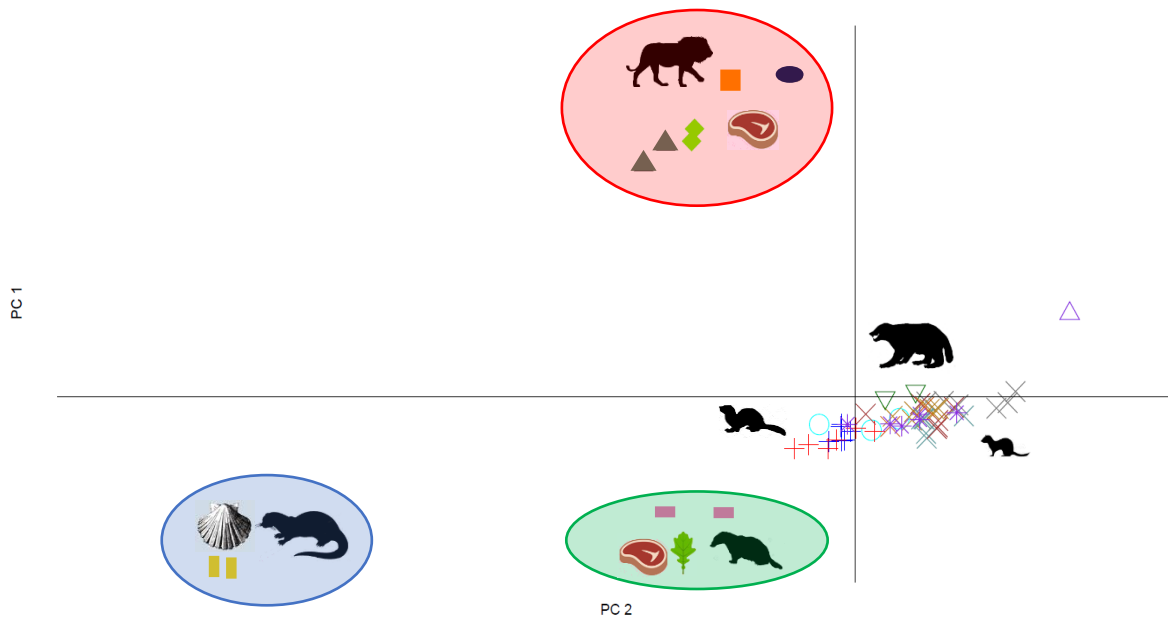
Figure 16: This graph includes the results of mesowear analysis from m1 and the P4 combined in a PCA.

The PCA in Fig. 16 are the results of the landmark analysis of the lower first molar and the upper fourth premolar are combined. The factor loadings of PC 1 (x-axis), explained by 57,64% of variance, is plotted against PC 2 (y-axis), which is explained by 18,83% of variance. Included taxa and the symbol explanation is identical to the PCA in Fig 4. Maximum number of each taxa is three to get a significant result. If the number is less than three, it is to the fact that no more suitable material was available.

Close grouped taxa are *Gulo gulo*, *Martes martes*, *Martes foina*, *Putorius putorius*, *Mustela eversmanni, Mustela nivalis*, *Neovison vison*. *Lutra lutra* and *Mustela erminea*. *Hyaena hyaena* plots to the right of this group. *Meles meles* forms an isolated group. Far on the left side in line with the badgers are the sea otters (*Enhydra lutris*). The felids form another well-defined group above the other constellations.
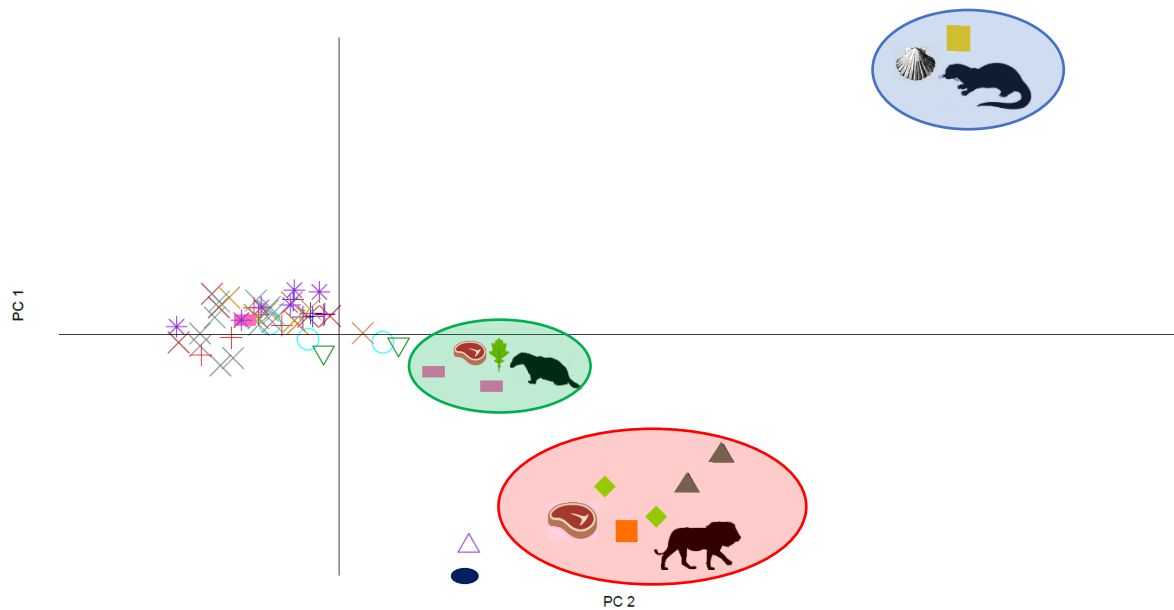
Figure 17: The PCA represents the landmark based mesowear analysis of the upper fourth premolar. The graphs include only extant mustelids and no fossil ones because the P4 are not received or to damaged.

Only the results of P4 landmark analysis are plotted in PCA, in Fig. 17. The sea otter is disconnected from all other taxa by PC 1 (y-axis) as well as PC 2 (x-axis). Also, the felids are separated from the mustelids. The badger is closely located to the wolverine. The other taxa, the martens as well as the mustelins, one group. Only the European mink and the European otter are slightly differentiated and reflect similarities to the wolverine and the badger. The factor loadings for the first principal components explains 56,31%% and the second principle component 24,13% of variance.
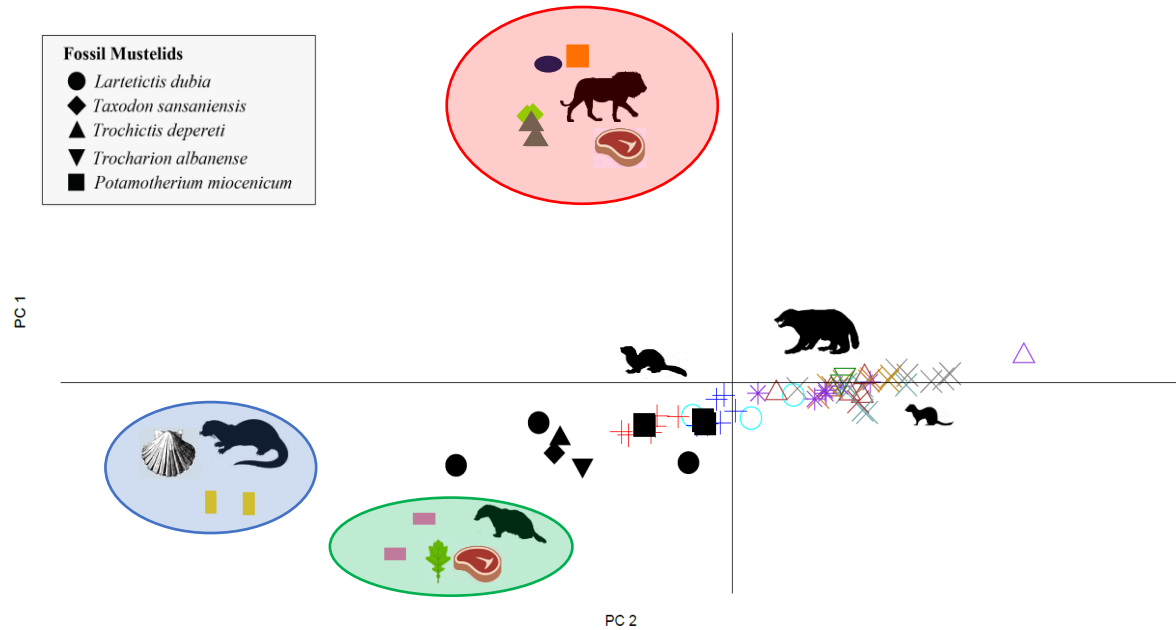
Figure 18: The PCA represents the landmark based mesowear analysis of the lower first molar. There are the recent mustelids included as well as the fossil *Potamotherium miocenicum, Lartetictis dubia, Trocharion albanense, Trochictis depereti* and *Taxodon sansaniensis.*

In Fig. 18 the results of the landmark analysis of the lower first molar is presented. The factor loadings for the first two principal components explaining 62,12% (PC1) and 18,24% (PC2) of variance. Principle component 1 (y-axis) mainly explains the influence of the procrusted coordinate nine and ten, while procrusted coordinate five, six and mainly seven is influenced by PC 2 (x-axis). The felids are segregated from all other taxa by PC 1. The other taxa are mainly distinguishable by PC 2. The sea otter is located on the left side, followed by the badger. Between the badgers and the martins is quite a distance to the other extant taxa interestingly filled by the fossil taxa. (*L. dubia, T. depereti, T. albanense* and *T. sansaniensis*) while *P. miocenicum* scatters in the middle of the pine and stone martin. The European otter is closely located to the martens. The other mustelins form one group. Among the smaller carnivora plots the bigger wolverine. On the right site in line with the mustelins, the hyena is segregated.

The group of smaller Mustelinae (*Mustela nivalis, M. erminea, M. eversmanni, Putorius putorius* and *Neovison vison*), as well as the larger member of the Martinae, *Gulo gulo,* are seen as more carnivorous. The Martinae, represented by *Martes martes* and *M. foina* as well

as *Vulpes vulpes*, a Canidae are slightly carnivore, but presenting more omnivorous characteristics than carnivorous in their dentition.

The dentition of the European otter, *Lutra lutra*, mirrors similarities to the sea otter, a crushing feeding type but more carnivorous.

The executed PCA´s of all European mustelids and the outgroups acquired through 12 calculated values represent clearly three different types of food preferences: carnivorous, omnivorous and crushing/hard object feeding. The NMDS and the mesowear studies provides similar results.

The mesowear study displays the fossil taxon *Potamotherium miocenicum,* usually described as otter-like (Savage, 2009), a more omnivorous, slightly carnivorous live style similar too *Vulpes vulpes, Martes martes* and *M. foina. Lartetictis dubia* plots absolutely more in the group of crushing/omnivorous, like *E. lutris* and *M. meles.* The dentition of *T. depereti* and *Taxodon sansaniensis* mirrors similar tooth morphologies like *L. dubia.*

This framework has a function as basement for future studies and for better understanding of the extant and fossil Mustelidae and their environmental behavior.

Discussion

The goal of this study was to create a framework of extant mustelids by metrical as well as non-metrical methods of dentition analysis, to distinguish the fossil Mustelidae (Early to Middle Miocene) from Göriach according to their food preferences. Principle component analysis 1 includes primary European mustelids felids (*Panthera leo, Lynx lynx*, *Felis silvestris* and *Megantereon cultridens*), hyena (*Hyaena hyaena*), a canid (*Vulpes vulpes*) and the sea otter *Enhydra lutris*.

The Felids (*Panthera leo, Lynx lynx, Felis silvestris* and the fossil *Megantereon cultridens*) are typically known to be **hypercarnivores** (Morlo, Gunnell & Nagel 2010). Overall, carnivorous taxa have relative longer blades on their carnassial and reduced grinding area. In the lower first molar the trigonid, built by para-, proto- and metaconid is accentuated in contrast to the talonid, which is often completely reduced like in the lion and the wild cat. The lower second and third molar, which are used for grinding are mostly reduced as in the upper jaw. The fourth upper premolar is built by an emphasized blade, without any grinding area. Only a strongly reduced first molar is enough as grinding area. These are adaptions to killing prey and cutting fresh flesh and skin (Van Valkenburgh, 1989; Biknevicius & Ruff, 1992; Van Valkenburgh & Koepfli, 1993; Friscia et al., 2007). These characteristics are responsible for the fact that this group is plotted far away in Fig. 4. More detailed it is shown in Fig. 11. The carnivoran feeding type is clearly separated by the RLGA (0) and the RBL (1). Appendix 2 and Fig. 12 mirrors similar results. Therefore, it can be assumed, that the premolars in the lower jaw are also influenced by this type of dietary. In the mentioned graphs the felids are well grouped so we can assume that size is successfully excluded. Appendix 4 and Fig. 10 and 15 confirms this. If the size has major effect, the taxa within the felids would be more spread, as well as the taxa within the mustelids, as the size differences within the mustelids range from the smallest predator, the 250 g heavy mouse weasel, to the 30 kg heavy wolverine (MacDonald 2006, Stubbe & Krapf 1993).

Omnivorous taxa have reduced carnassial blades and expended grinding areas and strong dentaries able to resist high stress. The true omnivores have no dominant food type. (Van Valkenburgh, 1989; Biknevicius & Ruff, 1992; Van Valkenburgh & Koepfli, 1993; Friscia et al., 2007). This assumption is supported by the PCA in Fig. 4. The location of the omnivorous feeding type, represented by the badgers, is mainly explained by enlarged RLGA as well as

the RUGA. For better understanding Appendix 1 and 2 as well Fig. 11 were executed. The badgers are located away from the felids because of an emphasized grinding area. The already mentioned graphs as well as graph in Appendix 4 show again when size is a mainly factor for separating species.

The food range of the **crushing/hard-object-feeding** group, also noted as a type of aquatic dietary, includes i.e. molluscs or large crustaceans (Würsig, Thewissen & Kovacs 2017, Rheingantz & Ruiz-Olmo 2018). *Enhydra lutris* is known as a full aquatic Lutrinae that feeds mostly on invertebrates (60%). *Lutra lutra,* the Eurasian otter, is more specialized on fish (Medina-Vogel et al. 2004, Krook 2006) and is also described as hypercarnivor but shows in the results crushing tendency. Until now no clearly separation between the omnivorous and the crushing feeding type is known by using tooth measurements. Principle component analysis in Fig. 4 the sea otter is clearly separated from the carnivorous and especially the omnivorous feeding type. The differentiation is manly influenced by RUPMZ, LP4S, UP4P and slightly by PMZ and P4Z, noticeable in Fig. 2 and 8. Frisca et al. (2007) mentioned already a strong influence of the premolars in hard object crushing able species. So, I assume, that the premolars are more important for the crushing feeding type. A closer look on the values of the premolars confirms this statement. The premolars are more wide and stronger developed than in other dietary types, an adaption to crushing hard objects. A taxon separated from the main group is the European otter. In contrast to the marten and the red fox, their dentition presents a trend towards the sea otter. The American mink is closer to the group of mustelins, but they have also slight similarities to the otters.

In NMDS (Fig. 6) the same taxa are evaluated as in Fig. 4. Additional to the twelve values, which were already used in Fig. 4, the landmark analysis based on mesowear data, the procrusted coordinates of the first lower molar as well as the procrusted coordinates of the fourth upper premolar are calculated. The landmark data are used to construct a multidimensional matrix. The twelve evaluated values are defined as environmental factors, which explain the calculated matrix.
In Fig. 6 are five different groups visible. The differentiation is clarified by the vectors. Based on the type of the m1 blade the felids or the carnivore feeding type is strongly segregated. On the other hand, are the badgers and the sea otters separated from each other and disassociated from the main group. The reasons for this plotting are the grinding area and the morphology of the premolars. The omnivorous feeding type is one more time specified by the grinding

area, whereas the crushing feeding type is mainly specified by the premolars, like in Fig. 4 and 7. Only the wolverine is tending towards the hyena. Slightly separated from the grouped mustelins are the martens, the stone marten is closer to the mustelins than the European pine marten. The European otter is also brief outside of the mixed group of ferret, American mink, steppe polecat, weasel, stoat and the Eurasian mink. Overall the results are similar to the PCA in Fig. 4 and 7. Only the martens and the European otters "change" places. In NMDS (Fig. 6) the European otter plots in line with the badgers, while the martens are in line with the sea otter. Reasons for changes in results could be the influence of the mesowear results. In Fig. 17 the badger and the sea otter are no separable. In Fig. 18 they are showing just slightly differentiation.

In Fig. 18 the first results of the landmark based mesowear analysis of the lower first molar is presented. A distinction the food preferences of mustelids based on their carnassial morphology is possible. The factor loadings for the first two principal components explaining 62,12% (PC1) and 18,24% (PC2) of variance. Principle component 1 (y-axis) mainly explains the influence of the procrusted coordinate nine and ten (landmark five, the lowest point of the talonid immediately after the trigonid) as well as eleven, thirteen and fourteen (landmarks six and seven, describing the talonid morphology) while procrusted coordinate five, six and mainly seven (landmark three, describes the lowest point of the trigonid and four, which marks the cusp of the protoconid) is influenced by PC 2 (x-axis).

The felids are grouped but strongly disassociated from all other taxa by PC 1. The other taxa are mainly distinguishable by PC 2. The sea otter is slightly segregated from the badger. Between the badgers and the martins is a huge gap in which the fossil taxa *L. dubia, T. depereti* and *T. sansaniensis* are plotting, meanwhile the otter-like described *P. miocenicum* (Savage 2009) scatters between the pine and stone martin. The European otter is close located to the martins. The other mustelins are a density group. Among the smaller carnivora plots the bigger wolverine.

The results can be explained by the tooth morphology. In carnivorous dietary the blade in m1, build by the trigonid and captured by landmark 1-5, is much more important than the talonid.

The separation of the group of felids is explainable by the strongly reduced or already missing talonid, which is common carnivores.

In omnivores the talonid, captured by landmark 5-7 is more stressed by chewing the food. To resist the stress the posterior part of the m1 is enlarged, what explains the separation of the badgers in mesowear analysis.

As well as in omnivorous the crushing feeding type is stressful for especially the grinding area. The talonid is also enlarged and strongly differentiable from carnivores. It is to assume that they are located close to the omnivores. They are so close that they are not clear differentiable only based on the m1 morphology.

In PCA (Fig. 17) only the results of P4 landmark analysis are incorporated. The factor loadings for the first two principal components explaining 55,26% (PC1) and 23,82% (PC2) of variance. Principle component 1 (y-axis) mainly explains the influence of the procrusted coordinate one, two, three, four, seven and nine, which landmarks 1, 2, 4 and 5 concern (landmarks describing length and high of upper fourth premolar), while procrusted coordinate one, three, five seven and nine is influenced by PC 2 (x-axis).

The sea otter is disconnected from all other taxa by PC 1 (y-axis) as well as PC 2 (x-axis). Also, the felids are segregated from the other mustelids. The badger is close located to the wolverine. The other taxa, the martens as well as the mustelins, building a densely group. Only the European mink and the European otter are slightly out grouped and reflect similarities to the wolverine and the badger.

The P4 is mainly a tool to cut food with the m1 as opponent. Especially between carnivores the P4 shape is similar. Only specialized taxa have noticeable P4 shape variations. For example, strict omnivores can have aa more compact P4 to crush nut shells.

In case of crushing/aquatic feeding type an enlarged P4 is necessary to resist the stress from crushing shells of bivalves and mollusks. That explains why the sea otter is such segregated from the other species in Fig. 17 and the badger not, like in the already discussed PCA´s.

The different characters of the carnassial of the three feeding types (carnivorous, omnivorous and crushing) could be optimized with more data and maybe diverse data selection. If using only the information of the buccal view of the carnassial some information could be lost.

Analysing the occlusal view could optimize the results of the landmark analysis, because more difference between the carnassial of the crushing and the omnivore feeding type are visual recognisable.

Conclusion

Not only the taxonomy and the systematic position of fossil mustelids are under discussion, also the lifestyle as well as the ecological segregation of this group. This work tries to clarify their dietary preferences for a better understanding of the ecological niche concept. In order to obtain only information on food preference in the graphs, factors such as size or phylogenetic effect had to be excluded. To eliminate the size simple equations for metric value were created and a generalized procrust transformation was performed in landmark analysis. The phylogenetic effect, on the other hand, is somewhat more difficult to exclude, since adaptation to the food source already has phylogenetic impacts.

Based on the metric method the European mustelids can clearly identified in three feeding types: 1) carnivore feeding type: 2) omnivore feeding type and 3) crushing/hard-object feeding type. Carnivores such as lions can cut fresh flesh, while the omnivores, as the badger or the bear, are more specialized on a wider food spectrum. The species with a crushing feeding type or also noted as aquatic feeding type such as the sea otter, can crush shells of bivalves and snails. The Mustelinae, *Mustela erminea, M. nivalis, M. lutreola, M. eversmanii* und *Putorius putorius* as well as the Gulolinae *Gulo gulo* are clearly more carnivorous than other sampled mustelids. *Neovison vison* is more detached from the just mentioned mustelins, closer to the following Gulolinae and the lutrins. *Martes martes* and *Martes foina* tend more to be more like the omnivore badgers. The Lutrinae presented by *Lutra lutra,* plots closer to the martens but tends to the crushing feeding type.

Metrically measurements of the RLGA, RLGA, RUPGA, m1Bs, m2S, RTalS, UP4P, PMZ, p4Z, RLCS and RUPMZ gave the best values and the clearest distinction between the three feeding types. the While for the hard-object crushing type the premolares are of some relevance, in general the carnassial still deliver the most stable results.

The mesowear analysis shows similar results. The carnivores are clearly separated from each other, meanwhile the crushing and the omnivore type are not that distinguishable as in metric

method. The mesowear analysis is simpler when it comes to data collection. While surveying takes a lot of time, the mesowear method makes it possible to work with images even without any scaling. For the classical measurements a lot of detailed information about the specific taxa is needed to understand the different morphologies and characteristics. Since there can be a bias in taking the measurements from different researchers one would have to remeasure all specimens for statistical analyses. The more measurements the more time consuming and the sample must be undamaged.

The fossil taxa: *Potamotherium miocenicum, Trochictis depereti, T. albanense, Taxodon* sp. and *Lartetictis dubia* in this work are evaluated through the mesowear technique for the first time. The lifestyle of *Lartetictis dubia* is usually described as semiaquatic fish predator (Heizmann & Morlo, 1998). In the mesowear analysis *L. dubia* is scattered between the *Meles meles*/*Enhydra lutris* and *Martes martes, M. foina*, who have a terrestrial lifestyle. Similar, but closer to the martens, plots also *Potamotherium miocenicum*, which is in literature associated with a semiaquatic way of life, which I cannot confirm clearly in this work at least according to its food preference.

Fossil material, is usually not completely preserved, making meaningful metric analysis almost impossible, whereas single teeth are enough for mesowear analysis. The mesowear technique is a possibility to gather information where traditional measurements are not enough.

The landmark or mesowear analysis does not provide as clear results as metrical evaluations yet. Nevertheless, the mesowear method has important advantages and it can be refined with more samples in future.

Acknowledgment

Literatur

BASKIN, J., A. (2011): A new species of Cernictis (Mammalia, Carnivora, Mustelidae) from the Late Miocene Bidahochi Formation of Arizona, USA. – Palaeontologia Electronica 14;3 (26A); 1-7

BERNOR, R., L., KORDOS, L., ROOK, L., AGUSTI, J., ANDREWS, P., ARMOUR-CHELU, M., BEGUN, D., R., CAMERON, D., W., DEMUTH, J., DAXNER-HÖCK, G., DE BONIS, L., FEJFAR, FESSAHA, N., FORTELIUS, M., FRANZEN, J., GASPARIK, M., GENTRY, A., HEISSIG, K., HERNYAK, G., SZYNDLAR, Z., TOPÁL, G., UNGAR, P., S., UTESCHER, T., VAN DAM, J., A., WERDELIN, L. & ZIEGLER, R. (2004): Recent Advances on Multidisciplinary Research at Rudabánya Late Miocene (MN9), Hungary: a compendium. – Palaeontographica Italica 89; 3-36

CARRANO, M., T., JANIS, C. & SEPKOSKI, JR., J., J. (1999): Hadrosaurs as ungulate parallels: Lost lifestyles and deficient data – Acta Palaeontologica Polonica 44(3); 237-261

CRUSAFONT-PAIRÓ, M. & TRUYOLS-SANTONJA, J. (1956): A Biometric Study of the Evolution of Fissiped Carnivores – Evolution 10(3); 314-332

DRYDEN, I., J. & MARDIA, K., V. (2016): Statistical shape analysis with applications in R – Second Edition - John Wiley and Sons Ltd. 1-479

FREEMAN, P., W. (1979): Specialized Insectivory: Beetle-Eating and Moth-Eating Molossid Bats – Journal of Mammology 60(3); 467-479

FRISCIA, A., R., VAN VALKENBURGH, B., & BIKNEVICUS, A., R. (2007): An ecomorphological analysis of extant small carnivorans. – Journal of Zoology 272: 82-100

GINSBURG, L. & MORALES, J. (2000): Origin et évolution des Melinae (Mustelidae, Carnivora, Mammalia). – C. R. Acad. Sci. Paris, Sciences de la Terre et des pianètes/ Earth and Planetary Sciences 330; 221-225

HAMMER, Ø., HARPER, D., T. & RYAN, P., D. (2001): PAST – Paleontological Statistics Software Package for Education and Data Analysis – Palaeontologia Electronica 4(1): 9

HELBING, H. (1926): Zur Definition des Genus Trochictis – Schweizer Paläontologische Gesellschaft 302-307

HEIZMANN, E., P., J. & MORLO, M. (1998): Die semiaquatische Lartetictis dubia (Mustelinae, Carnivora, Mammalia) von Goldberg/Ries (Baden-Württemberg). – Mainzer naturwissenschaftliches Archiv/Beiheft 21; 141-153

JAKSIC, F., M., FEINSINGER, P. & JIMÉNEZ, J., E. (1993): A long-term study on the dynamics of guild structure among predatory vertebrates at a semi-arid Neotropical site – OIKOS 67(1); 87-96

KAY, R., F. (1975): The Functional Adaptions of Primate Molar Teeth – American Journal of Physical Anthropology 43; 195-216

KLINGENBERG, C., P. (2011): MorphoJ: an integrated software package for geometric morphometrics – Molecular Ecology Resources 11: 353-357

KORETSKY, I., A., & DOMING, D., P. (2014): One of the oldest seals (Carnivora, Phocidae) from the Old World – Jounal of Vertebrate Paleontology 34:1 224-229

LITVAITIS, J., A. (2000): Investigatin Food Habits of Terrestrial Vertebrates. In Research Techniques in Animal Ecology: Controversies and Consequences – Columbia University Press 165-183

KRUUK, H. (2006): Otters: Ecology, Behaviour and onservation. – Oxford University Press 278

MAAS, M., C., KRAUSE, D., W. & STRAIT, S., G. (1988): The decline and extinction of Plesiadapiformes (Mammalia: ?Primates) in North America: displacement or replacement? – Paleobiology 14(4); 410-431

MARDIA, K., V. & DRYDEN, I., L. (1989): The statistical analysis of shape data – Biometrika 76(2): 271-281

MACDONALD, D., W. (2006): The encyclopedia of mammals - Oxford: Oxford University Press 485-509

MEDINA-VOGEL, G. (2004): Feeding ecology of the marine otter (*Lutra Felina*) in a rocky seashore of the south of Chile – MarineMammal Science 20(1): 134-144

MILLER, G., S. (1912): Cataloge of the Mammals of Western Europe (Europe Exclusive of Russia). In the Collection of the British Museum – Cornell University Library 365-380

MORLO, M. (1996): Carnivoren aus dem Unter-Miozän des Mainzer Beckens (2. Mustelida, Pinnipedia, Feliformia, Palaeogale) – Senckenbergiana lethaea 76(1); 193-249

MORLO, M., GUNNELL, G., F. & NAGEL, D. (2010): Ecomorphological analysis of carnivore guilds in the Eocene through Miocene of Laurasia. In Carnivoran Evolution: New Views on Phylogeny, Form, and Function – Cambridge University Press. 269-310

MÖRS, T., VON DER HOCHT, F. & WUTZLER, B. (2000): Die erste Wirbeltierfauna aus der miozänen Braunkohle der Niederrheinischen Bucht (Ville-Schichten, Tagebau Hambach) – Paläontologische Zeitschrift 74(1/2); 145-170

POPOWICS, T., E. (2003): Postcanine Dental Form in the Mustelidae and Viverridae (Carnivora: Mammalia) – Journal of Morphology 256; 322-341

POLLY. P., D. (2018): Geometric Morphometrics. In The Encyclopedia of Archaeological Sciences – John Wiley & Sons Inc. 1-5

RABI, M., BASTL, K., BOTFALVAI, G., EVANICS, Z. & PEIGNÉ S. (2017): A new carnivoran fauna from the late Oligoene of Hungary – Palaeobiodiversity and Palaeoenvironments 13

RENSBERGER, J., M. (1978): Scanning electron microscopy of wear and occlusal events in some small herbivores. In: Butler, P.M., Joysey, K.A. (Eds.), Development, Function and Evolution of Teeth. Academic Press, New York 415–438.

RHEINGANTZ, M., L. & RUIZ-OLMO, J. (2018): Mustelidae Diet. In Encyclopedia of Animal Cognition and Behavior – Springer International Publishing AG 1-8

ROTH, C., H. (1989): Die Raubtierfauna (Carnivora, Mamm.) der untermiozänen Spaltenfüllung von Erkertshofen 2 bei Eichstätt/Bayern – Mitteilung der Bayerischen Staatssammlung für Paläontologie und Historische Geologie 29; 163-205

ROBLES, J. M., ALBA, D., M. & MOYÀ-SOLÀ, S. (2009): The Morphology of the upper forth premolar in *Trocharion albanense* Major, 1903 (Mustelidae: Leptarctinae) and the independent loss of the carnassial notch in Leptarctines and other Mustelids – Paleolusitana 1: 403-409

ROBLES, J., M., ALBA, D., M., MOYÀ-SOLÀ, S., CASANOVAS-VILLAR, I., GALINDO, J., ROTGERS, C., ALMÉCIJA, S. & CARMONA, R. (2010): New craniodental remains of *Trocharion Albanense* Major, 1903 (Carnivora, Mustelidae), from the Vallès-Penedès Basin (middle to late Miocene, Barcelona, Spain). – Journal of Vertebrate Paleontology 30/2: 547-562

ROHLF, F., J. & SLICE, D. (1990): Extensions of the Procrustes Method for the Optimal Superimposition of Landmarks – Systematic Zoology 39 (1): 40-59

ROHLF, F. J. (2005): tpsDig, digitize landmarks and outlines, version 2.05 - Department of Ecology and Evolution, State University of New York at Stony Brook

ROHLF, F., J. (2015): The tps series of software – Hystrix, the Italian journal of Mammalogy 26(1): 9-12

ROHLF, F. J. (2015): tpsUtil, file utility program. version 1.61 - Department of Ecology and Evolution, State University of New York at Stony Brook.

RYBCZYNSKI, N., DAWSON, M., R. & TEDFORD, R., H. (2009): A semi-aquatic Arctic mammalian carnivore from the Miocene epoch and origin of Pinnipedia – Nature 458; 1021-1024

SALAS, L., A. & FULLER, T., K. (1996): Diet of the lowland tapir (*Tapirus terrestris* L.) in the Tabaro River valley, southern Venezuela – Canadian Journal of Zoology 74; 1444-1451

SACCO, T. & VAN VALKENBURGH, B. (2004): Ecomorphological indicators of feeding behavior in the bears (Carnivora: Ursidae) – The Zoological Society of London 263: 41-54

SATO, J., J., WOLSAN, M., PREVOSTI, F., J., D`ELÍA, G., GEBB, C., BEGG, K., HOSODA. T., CAMPBELL, K., I. & SUZUKI, H. (2012) Evolutionary and biogeographic history of weasel-like carnivorans (Musteloidea) – Molecular Phylogenetics and Evolution 63: 745-757

SALESA, M., J., ANTÓN, M., SILICEO, G., PESQUERO, M. D., MORALES, J. & ALCALÁ, L. (2013): A non-aquatic otter (Mammalia, Carnivora, Mustelidae) from the Late Miocene (Vallesian, MN 10) of La Roma 2 (Alfambra, Teruel, Spain): systematics and functional anatomy. – Zoological Journal of the Linnean Society 169; 448-482

SEMPREBON, G., JANIS, C. & SOLOUNIAS, N. (2004): The Diets of the Dromomerycidae (Mammalia: Artiodactyla) and their Response to Miocene Vegetational Change – Journal of Vertebrate Paleontology 24(2); 427-444

SEVAGE, R., J., G. (2009): The anatomy of Potamotherium an Oligocene lutrine. – Journal of Zoology 129(2): 151-244

SMITH, K., CZAPLEWSKI, N. & CIFELLI, L., R. (2016) Middle Miocene carnivorans from the Monarch Mill Formation, Nevada. – Acta Palaeontologica Polonica 61 (1); 231-252

STUBBE, M., KRAPP, F. (1993a): Handbuch der Säugetiere Europas; Raubsäuger (TeilI). – AULA-Verlag Wiesbaden. 9-527

STUBBE, M., KRAPP, F. (1993b): Handbuch der Säugetiere Europas; Raubsäuger (TeilII.) – AULA-Verlag Wiesbaden. 529-1215

STRAIT, S., G. (1993b): Molar Morphology and Food Texture Among Small-Bodied Insectivorous Mammals – Jounal of Mammology 74(2); 391-402

STRAIT, S., G. & VINCENT, J., F., V. (1998): Primate Faunivores: Physical Properties of Prey Items – International Jounal of Primatology 19(5); 867-878

SZUMA, E. & GERMONPRÉ, M. (2020): Were ancient foxes far more carnivorous than recent ones? – Carnassial morpholigal evidence – PloS ONE 15(1); 26

TAGUCHI, Y.-H., OONO, Y. (2005): Relational patterns of gene expression via non-metric multidimensional scaling analysis. – Bioinformatics 21(6):730-40

TEDFORD, R., H. (1976): Relationship of Pinnipeds to other Carnivores (Mammalia) – Systematic Zoology 25:363-374

TINKER, M., T., BODKIN, J. L., BEN-DAVID, M. & ESTES, J., A. (2018): Otters: *Enhydra lutris* and *Lontra felina*. In Encyclopedia of Marine Mammals - – Elsevir 3: 664-671

THENIUS, E. (1949): Die Lutrinen des steirischen Tertiärs (Beiträge zur Kenntnis der Säugetierreste des steirischen Tertiärs I.). – Akademie d. Wissenschaften 299-322

TOULA, F. (1884): Ueber einige Säugethierreste von Göriach bei Turnau (Bruck a|M. Nord) in Steiermark. – Jahrbuch der Kais. Kön. Geologischen Reichsanstalt. 34 (III) 385-402

VAN VALKENBURGH (1989): Carnivore dental adaptations and diet: A Study of Trophic Diversity within guilds – Paleobiology 14(2): 155-173

VAN VALKENBURGH (1991): Iterative evolution of hypercarnivory in canids (Mammalia: Carnivora): evolutionary interactions among sympatric predators – Paleobiology 17(4): 340-362

VAN VALKENBURGH, B. & KOEPFLI, K-P. (1993): Cranial and dental adaptions to predation in canids – The Zoological Society of London 65: 15-37

VALENCIANO, A., MAYDA, S. & ALPAGUT, B. (2019): First record of *Lartetictis* (Carnivora, ustelidae, Lutrinae) in Turkey from the middle Miocene hominoid locality of Paşalar. – Historical Biology 1-15

VIRET, J., M. (1951): Catalogue Critique de la Faune des Mammiféres Miocénes de la Grive Saint-Alban (Isére). Première parie: Chiroptéres, Carnivores, Édentés pholidotes. In: Nouvelles archives du Muséum d´histoire naturelle de Lyon, tome 3, 48-66

VIRANTA, S. & ANDREWS, P. (1995): Carnivora guild structure in the Paşalar Miocene fauna – Journal of Human Evolution 28; 359-372

WANK, M. (1977): Fischotter- und Schildkrötenfunde im Mittelmiozän von Schönweg (Lavanttal, Kärnten). – Carinthia II 167./87; 153-156

WALKER, A., HOECK, H., N. PEREZ, L. (1978): Microwear of mammalian teeth as an indicator of diet. Science 201 (4359), 908–910

WANG, X., QIU, Z. & WANG, B. (2004): A new leptarctine (Carnivora: Mustelidae) from the early Miocene of the northern Tibetan Plateau: implications for the phylogeny and

zoogeography of basal mustelids. – Zoological Journal of the Linnean Society 142; 405-421

WANG, X. MCKENNA, M., C. & DASHZEVEG, D. (2005): *Amphicticeps* and *Amphicynodon* (Arctoidea, Carnivora) from Hsanda Gol Formation, Central Mongolia and Phylogeny of Basal Arctoids with Comments on Zoogeography. – American Museum of Natural History 3483; 57

WERDELIN, L. (2005): The Carnivora of Rudabánya (MN 9, Late Miocene, Hungary). – Palaeontographica Italica 90; 163-180

WOLSAN, M. (1993): Phylogeny and classification of early European Mustelida (Mammalia: Carnivora). – ACTA Theriologica 38 (4): 345-384

YONEZAWA, T., NIKAIDO, M., KOHNO, N., FUKUMOTO, Y., OKADA, N. & HASEGAWA, M. (2007): Molecular phylogenetic study on the origin and evolution of Mustelidae – Gene 396: 1-12

XAFIS, A., NAGEL, D. & BASTL, K. (2017): Which toot to sample? A methodological study of the utility of premolar/non-carnassial teeth in the microwear analysis of mammals – Palaeogeography, Palaeoclimatology, Palaeoecology 487; 229-240

ZAPFE, H. (1950): Die Fauna der miozänen Spaltenfüllung von Neudorf an der March (CSR.): Carnivora – Akademie der Wissenschaften Wien 159; 109-141
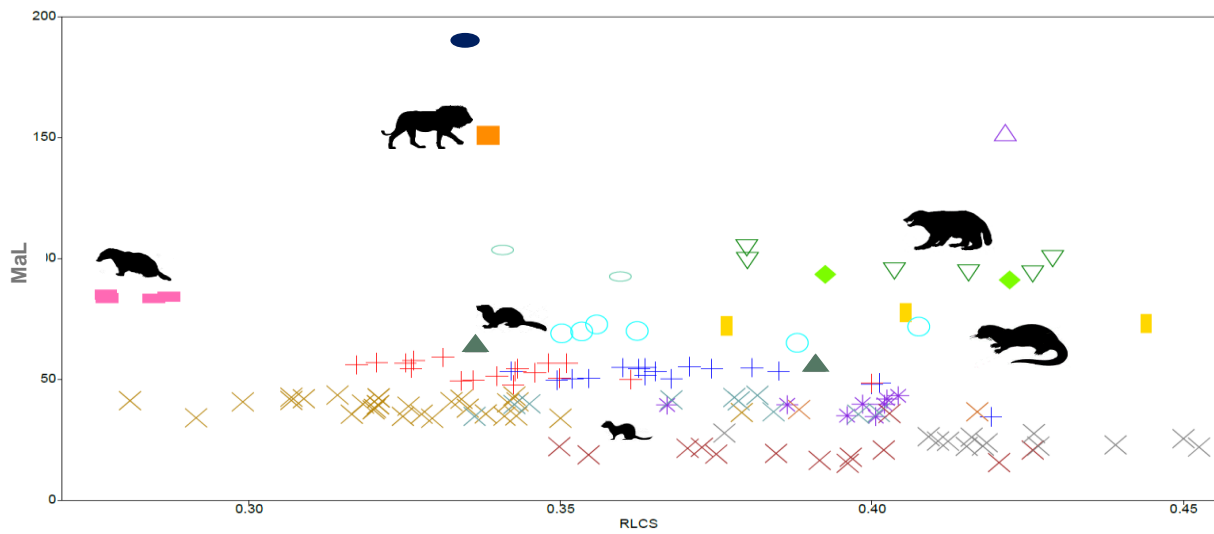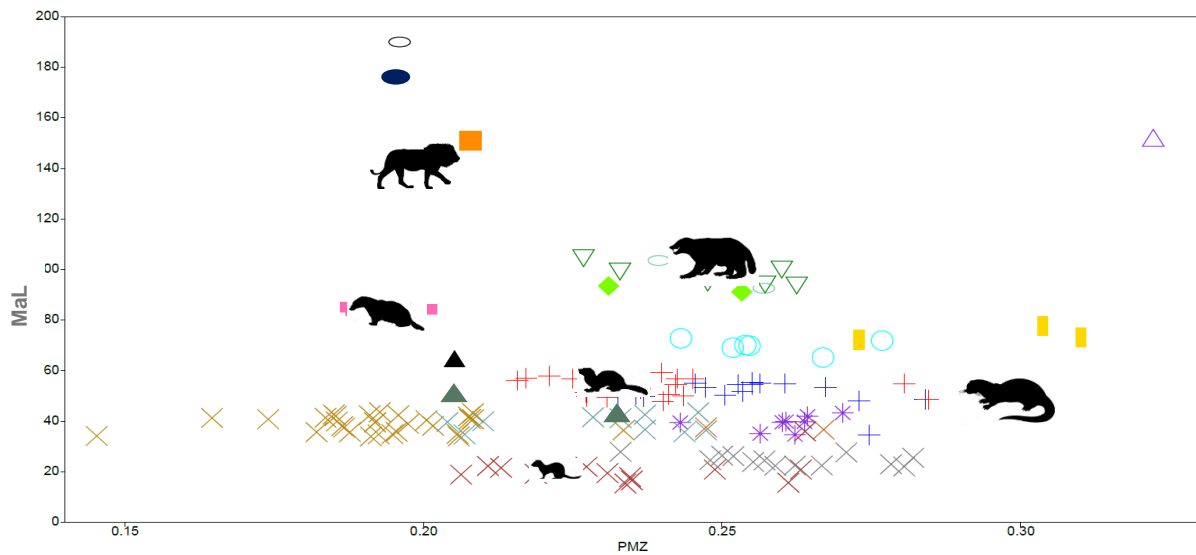
Appendix
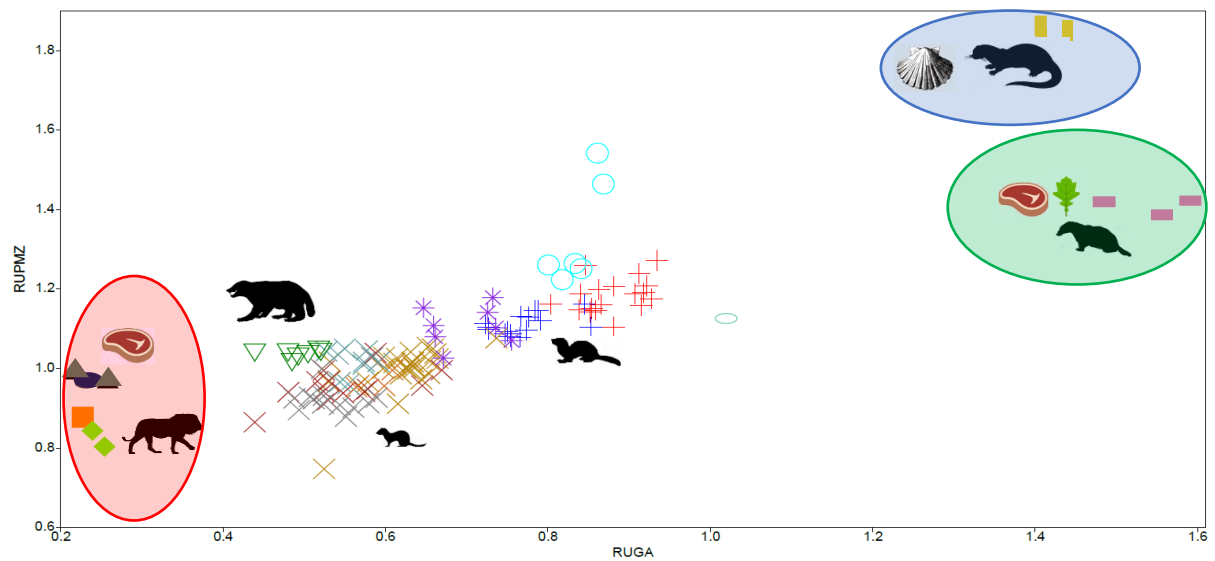
Appendix 1: The relative upper grinding area (x-axis) plotted against the relative total length of the upper premolars (y-axis) in a simple x/y graph.
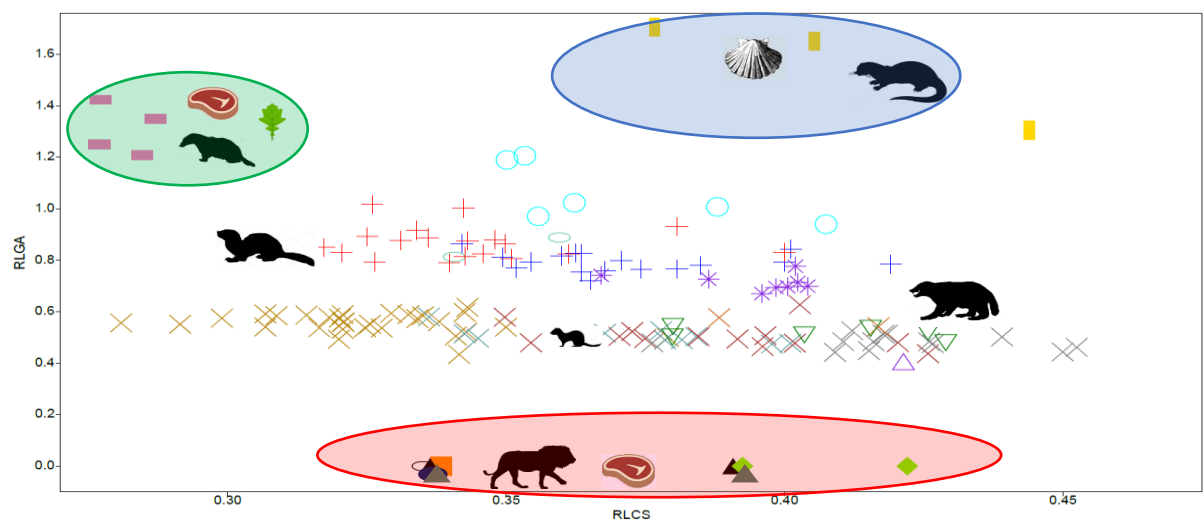

Appendix 2: Relative lower grinding area (y-axis) is plotted against the relative cusping size (x-axis). A clear differentiation between omnivorous, carnivorous and crushin is recognizable.

Appendix 3: The mandibular length is plotted against the relative lower cusping size. The taxa are strongly spreaded. One reason is the included size which has in this case a major effect.


Appendix 4: To visualize the effect of the size the mandibular length (y-axis) is plotted against the relative total length of premolars (x-axis).
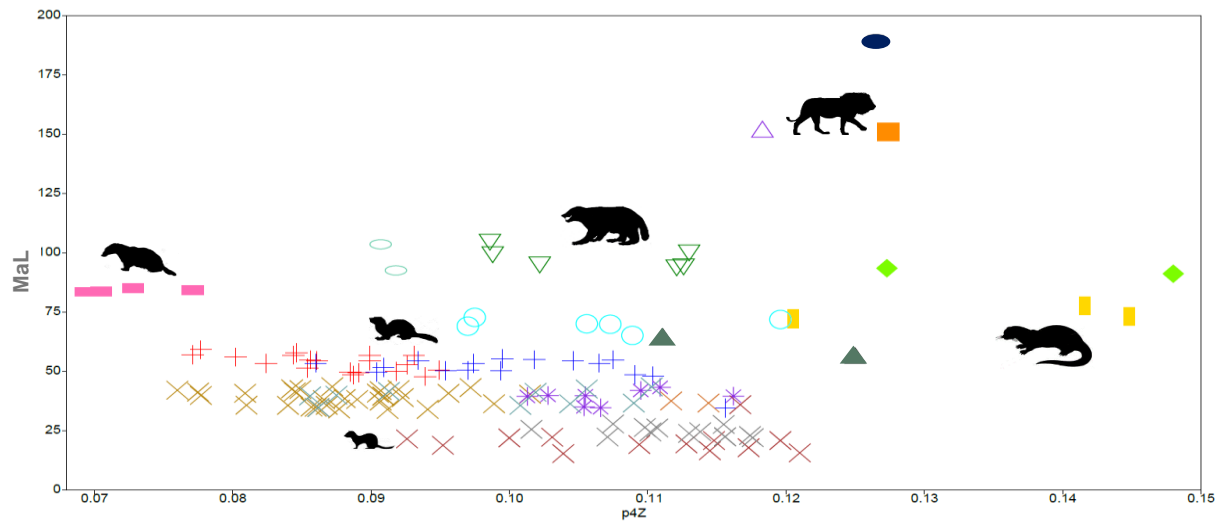
Appendix 5: The mandibular length (y-axis) is plotted against the relative length of fourth lower premolar s (x-axis). The taxa are spread by the p4Z values as well by the MaL values.
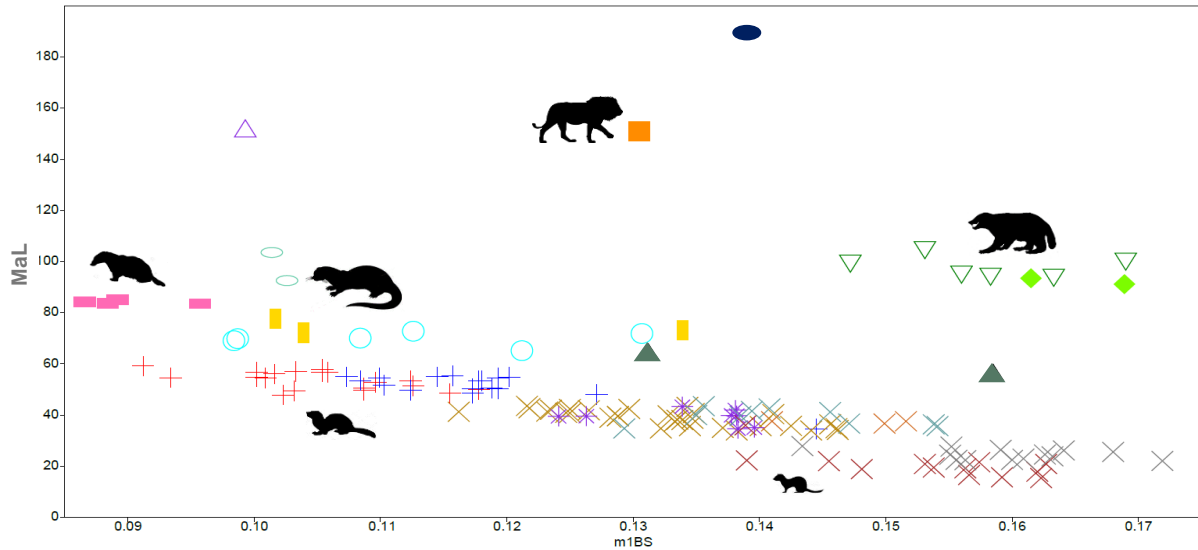
Appendix 6: The graph is an explanation how the size effects the scattering of the taxa. The MaL (y-axis) is plotted versus the m1BS.
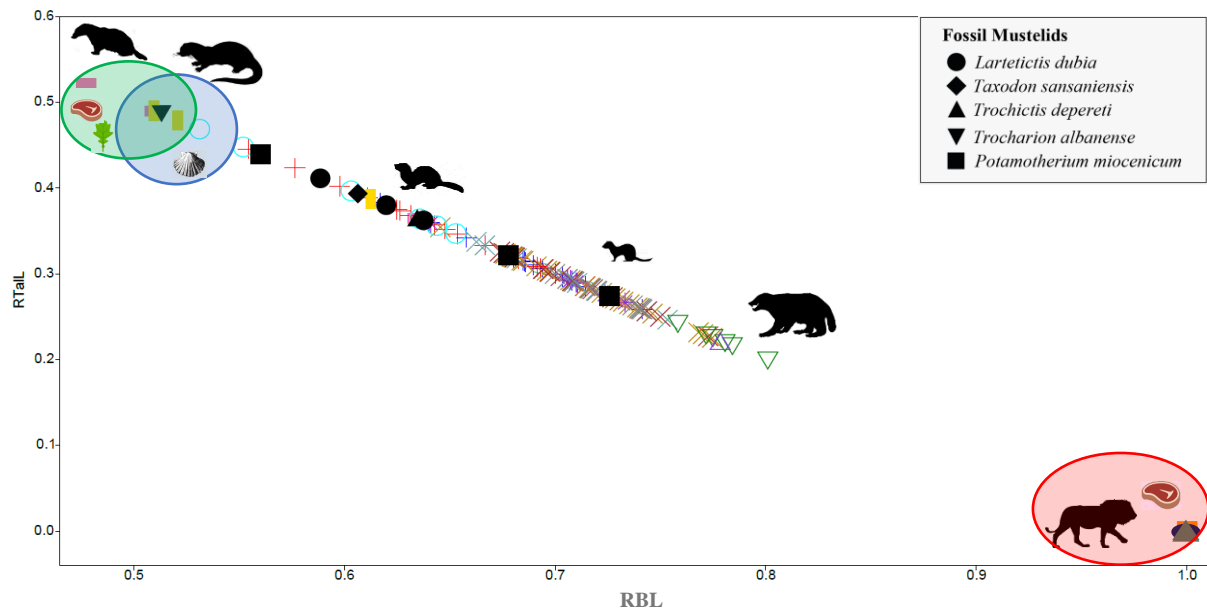
Appendix 7: In the graph the values of the lower first molar is plotted. On the y-axis the RTalL and on the x-axis the RBL. A clear separation between the carnivorous and the non-carnivorous are visualized. The carnivores have a prominent blade which is built by the trigonid, while the omnivores and the crushing have reduced blade but emphasized talonid. Between those extremes the other taxa plotted and can be assigned to the respective food preference.