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The carnivorans (Carnivora, Mammalia) from the hominid locality of Hammerschmiede (Bavaria, Germany)

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Doctoral Thesis

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Cover Image: Artistic illustration of the Hammerschmiede ecosystem, depicting the felid *Pseudaelurus* hunting the hominid *Danuvius*. Artwork: M. Antón

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Abstract

The present Thesis is focused on the study of the carnivorans that have been discovered in the hominid locality of Hammerschmiede. The age of the locality is at the base of Late Miocene and it is situated in Bavaria, Germany. Five articles have already been conducted based on this material, while more specimens are presented here accompanied by a discussion concerning the carnivoran guild of the locality.

The main part of this Thesis includes three introductory chapters. The first chapter deals with the order Carnivora. The phylogenetic relationships of this group are discussed, followed by an extensive presentation of the representatives of this order during the Miocene of Europe. This part was considered essential, because of the extreme diversity of the Hammerschmiede carnivorans that made required a deep understanding of the current knowledge on this group. The second part of the introduction deals with some characteristics of the Miocene of Europe. The carnivoran guilds of several localities are studied, followed by some remarks on palaeogeography and palaeoclimatology. Finally, the last part of the introduction has to do with the locality of Hammerschmiede. The most updated data for the faunal, floral and abiotic components of the locality are demonstrated, together with a historical summary of the studies concerning Hammerschmiede.

The chapter 4 of material and methods includes a detailed table containing the material used in this project, as well as the methodologies used for its study (dental nomenclature, anatomical nomenclature, measurements, guild analysis).

The next part (chapter 5) of the Thesis includes the five articles that have already been conducted for peer-review academic journals. The first paper consists of a taxonomic, biostratigraphic and palaeoecologic review of the genus *Semigenetta* (Viverridae), reporting some material of *Semigenetta sansaniensis* and *Semigenetta grandis* from Hammerschmiede. The second paper reports the presence of a new species of otter, *Vishnuonyx neptuni* (Mustelidae), accompanied by palaeogeographical and palaeoecological notes. The third paper concerns the material of hyenas (Hyaenidae) found in the locality, presenting dental material of the ictithere *Thalassictis montadai*, together with a large bone-cracking hyaenid, as well as a biostratigraphic review of relevant forms in Europe. The fourth paper presents the extreme diversity of the small carnivoran forms found in Hammerschmiede, together with a preliminary palaeoecological comparison. The discovered species include: "*Martes*" *sansaniensis*, "*Martes*" cf. *munki*, "*Martes*" sp., *Circamustela hartmanni* (a new species for this genus), *Laphyctis mustelinus*, Guloninae indet., *Eomellivora moralesi*, *Vishnuonyx neptuni*, *Lartetictis* cf. *dubia*, *Paralutra jaegeri*, *Trocharion albanense*, *Palaeomeles pachecoi*, *Proputorius sansaniensis*, *Proputorius pusillus*, *Alopecocyon goeriachensis*, Simocyoninae indet., *Potamotherium* sp., *Semigenetta sansaniensis*, *Semigenetta grandis* and *Viverrictis modica*. Finally, the fifth paper concerns material of the primitive giant panda *Kretzoiarctos beatrix* (Ursidae) accompanied with a diet estimation for this species based on dental texture microwear analysis.

More material, which either was discovered after the publications or was considered to consist of a separate subject, was studied for the families: Amphicyonidae (1 species), Ailuridae (more material of *Alopecocyon goeriachensis*), Mephitidae (more

material of *Proputorius sansaniensis*), Mustelidae (more material of *Paralutra jaegeri* and *Lartetictis* cf. *dubia*), Phocidae (1 species), Felidae (*Pseudaelurus quadridentatus* and Metailurini indet.), Barbourofelidae (1 species) and Hyaenidae (more material of *Thalassictis montadai*). Additionally, a preliminary description of the coprolites found in the locality has been attempted.

Consequently, the carnivoran guild of the locality includes 28 species. This makes Hammerschmiede the third most diverse locality in the Miocene of Europe (surpassed only by the fissure-fillings Wintershof-West and La Grive-Saint-Alban). This is especially impressive, based on the relatively low number of identifiable specimens (n=122), as also shown in rarefaction analysis. The HAM 5 layer alone has yielded 21 species, in comparison to the 15 species found in HAM 4. A biostratigraphic analysis demonstrated that the locality includes mostly Aragonian, but also some Vallesian forms, including several First Occurrence Dates and Last Occurrence Dates. Species diversity for the discovered families reveals that the profile seen in Hammerschmiede does not resemble that of any other Miocene locality of Europe. A detailed attribution of all the discovered species to the available categories for Dietary Habits, Locomotor Lifestyle and Body Mass has been presented. Quantitative analysis of these data show that the locality mostly includes small- to medium-sized carnivorans, especially in HAM 4. Additionally, many species are scansorial or semi-aquatic, proving the strong influence of the forested river in the locality. Palaeoecological comparison of the discovered species (through cluster analysis and 2D+ plots) shows that most species are able to coexist without competition, whereas other were found to occupy very similar niches.

Concluding, the locality of Hammerschmiede has proven to conceal an astonishing diversity of mammalian carnivores. Based on the presented data, it is sure that it will be a reference locality for the study of the Miocene carnivorans of Europe in terms of taxonomy, biostratigraphy and palaeoecology. Some possible future objectives are mentioned at the end of the discussion.

Zusammenfassung

Die vorliegende Arbeit konzentriert sich auf die Erforschung der in der Hominidenfundstelle Hammerschmiede entdeckten Fleischfresser. Die Lokalität befindet sich in Bayern, Deutschland und ihr Alter liegt am Anfang des Späten Miozäns. Basierend auf diesem Material wurden bereits fünf Artikel geführt, während weiteres Material hier präsentiert wird, begleitet von einer Diskussion über die Raubtiere der Fundstelle als Ganzes.

Die Einleitung dieser Arbeit umfasst drei Kapitel. Das erste Kapitel befasst sich mit der Ordnung Carnivora. Die phylogenetischen Beziehungen dieser Gruppe werden diskutiert, gefolgt von einer ausführlichen Präsentation der Vertreter dieser Ordnung während des Miozäns in Europa. Dieser Teil wurde als wesentlich erachtet, da die extreme Vielfalt der Hammerschmiede-Raubtiere ein tiefes Verständnis des aktuellen Wissens über diese Gruppe erforderte. Der zweite Teil der Einführung befasst sich mit einigen Merkmalen des Miozäns Europas. Die Raubtiere mehrerer Lokalitäten werden untersucht, gefolgt von einigen Bemerkungen zur Paläogeographie und Paläoklimatologie. Schließlich hat der letzte Teil der Einleitung mit dem Fundort Hammerschmiede zu tun. Dargestellt sind die aktuellsten Daten zu Fauna, Flora und abiotischen Bestandteilen des Fundortes, zusammen mit einer historischen Zusammenfassung der Studien zur Hammerschmiede.

Das Kapitel Material und Methoden enthält eine detaillierte Tabelle mit dem in diesem Projekt verwendeten Material sowie den für seine Untersuchung verwendeten Methoden (Zahn Nomenklatur, anatomische Nomenklatur, Messungen, Gildenanalyse).

Der nächste Teil der Dissertation umfasst die fünf Artikel, die bereits in akademischen Peer-Review-Zeitschriften veröffentlicht wurden. Die erste Veröffentlichung besteht aus einer taxonomischen, biostratigraphischen und paläoökologischen Übersicht der Gattung *Semigenetta* (Viverridae) und berichtet über Material von *Semigenetta sansaniensis* und *Semigenetta grandis* von Hammerschmiede. Die zweite Veröffentlichung berichtet über das Vorkommen einer neuen Otterart, *Vishnuonyx neptuni* (Mustelidae), begleitet von paläogeographischen und paläoökologischen Notizen. Der dritte Artikel betrifft das Material von Hyänen (Hyaenidae), die in der Lokalität gefunden wurden, und präsentiert Zahnmaterial der ictithere *Thalassictis montadai* zusammen mit einer großen knochenbrechenden Hyäne sowie eine biostratigraphische Übersicht über relevante Formen in Europa. Der vierte Beitrag präsentiert die extreme Diversität der Kleinraubtierformen in Hammerschmiede, zusammen mit einem vorläufigen paläoökologischen Vergleich. Zu den entdeckten Arten gehören: “*Martes*” *sansaniensis*, “*Martes*” cf. *munki*, “*Martes*” sp., *Circamustela hartmanni* (eine neue Art für diese Gattung), *Laphyctis mustelinus*, Guloninae indet., *Eomellivora moralesi*, *Vishnuonyx neptuni*, *Lartetictis* cf. *dubia*, *Paralutra jaegeri*, *Trocharion albanense*, *Palaeomeles pachecoi*, *Proputorius sansaniensis*, *Proputorius pusillus*, *Alopecocyon goeriachensis*, Simocyoninae indet., *Potamotherium* sp., *Semigenetta sansaniensis*, *Semigenetta grandis* und *Viverrictis modica*. Schließlich befasst sich die fünfte Arbeit mit Material des primitiven

Riesenpandas *Kretzoiarctos beatrix* (Ursidae), begleitet von einer Einschätzung der Ernährung diese Art, basierend auf einer Analyse der Zahntextur von Microwear.

Weiteres Material, das entweder nach den Veröffentlichungen entdeckt oder als eigenständiges Thema angesehen wurde, wurde für folgende Familien untersucht: Amphicyonidae (1 Art), Ailuridae (weiteres Material von *Alopecocyon goeriachensis*), Mephitidae (weiteres Material von *Proputorius sansaniensis*), Mustelidae (weiteres Material von *Paralutra jaegeri* und *Lartetictis* cf. *dubia*), Phocidae (1 Art), Felidae (*Pseudaelurus quadridentatus* und Metailurini indet.), Barbourofelidae (1 Art) und Hyaenidae (weiteres Material von *Thalassictis montadai*). Zusätzlich wird eine vorläufige Beschreibung der in der Lokalität gefundenen Koprolithen erbracht.

Folglich umfassent die Raubtiere die Lokalität 28 Arten. Damit ist Hammerschmiede der drittreichste Fundort im Miozän Europas (übertroffen nur von Spaltenfüllungs Wintershof-West und La Grive-Saint-Alban). Dies ist besonders beeindruckend, basierend auf der relativ geringen Anzahl identifizierbarer Exemplare (n = 122), wie auch die Verdünnungsanalyse zeigt. Allein die HAM 5-Schicht hat 21 Arten hervorgebracht, im Vergleich zu den 15 Arten, die in HAM 4 gefunden wurden. Eine biostratigraphische Analyse zeigte, dass die Lokalität hauptsächlich aragonische, aber auch einige vallesische Formen umfasst, darunter mehrere Daten des ersten und letzten Auftretens. Die Artenvielfalt der entdeckten Familien zeigt, dass das Profil in Hammerschmiede nicht dem anderer miozäner Fundorte in Europa ähnelt. Eine detaillierte Zuordnung aller entdeckten Arten zu den verfügbaren Kategorien für Ernährungsgewohnheiten, lokomotorische Lebensweise und Körpermasse wurde vorgelegt. Die quantitative Analyse dieser Daten zeigt, dass der Fundort hauptsächlich kleine bis mittelgroße Fleischfresser umfasst, insbesondere in HAM 4. Außerdem sind viele Arten Kletterer oder semi-aquatisch, was den starken Einfluss des bewaldeten Flusses in dem Fundort beweist. Der paläoökologische Vergleich der entdeckten Arten (durch Clusteranalyse und 2D+-Plots) zeigt, dass die meisten Arten ohne Konkurrenz koexistieren können, während andere sehr ähnliche Nischen besetzen.

Zusammenfassend lässt sich sagen, dass der Fundort Hammerschmiede eine erstaunliche Vielfalt an Raubsäugern beheimatet. Aufgrund der präsentierten Daten ist es sicher, dass es sich um eine Referenzlokalität für die Studie der miozänen Raubtiere Europas in Bezug auf Taxonomie, Biostratigraphie und Paläoökologie handeln wird. Einige mögliche zukünftige Ziele werden am Ende der Diskussion erwähnt.

Introduction and Objectives

This Thesis is focusing on the taxonomy and palaeoecology of the carnivorans that has been unearthed from the locality of Hammerschmiede (Bavaria, Germany). Even though previous studies have included members of Carnivora in their faunal lists, there hadn't been thorough research on this group. The excavations conducted by the University of Tübingen (under the supervision of Prof. M. Böhme) have uncovered an astonishing diversity in the locality, including numerous species of mammalian carnivores.

The objectives of the present study are:

- The taxonomic identification of the carnivorans found in the locality of Hammerschmiede
- The report of any species that are new to science
- The discussion on the biostratigraphy and palaeogeography of the discovered species
- The estimation of palaeoecological parameters for the discovered species, in terms of diet, locomotor behavior and body mass
- The study of the carnivoran guild of the locality, including possible interspecific competition cases
- The indicators concerning the palaeoecology of the locality based on carnivorans, including possible differences between the main layers

Chapter 1

Order Carnivora: General Information and their Miocene Representatives in Europe

Fig. 1.1: Skeleton of *Smilodon fatalis*. Source: https://artsandculture.google.com.

General Information

Today the mammalian order Carnivora BOWDICH, 1821, includes 16 families and approximately 280 species that occupy nearly the total surface of the Earth, expressing an astonishing diversity of:

> (1) size: from the 25 g *Mustela nivalis* LINNAEUS, 1766, to the >3500 kg *Mirounga leonina* (LINNAEUS, 1758) (Ling & Bryden, 1992; Sheffield & King, 1994)
>
> (2) locomotor abilities: from the arboreal *Ailurus fulgens* CUVIER, 1825, to the marine pinnipeds (Roberts & Gittleman, 1984; Perrin et al., 2009)
>
> (3) hunting strategies: from the strictly herbivorous *Ailuropoda melanoleuca* (DAVID, 1869) to the strictly flesh-eating *Panthera pardus* (LINNAEUS, 1758) and the bone-crushing *Hyaena hyaena* (LINNAEUS, 1758) (Chorn & Hoffmann, 1978; Rieger, 1981; Stein & Hayssen, 2013).

This variability is even greater when the fossil record of the order is studied, as several extinct forms correspond to lineages and ecomorphs with no living representatives. One typical example is the subfamily Machairodontinae GILL, 1872, the sabertooth cats, which includes species with unique adaptations for the killing of large prey through the canine-shear bite (e.g. Akersten, 1985; Antón and Galobart, 1999; Antón et al., 2004; Antón, 2013).

The next pages will deal with the diversity of carnivorans focusing on the state-of-the-art knowledge for the Miocene representatives of the group.

The phylogeny of Carnivora

Many alternative scenarios have been proposed concerning the exact position of the order Carnivora in the mammalian phylogenetic tree. The modern consensus for this problem is that Carnivora belong to the mammalian mirorder Ferae LINNAEUS, 1758. These relationships were recently discussed in detail by Lv et al. (2021), who presented all the well-known hypotheses concerning the relationships of carnivorans. It is demonstrated in Fig. 1.2 that in all these hypotheses the most closely related extant order to the Carnivora is Pholidota WEBER, 1904. In particular, Ferae are divided in two clades: the Pan-Carnivora FLYNN, WYSS & WOLSAN, 2020 (the group that includes the carnivorans and their fossil relatives) and the Pholidotamorpha GAUDIN, EMRY & WIBLE, 2009 (the group that includes the extant pangolins and their fossil relatives).

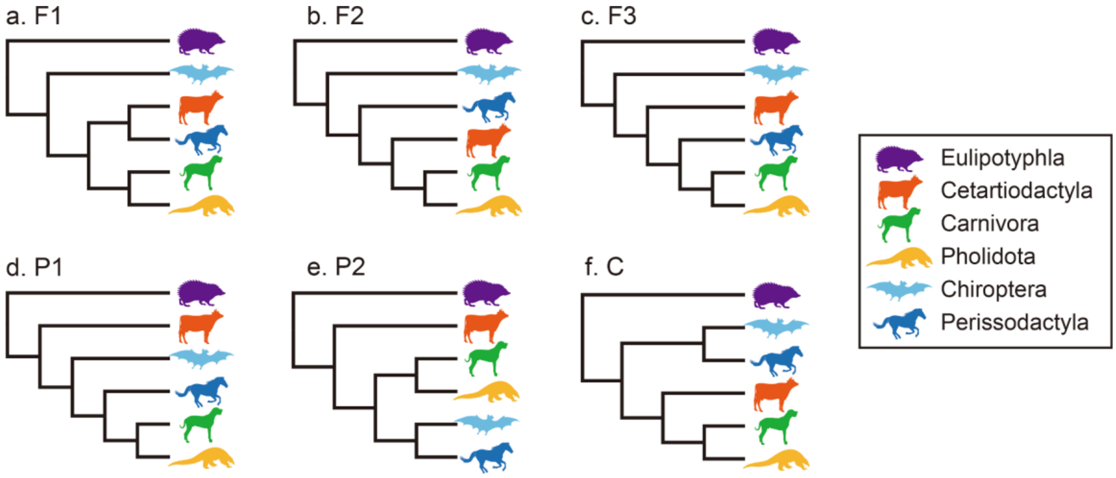

Fig. 1.2: Different hypotheses concerning the position of the order Carnivora, based on 23 previous studies. Source: Lv et al. (2021).

The Pan-Carnivora are also divided in two clades: the Carnivoramorpha WYSS & FLYNN, 1993 (that include the Carnivora and the Miacoidea SIMPSON, 1931) and the Creodonta COPE, 1875 (Matthew, 1909; Wyss & Flynn, 1993; Wesley-Hunt & Flynn, 2005; Flynn et al., 2010). The creodonts are divided in the Hyaenodonta VAN VALEN, 1967, and the Oxyaenodonta VAN VALEN, 1971 (e.g. Egi et al., 2005; Flynn et al., 2010). The carnivorans are differentiated from the paraphyletic Miacoidea (the other group of Carnivoramorpha), which are split into the families Miacidae COPE, 1880a, and Viverravidae WORTMAN & MATTHEW, 1899 (Flynn et al., 2010). Finally, the Carnivora include the suborders Caniformia KRETZOI, 1943, and Feliformia KRETZOI, 1945 (e.g. Wozencraft, 1989; Flynn & Nedbal, 1998; Wesley-Hunt & Flynn, 2005). A simplified depiction of the aforementioned relationships between these groups can be seen in Fig. 1.3.

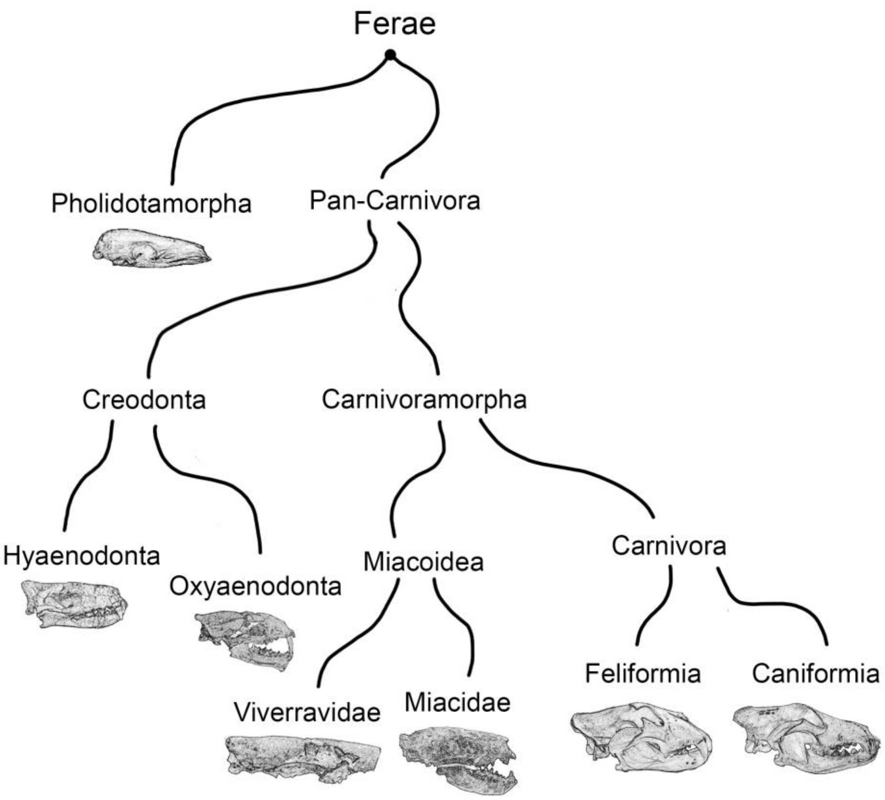

Fig. 1.3: Simplified depiction of the relationships between the major groups of Ferae.

The order Carnivora includes 16 extant and at least 11 extinct families, divided in the two suborders, Feliformia and Caniformia. A consensus list of the carnivoran families can be seen in Table 1.1.

Table 1.1: List of the carnivoran families and their suborder position. Extinct families are marked with an “†”.

Feliformia	**Caniformia**
Felidae	Canidae
Barbourofelidae†	Amphicyonidae†
Prionodontidae	Ursidae
Hyaenidae	Hemicyonidae†
Percrocutidae†	Amphicynodontidae†
Lophocyonidae†	Enaliarctidae†
Herpestidae	Desmatophocidae†
Eupleridae	Phocidae
Viverridae	Otariidae
Stenoplesictidae†	Odobenidae
Nandiniidae	Ailuridae
Nimravidae†	Mephitidae
Palaeogalidae†	Procyonidae
	Mustelidae

Several different approaches have provided different views of the phylogenetic relationships between these families. The image becomes clearer when only the extant families are studied, as several studies result in similar patterns (Bininda-Emonds & Gittleman, 2000; Flynn et al., 2005; Finarelli, 2008; Agnarsson et al., 2010; Nyakatura & Bininda-Emonds, 2012; Antón, 2013; Paterson et al., 2020; Hassanin et al., 2021). A consensus of these studies, based on Hassanin et al. (2021) can be seen in Fig. 1.4.

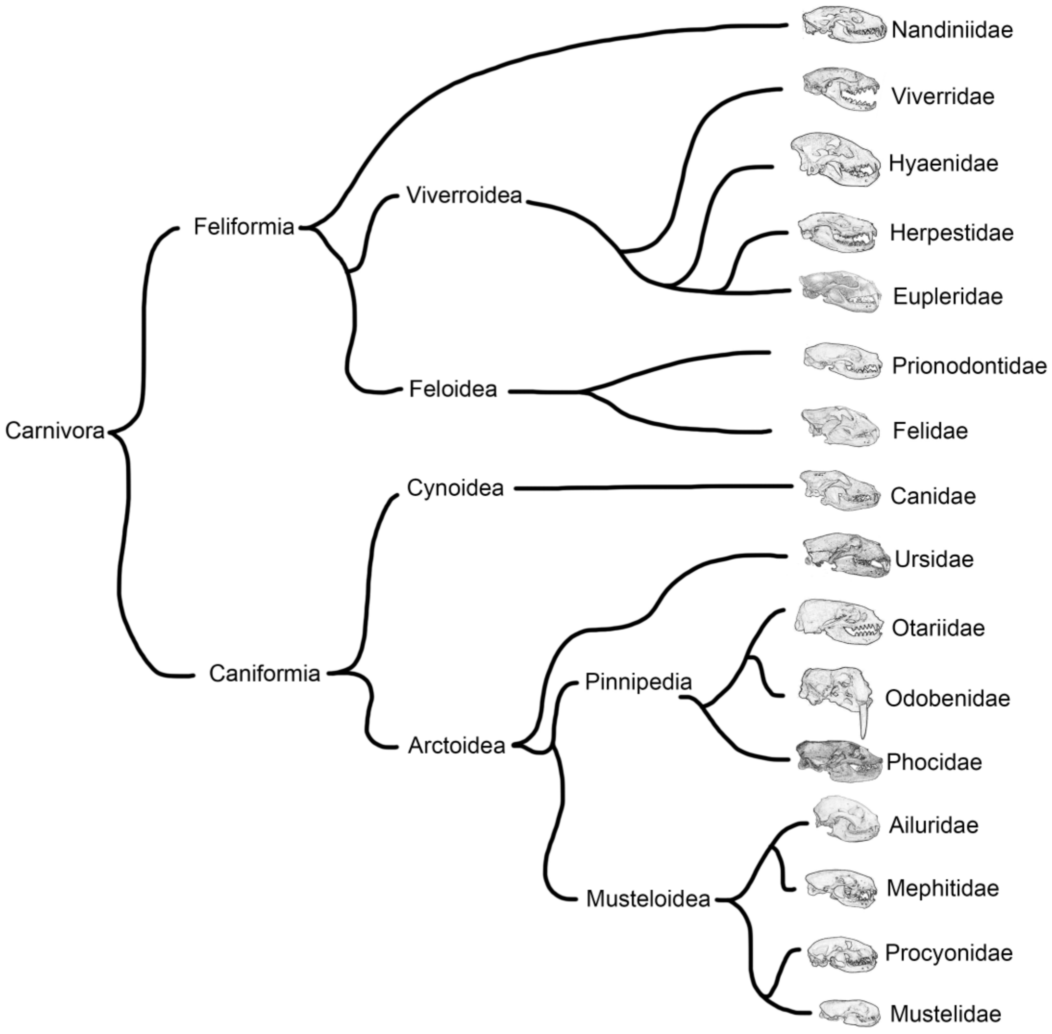

Fig. 1.4: Simplified depiction of the relationships between the carnivoran families based on Hassanin et al. (2021) and references therein.

Regarding the extinct families, their exact positions are still debatable and each one of them will be dealt with separately.

The family Percrocutidae WERDELIN & SOLOUNIAS, 1991, is considered to be a sister group of the hyaenids (Thenius, 1966; Schmidt-Kittler, 1976; Werdelin & Solounias, 1991; Radović et al., 2021). Xiong (2019) supported the re-inclusion of the percrocutids into the Hyaenidae Gray, 1821, but, in agreement with Radović et al. (2021), the former group still exhibits some clear apomorphies (such as the mesially situated orbit and the widely connected trigonid and talonid of dp4), so here they are considered as a distinct taxon that can possibly be interpreted as an early branch of the hyaenids.

The families Barbourofelidae SCHULTZ, SCHULTZ & MARTIN, 1970, and Nimravidae COPE, 1880b include felid-like forms, which were thought to belong to the same family for decades (e.g. Bryant, 1991 and references therein). However, a number of recent studies suggest that the two groups are distinct: the Barbourofelidae are a sister group of Felidae and the Nimravidae are a primitive outgroup inside the Feliformia (Hunt, 1987; Flynn et al., 1988; Flynn & Galiano, 1982; Morales et al., 2001; Morlo et al., 2004; Antón, 2013; Robles et al., 2013b). In fact, Hunt (1987) placed the nimravids as even more basal than the nandiniids, based on the structure of their auditory region. Though, none of these studies considered the recently established close relationship between Felidae and Prionodontidae, so the relationships between these two families and Barbourofelidae is unclear.

The family Lophocyonidae FEJFAR, SCHMIDT-KITTLER & ZACHAROV, 1987, includes some rare, small-sized feliforms with dilambdodont upper molars, lophodont lower molars and molarized premolars (Morales et al., 2019b). Only four genera are known and the remains are usually fragmentary, so there are not sufficient data to solidly estimate the phylogenetic position of the family. The only available data suggest that the group exhibits some affinities to the basal hyaenids (Morales et al., 2019b).

Similarly to the lophocyonids, the family Stenoplesictidae SCHLOSSER, 1923, is also very poorly known. Morales et al. (2000) and Morlo et al. (2007) have supported the validity of the family, while Peigné & de Bonis (1999) preferred to refer to this group as “Family Incertae Sedis”. Peigné & de Bonis (1999), in their review of the genus *Stenoplesictis* FILHOL, 1880 considered it as a feliform closely related to *Nandinia* GRAY, 1843, but more derived.

Another group that our knowledge about it is still restricted, is the family Palaeogalidae MARTIN & LIM, 2001. Very few efforts have been made to pinpoint the phylogenetic position of the family in the carnivoramorphan tree. Flynn & Galiano (1982) suggested that the group of *Palaeogale* VON MEYER, 1846, must be included into the Viverravidae. However, the following aforementioned studies concerning the phylogeny of carnivorans changed our point of view for several relationships inside the group. A more recent approach by Wang & Zhang (2015) suggested that the family Palaeogalidae is in fact a basal feliform lineage. The resulting tree (Wang & Zhang, 2015, Fig. 7) indicates that the family is even more basal than the Nimravidae.

The family Amphicyonidae TROUESSART, 1885, is one of the richest in the Miocene carnivoran fossil record, with numerous species grouped in several tribes and genera. The group is colloquially called as “bear-dogs”, pointing out the initial phylogenetic problem of the taxon: is it closer to the bears (Arctoidea) or to the dogs (Cynoidea)? The traditional point of view included the amphicyonids in the dog lineage and, often, in the family Canidae (e.g. Trouessart, 1885; Schlosser, 1899a; Pilgrim, 1931; Viret, 1951). However, the most widely accepted point of view today is the inclusion of the Amphicyonidae into the Arctoidea (e.g. Viranta, 1996; Peigné, 2012; Hunt & Stepleton, 2015; Jiangzuo et al., 2019a, 2019b, 2020). The study of Tomiya & Tseng (2016) provides an interesting exception, suggesting that the bear-dogs differentiated from the caniformian branch before the split of Cynoidea and Arctoidea. Herein, the common opinion that the amphicyonids are arctoids is followed.

The family Amphicynodontidae SIMPSON, 1945, is an enigmatic group that combines bear-like and pinniped-like characteristics. Its monophyly is still debated (Rybczynski et al., 2009; Paterson et al., 2020). Some studies suggest a closer relationship to the bears (e.g. Wang et al., 2005; Finarelli, 2008), while some others place at least some of the genera into the pinniped lineage (e.g. Tedford et al., 1994; Paterson et al., 2020). Herein, they are considered as an early branch of the pinniped group.

The family Hemicyonidae FRICK, 1926, was traditionally considered to belong to the family Ursidae FISCHER DE WALDHEIM, 1817 (e.g. McLellan & Reiner, 1994; Ginsburg & Morales, 1998; Peigné et al., 2006b; de Bonis, 2013). However, their distinctiveness inside the bear linage has been considered granted in all the relevant phylogenetic studies (McLellan & Reiner, 1994; Ginsburg & Morales, 1998; Abella et al., 2012; Qiu et al., 2014). Therefore, the attribution of these genera into a distinct family depends on the point of view of each author. In the present manuscript, based on the detailed comparisons made by Hontecillas (2019), the group is recognized to have a sufficient number of apomorphies in order to be considered as a distinct family.

The family Enaliarctidae MITCHEL & TEDFORD, 1973, is a group of primitive pinnipeds, originally described as members of the family Otariidae GRAY, 1825 (Mitchel & Tedford, 1973). However, further studies have suggested that this taxon occupies a more basal position than the extant pinnipeds and it should be considered as a distinct family (Tedford, 1976; Berta et al., 2018; Poust & Boessenecker, 2018; Paterson et al., 2020). However, the monophyly of the group is still debated (Paterson et al., 2020).

Finally, the last extinct carnivoran family is Desmatophocidae HAY, 1930, another pinniped group that has been often considered as a sister group of Phocidae GRAY, 1821 (Berta et al., 2018; Boessenecker & Churchill, 2018; Poust & Boessenecker, 2018). However, other points of view suggest that they are in fact closer to the otariid-odobenid group (Paterson et al., 2020). Herein, it is preferred to retain the sister-group relationship with the phocids that is followed in the majority of the literature sources.

A simplified depiction that is summarizing the aforementioned relationships at family level can be seen in Figure 1.5. However, it must be noted that this figure doesn’t represent a total consensus of the current knowledge on carnivoran phylogeny. There are many remaining questions concerning several genera or even larger groups of unknown position. One example is the group of *Potamotherium* GEOFFROY SAINT-HILAIRE, 1833, which is discussed in a following chapter. Though, the figure depicts the latest and most widely accepted point of views for the studied taxa and it aims into enabling the reader to set a wider frame before entering into a more detailed taxonomy.

In the following pages, each family will be reviewed in some detail, in order to provide the current knowledge on the Miocene representatives of them.

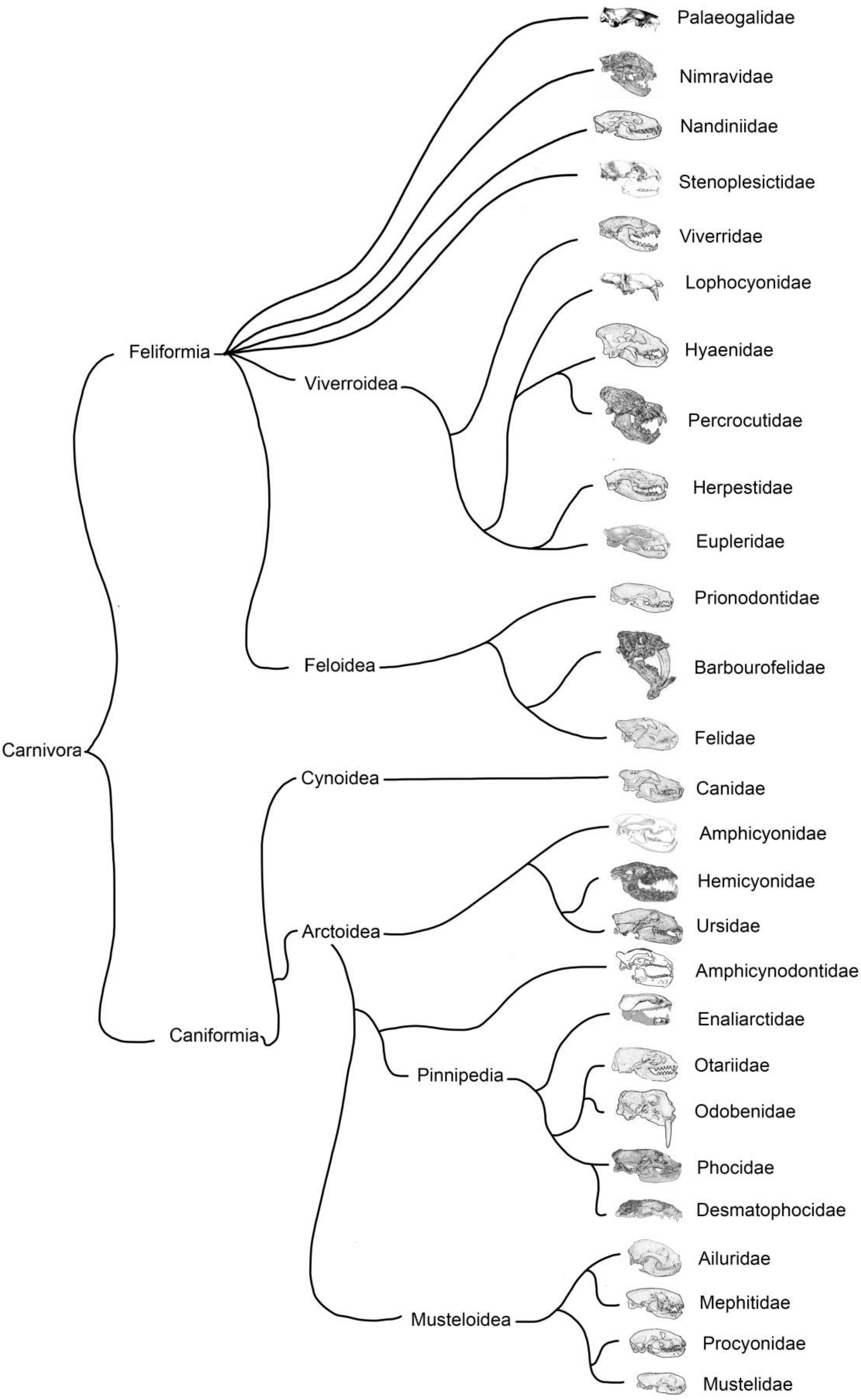

Fig. 1.5: Simplified depiction of the relationships between the extant and extinct families of Carnivora. For references see text above.

Felidae FISCHER DE WALDHEIM, 1817

A review of the fossil record of the felids has been made by Werdelin et al. (2010) and Antón (2013) and a detailed overview is beyond the scope of this Thesis. However, a short chronicle of this family's history in the Miocene fossil record will be provided.

The oldest genus attributed to the family Felidae FISCHER DE WALDHEIM, 1817, is *Proailurus* FILHOL, 1879, which has been found in the Late Oligocene and Early Miocene mainly of Europe (Peigné, 1999 and references therein) and North America (Hunt, 1998a). A diagnosis for *Proailurus* is given by Peigné (1999): "European felid carnivore which varies in size from that of *Lynx rufus* to that of *Lynx lynx*. Short rostrum and mandible; no diastemas between premolars; p1 absent in 1/3 of the specimens attributed to the genus; p2 significantly reduced in size compared to p3; p3 lower and shorter than p4; posterior cingulum of p3 and p4 cutting and turning up; very open m1 trigonid with a very reduced metaconid, very distally positioned and very low; m1 talonid very short (between 10 and 15% of the total length of m1), not hollow and cutting, distal to the protoconid; m2 uniradiculate, with blunt and low trigonid, very reduced or absent talonid; P1 present, small; P3 lower than the paracone of P4; without lingual cusp and with developed distal accessory cusp; parastyle of P4 sharp and highly developed compared to other Feliformia of the Oligocene; M1 reduced and stretched lingually, without cusps; M2 absent. Sagittal and lambdoid crests developed; auditory region derived from older Feliformia: developed auditory bulla, divided by a septum into two unequal parts consisting in particular of a bony ectotympanic and a highly developed caudal entotympanic, probably cartilaginous; antero-internal part of the petrosal forming a lamella pressing against the lateral face of the basicranium (see Hunt, 1998a for more details)".

This genus is considered as the base for two large lineages: the machairodontines (saber-toothed cats) and the extant felids, which include the subfamilies Felinae FISCHER DE WALDHEIM, 1817, and Pantherinae POCOCK, 1917. A simplified depiction of these clades (and some of their included genera) is demonstrated in Fig. 1.6, edited from Werdelin et al. (2010, fig. 2.2).

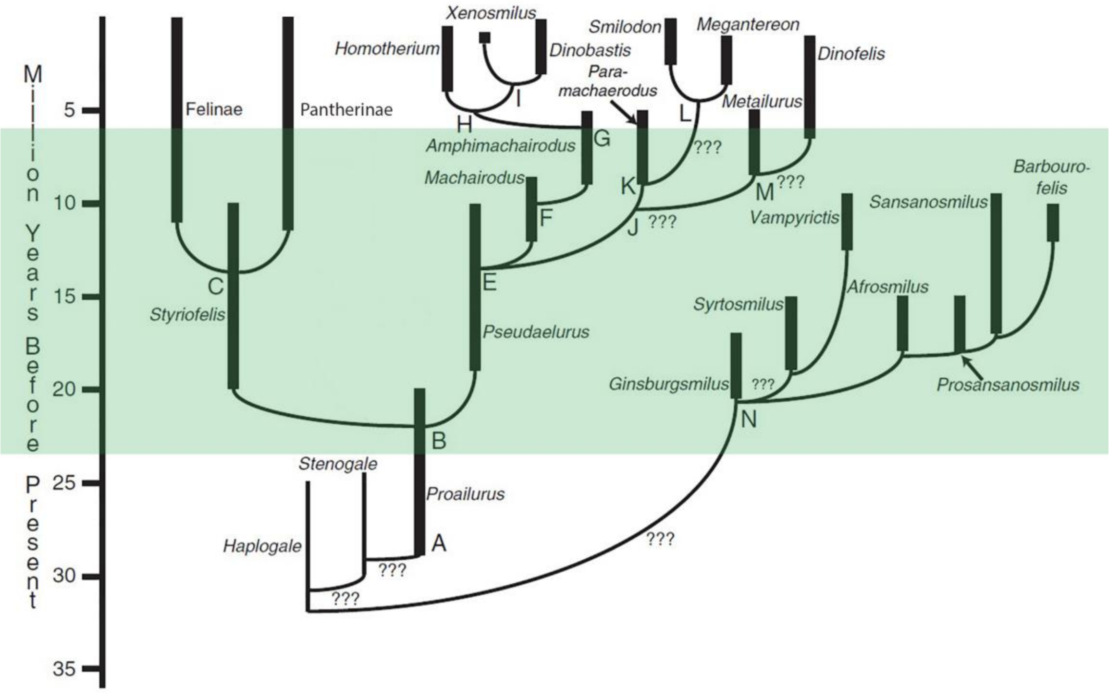

Fig. 1.6: Phylogeny of the family Felidae. Edited from: Werdelin et al. (2010). The nimravid clade was removed and the pantherine clade was added. The green transparent part represents the Miocene.

After the disappearance of *Proailurus* from the fossil record, the dominant felid in Europe and North America is *Pseudaelurus* GERVAIS, 1850. Traditionally, four European species of this genus were considered to be valid: *Pseudaelurus quadridentatus* (DE BLAINVILLE, 1843), *Pseudaelurus romieviensis* (ROMAN & VIRET, 1934), “*Pseudaelurus*” *turnauensis* (HOERNES, 1882) (including “*Pseudaelurus transitorius*” DEPÉRET, 1892) and “*Pseudaelurus*” *lorteti* GAILLARD, 1899. However, recent approaches placed the two latter species into the genus *Styriofelis* KRETZOI, 1929 (Werdelin et al., 2010; Turner et al., 2011; Salesa et al., 2012; Robles et al., 2013a). These two genera are considered the most basal taxa for the Machairodontinae and Felinae/Pantherinae lineages respectively (Figure 1.6).

More specifically, “*Styriofelis*” *lorteti* has been considered to be closer to the pantherines and it has been grouped with “*Felis*” *pamiri* OZANSOY, 1965, into the genus *Miopanthera* KRETZOI, 1938, by Geraads & Peigné (2017). An emended diagnosis for the genus *Miopanthera* has been provided by Geraads & Peigné (2017): “a feline ranging in size from that of a large caracal to that of a small leopard. Canines without grooves. Upper canines conical, moderately compressed. P4 with small protocone; M1 short but broad; p2 vestigial or absent; p3 low; m1 without metaconid, m2 absent”.

The stratigraphic range of *Pseudaelurus*, *Styriofelis* and *Miopanthera* spans from the late Early Miocene (MN 3; e.g. Wintershof-West; Dehm, 1950) until the early Late Miocene (MN 9; e.g. Rudabánya; Werdelin, 2005). Unfortunately, no recent diagnoses for *Pseudaelurus* or *Styriofelis* (the so-called “*Pseudaelurus*-grade”) have been published, even though they are the most characteristic representatives of the family during the Middle Miocene.

Fig. 1.7: *Styriofelis lorteti*. Source: chasingsabretooths.wordpress.com. Artist: M. Antón

A transitional form between the *Pseudaelurus*-grade and the derived sabertooths has been described from the Turkish localities of Yassiören (MN 9 or also possibly MN 7/8; Viranta & Werdelin, 2003) and Akçaköy as *Miomachairodus pseudaeluroides* SCHMIDT-KITTLER, 1976. The original diagnosis of this form is the following: "machairodontine of approximately the size of *Machairodus aphanistus,* with highly specialized saber C and *Pseudaelurus*-like premolars and molars; C with serrated mesial and distal cutting crests; C mesial cutting crest split into two edges; P4 protocone very large; P3 with high main cusp and diagonally oriented mesial and distal borders; P3 accessory cusp situated right on the lingual margin of the tooth; m1 with *Pseudaelurus*-like talonid; p3 slightly reduced". The presence of long, serrated upper canines is the most notable character that differentiates this form from the *Pseudaelurus*-grade.

The first derived, large-sized true sabertooth cat is *Machairodus aphanistus* (KAUP, 1832), which has been found in several localities of the Vallesian of Europe. Some of them include Eppelsheim (Kaup, 1832), Dorn-Dürkheim (Morlo, 1997), Höwenegg (de Beaumont, 1986), Can Llobateres, Can Ponsic (Crusafont Pairó & Kurtén, 1976), Batallones-1 (Antón et al., 2004) and Batallones-3 (Monescillo et al., 2014). A diagnosis for this form is provided by Antón et al. (2004): "A lion-sized extinct felid with small lower incisors arranged in a straight row, large lower canines with flattened roots and an oval cross section to the crown, a small diastema between the lower canine and p3, large lower premolars with a complete set of additional cusps and p3 large relative to p4, a well-developed metaconid-talonid complex on the lower carnassial, mandibular horizontal ramus thick and high, an undeveloped mandibular flange, coronoid process high and posteriorly inclined, relatively large upper incisors set in a shallow arc anterior to the upper canines, high-crowned and very flattened upper canines, P2 variably present, P3 with a very developed posterior expansion, an upper carnassial with a distinct protocone and preparastyle and all teeth probably serrated, a moderately convex dorsal profile of the skull, a well-developed sagittal crest, skull narrow in dorsal view across the zygoma, zygomatic arch low and gently curved in side view, temporal fossa elongated, paraoccipital process well-developed and projecting inferiorly beyond the relatively small mastoid process, nasofrontal suture intermediate between pantherine (pointed) and evolved machairdontine (straight) condition, postorbital processes large but low."

The species *Promegantereon ogygia* (Kaup, 1832) is the only member of its genus. It has been described from Eppelsheim (Kaup, 1832), Dorn-Dürkheim (Morlo, 1997), Batallones and Crevillente-2 (Salesa et al., 2010). Salesa et al. (2010) provided a diagnosis for this form as follows: “Machairodontinae of the size of a puma, Puma concolor. Dentition without crenulations. Premaxilla only slightly projected rostrally, with a nonprocumbent incisor arcade. Upper canines with a moderately inflated root, with smooth and laterally flattened crown; both mesial and distal borders of the crown show a soft ridge, more marked on the mesial side, which continues lingually at the base of the crown. P1, p1, and P2 are absent. The P3 is wide, with a marked disto-lingual expansion; it has a small distal cusp and a minute or absent mesial cusp. P4 without ectostyle and with a well-developed protocone, placed between the parastyle and paracone and buccally oriented. Lower canines very much reduced in comparison with the upper ones; p2 vestigial but present; p3 smaller than p4, without mesial cuspid and with a very much reduced distal cuspid; p4 with developed mesial and distal cuspids, the former located lingually and the latter buccally. Both p3 and p4 are wider distally than mesially. Lower carnassial with high paraconid and protoconid, the latter being higher than the former; the m1 shows a small talonid, and a tiny metaconid above it. Mandible with moderately verticalized symphysis and high coronoid process.”

The monospecific genus *Leptofelis vallesiensis* (SALESA et al., 2012a) is perhaps the oldest undoubtedly true feline, as it has been found in Batallones and Maragheh (Salesa et al., 2012a, 2019). A combined diagnosis for this form based on Salesa et al. (2012a, 2019) includes: “Feline intermediate in size between a wildcat and a serval; skull without postorbital processes of frontal and zygomatic; moderately inflated tympanic bullae; well-developed mastoid and paramastoid process, the latter being markedly caudally projected. Moderately developed upper and lower canines, the latter having a buccal vertical groove; absence of P2; presence of retained D1 and D2; P3 without mesial cusp, with a high main cusp, and a well-developed distal one; with lingual expansion of crown placed distally to the main cusp; P4 with a weak protocone, placed at the level of parastyle, well-developed paracone, small parastyle, and short metacone and metastyle; presence of ectostyle on P4 is variable; M1 buccolingually elongated, triangle shaped, and with clearly distinguished paracone and metacone. Mandibular symphysis curved in lateral view; the dorsal border of the coronoid process of the mandible is not sharp, as in most of the small felines, but flattened. Presence of a small premolar mesial to p3, probably a d2; p3 relatively high, with small mesial and distal cuspids; p4 larger than p3, with strong mesial and distal cuspids; m1 with paraconid slightly lower than protoconid, with a distally expanded talonid that may have a metaconid separated from the distal border of the protoconid by mean of a ridge. postcranial skeleton with a combination of primitive and derived features: humerus with a well proximally projected greater tubercle and an almost non-projected medial epicondyle; medial tubercle of the ulna well developed, markedly proximally projected, and surpassing the level of the lateral tubercle; slender Mc I, much less robust than those of middle Miocene felines such as *S. turnauensis* and *M. lorteti*; mediopalmar facet of the Mc IV base relatively less proximodistally expanded than in most felines; relatively short L7; dorsal sacral foramina absent; relatively proximodistally elongated femoral trochlea; relatively reduced attachment area for the m. quadratus plantae on the lateral face of the calcaneus; presence of a marked proximodistally developed ridge on the caudal face of the tibia.”

Another small feline, *Pristifelis attica* (WAGNER, 1857), has been described from Pikermi (Wagner, 1857; Roussiakis, 2002), Vathylakkos (Arambourg & Pivetau, 1929; Koufos, 2000), Samos (de Beaumont, 1961; Koufos et al., 2011) and Akkaşdaği (de Bonis, 2005). The diagnosis provided by Salesa et al. (2012a) for this form is the following: "Feline intermediate in size between a wildcat and a serval; skull elongated and with small postorbital processes of frontal and zygomatic; inflated tympanic bullae, with a marked ridge between ectotympanic and caudal entotympanic; well-developed mastoid process, and small paramastoid process, with a tiny caudal projection. Moderately developed upper and lower canines, both having buccal vertical groove; double-rooted P2, with a low crown; P3 without mesial cusp, with a high main cusp, and a well-developed distal one; with lingual expansion of crown placed distally to the main cusp; P4 with a weak protocone, placed at the level of parastyle, well-developed paracone, moderately developed parastyle, metacone and metastyle; presence of ectostyle on P4 is variable; M1 buccolingually elongated, triangle shaped, and with clearly distinguished paracone and metacone. Mandibular symphysis curved in lateral view; the dorsal border of the coronoid process of the mandible is not sharp, as in most of the small felines, but flattened. Absence of d1, d2 and p2; p3 relatively high, with small mesial and distal cuspids; p4 larger than p3, with strong mesial and distal cuspids; m1 with paraconid slightly lower than protoconid, without talonid, although a small distal lump may be present."

The genus *Metailurus* ZDANSKY, 1924, originally included two mainly Turolian (with rare Vallesian occurrences) species: the large-sized *Metailurus major* ZDANSKY, 1924 and the small-sized "*Metailurus parvulus*" (HENSEL, 1862) (=*Metailurus minor* ZDANSKY, 1924). These forms were very common in the Mediterranean region, found e.g. in Las Casiones, Hadjidimovo, Pikermi, Samos, Kerassia and Axios Valley (Kovatchev, 2001; Roussiakis et al., 2006; Koufos et al., 2011; Koufos, 2012a; Salesa et al., 2012b; Roussiakis et al., 2019). However, Spassov & Geraads (2015) reviewed the material of the small-sized "*Metailurus*", reporting the presence of a new form: *Yoshi garevskii* SPASSOV & GERAADS, 2015. These authors differentiated the new genus from *Metailurus* and suggested that the small-sized "*Metailurus parvulus*" should be included in *Yoshi*. However, they pointed out that the holotype of "*Metailurus parvulus*" was not diagnostic, so they considered this as a nomen dubium, suggesting that all the material attributed previously to this form should be included to *Yoshi garevskii* or to *Yoshi minor*. The diagnosis of *Yoshi* provided by Spassov & Geraads (2015) is the following: "A felid intermediate in size between a lynx, *Lynx* Kerr, 1772, and a cheetah, *Acinonyx* BROOKES, 1828. The skull is short, wide (rather cat-like in proportions), with a broad frontal area and a deep face; profile vaulted to strongly vaulted in the frontal region; rostral part short and broad; zygomatic processes of the frontal bones short and rounded; postorbital constriction weak, area of postorbital constriction short; frontal sinuses invading the whole bone, from the nasals to the parietals, as well as the zygomatic processes of the frontals; sagittal crest weak; median part of the nuchal crest concave in dorsal view. Upper canines short, without crenulations but with an anterior keel located mesially rather than mesio-lingually, lingual surface almost flat or slightly convex, buccal one slightly flattened to convex. P3 and p3 without distinct mesial accessory cuspid, m1 with distinct talonid. Symphysis of the mandible not elevated, without any mandibular flange". Additionally, a diagnosis of *Metailurus major* has been provided by Roussiakis (2001a): "*Metailurus* of large size, P3 relatively wide in front, with strong posterior accessory cusp, anterior accessory cusp smaller and situated slightly lingually; M1 relatively large”. However, this diagnosis mainly differentiates this form from *Yoshi*, so an emended diagnosis is considered vital for future studies. Another enigmatic member species of this lineage is *Metailurus boodon* BELYAEVA, 1948, from the Miocene locality of Grebeniki.

The genus *Paramachaerodus* PILGRIM, 1913, has been known with two species from Europe. The species *Paramachaerodus maximiliani* (ZDANSKY, 1924) has been found mainly in China, but also in the locality of Venta del Moro (Salesa et al., 2010). On the contrary, the species *Paramachaerodus orientalis* (KITTL, 1887) has been found in several localities in Europe, including Pikermi (Roussiakis et al., 2019), Dorn-Dürkheim (Morlo, 1997), Chobruchi, Taraklia (Lungu & Rzebik-Kowalska, 2011), Crevillente-15, Crevillent-16, Puente Minero and Concud (Salesa et al., 2010). A diagnosis for this genus is provided by Salesa et al. (2010): “Machairodontinae with moderately enlarged and laterally flattened upper canines, and reduced lower canines; presence of crenulations in the borders of both upper and lower canines. I1 and I2 smaller than I3, which has a caniniform crown; absence of P1, p1, P2 and p2; P3 with a mesiodistally elongated crown, a small or absent mesial cusp, and a well-developed distal one; P4 with a straight buccal border, a small ectostyle, a well-developed parastyle and a relatively reduced protocone, mesiolingually oriented; relatively reduced M1; p3 clearly smaller than p4; m1 with a very much reduced talonid, composed of a simple crest. Mandibular symphysis without flange, but clearly verticalized, with a flat and rough rostral surface. Relatively wide nasal bones. Moderately developed sagittal crest.”

The species *Stenailurus teilhardi* CRUSAFONT PAIRÓ & AGUIRRE, 1972, is the only member of its genus. It has been described only based on one partial skull from the Spanish Turolian of Piera (specifically in the “breach 1” near Torrentet dels Traginers). Some of the diagnostic features pointed out by these authors are: mesiodistally reduced premaxilla; cutting crests of the upper canines being diametrically opposed to the sagittal plane, without being oriented lingually (as in *Metailurus* or *Pseudaelurus*); the presence of faint serrations in the upper canine; the presence of P2; low and elongated P3 with a low distal rim; large, individualized and mesially situated P4 protocone.

Another scarcely known species is *Fortunictis acerensis* PONS-MOYÀ, 1987, which has been described based on some dental remains from the Spanish Turolian localities of Casa del Acero and El Arquillo de la Fontana. The diagnosis given by the author was: “Metailurini with very laterally compressed and curved upper canines; P3 without mesial cusp and elongated crown; P4 and lower premolars with transversely compressed and high cusps; m1 highly compressed, without metaconid, and with a long talonid with hypoconid.”

Finally, the last sabertooth of the Miocene of Europe is *Amphimachairodus giganteus* (Wagner, 1848). This was a larger species than *M. aphanistus* that was the dominant large felid during the Turolian in Europe. Recently, Geraads & Spassov (2021) argued that this species shall be included in the same genus as *M. aphanistus*, but several publications of the past decades follow the generic separation (Salsa et al., 2012b; Antón, 2013; Monescillo et al., 2014). This subject is still debatable, but in general, the two forms are considered to be closely related. *Amphimachairodus* *giganteus* has been found in Pikermi (Roussiakis, 2002), Samos (Koufos et al., 2011), Axios Valley (Koufos, 2012a), Las Casiones (Salesa et al., 2012b), Hadjidimovo (Geraads & Spassov, 2021) and Mt Luberon (Gaudry, 1873).

The transition to the Pliocene was critical for the extinction of all the aforementioned forms. The niche of the small-sized to large-sized felids was gradually covered by the typical Villafranchian cats, such as *Homotherium* Fabrini, 1890, *Megantereon* Croizet & Jobert, 1828, *Dinofelis* Zdansky, 1924, *Panthera* Oken, 1826, *Felis* Linnaeus, 1758, *Lynx* Kerr, 1792, *Acinonyx* Brookes, 1828, and *Puma* Jardine, 1834.

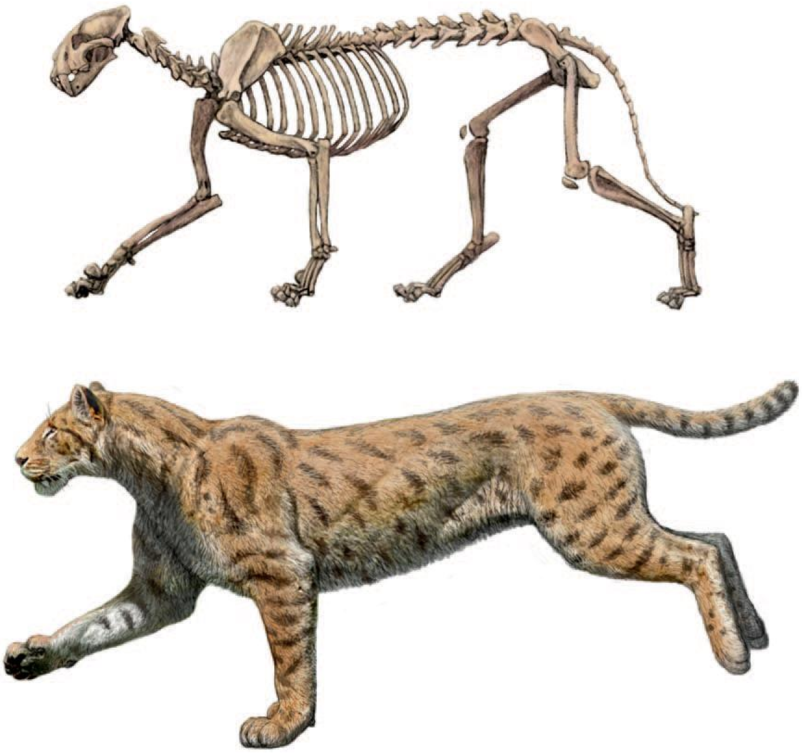

Fig. 1.8: *Machairodus aphanistus*. Source: Antón (2013). Artist: M. Antón.

Barbourofelidae SCHULTZ, SCHULTZ & MARTIN, 1970

The family Barbourofelidae includes extinct (usually large-sized) feliforms with sabertooth adaptations. Its fossil record is restricted in the Miocene, including rare occurrences in Europe, Asia, Africa and North America. From the first report of this group, made by de Blainville (1843) for "*Felis palmidens*", now called *Sansanosmilus palmidens* (DE BLAINVILLE, 1843), the taxonomy of this group has been controversial. However, recent overviews have now established its monophyly, its close affinities with the felids and its separation from the nimravids (Geraads & Güleç, 1997; Morales et al., 2001; Morlo et al., 2004; Morlo, 2006; Antón, 2013; Robles et al., 2013b).

Morlo et al. (2004) provided an emended diagnosis for the family: "Barbourofelidae are distinguished by the following: loss of P1/, M2/, P/1 and M/2; plesiomorphic tooth formula 3131/3131; apomorphic species additionally lose P2/ and P/2; scimitar-like sabreteeth with crenulations on, at least, the posterior border of upper canines; upper canines markedly compressed with vertical grooves present; strong relationships between the eruption of the upper canines and the development of other sabretooth features, especially the mandibular flange (see Peigné & de Bonis, 2003); no anterior cusp on P/3, but distinct and sometimes large posterior accessory cusp on P/3-4; protoconid of M/1 relatively tall (at least in early taxa); talonid of M/1 extremely reduced, and markedly more so than the metaconid; reduction of the talonid before the metaconid on M/1; angular chin on mandible (genial flange in the apomorphic genera) and slightly (*Afrosmilus turkanae*) to strongly (other taxa) curved mandibular body; short horizontal proseptum in the anteromedial corner of the auditory bulla; early and complete fusion of elements making up the bulla. In addition to those features, the Barbourofelidae differ from the Nimravidae (primitive taxa) by the following: fully ossified bulla invading the mastoid; thin wall of the caudal entotympanic, not composed of three layers as in Nimravidae; petrosal not deeply recessed in the basicranium; absence of the postglenoid foramen; presence of a parastyle on P4/; protocone on P4/ located further back; bulla more anteriorly located (than in the most primitive felid genera such as *Proailurus* and *Pseudaelurus*) and consequently a more anteriorly placed foramen ovale which is close to the posterior opening of the alisphenoid canal (except *Barbourofelis*); a shortened palate; lateral walls of the nasopharynx converging posteriorly; broad metacarpals (known from *Sansanosmilus palmidens* and *Barbourofelis fricki* only). "

Two major clades (interpreted as tribes) are recognized today: Afrosmilini MORALES et al., 2001, and Barbourofelini SCHULTZ, SCHULTZ & MARTIN, 1970 (Robles et al., 2013b). The former group includes the genera *Prosansanosmilus* HEIZMANN et al., 1980 (Early and Middle Miocene of Europe) and *Afrosmilus* KRETZOI, 1929 (Early Miocene of Africa and Spain). The latter includes *Sansanosmilus* KRETZOI, 1929 (Middle and Late Miocene of Eurasia), *Albanosmilus* KRETZOI, 1929 (Middle and Late Miocene of Europe, Asia and North America) and *Barbourofelis* SCHULTZ, SCHULTZ & MARTIN, 1970 (Middle and Late Miocene of North America and Anatolia). The positions of *Ginsburgsmilus* MORALES et al., 2001 (Early Miocene of Africa), *Syrtosmilus* GINSBURG, 1978 (Early Miocene of Africa) and *Vampyrictis* KURTÉN, 1976 (Late Miocene of Africa) remain uncertain, due to lack of phylogenetically informative material. Therefore, the European record of barbourofelids includes the genera *Prosansanosmilus*, *Afrosmilus*, *Sansanosmilus* and *Albanosmilus*, while *Barbourofelis* has been reported in the neighboring Anatolia.

The genus *Prosansanosmilus* includes the species *Prosansanosmilus peregrinus* HEIZMANN et al., 1980 (from the MN 4 and MN 5 of Langenau 1, Petersbuch 2, Baigneux, Artenay, Channay-sur-Lathan and Bézian; Heizmann et al., 1980; Ginsburg & Bulot, 1982; Ginsburg, 1999; NOW, 2021) and *Prosansanosmilus eggeri* MORLO et al., 2004 (from the MN 5 of Sandelzhausen; Morlo et al., 2004). Morlo et al. (2004) provided an emended diagnosis for the genus: “Relatively short genial flange, well developed P/3 presenting a clear posterior cingulid, relative to *Ginsburgsmilus* and *Afrosmilus* large posterior accessory cusp on P/4, small preparastyle and well developed protocone on P4/, and P/2 vestigial or absent.”

The genus *Afrosmilus* has only been described based on the species *Afrosmilus hispanicus* MORALES et al., 2001 from the Spanish localities of Artesilla and Buñol (MN 4). The diagnosis given by the authors for this genus is: “Barbourofelines in which P4 tends to have a reduced protocone, some species with incipient ectostyle, P3 elongated, with strong reduction of the antero-lingual expansion, m1 with talonid present. Mandibular symphysis sub-quadrate, moderately well developed.”

The only European representative of the genus *Albanosmilus* is *Albanosmilus jourdani* (FILHOL, 1883). This is the most common barbourofelid in Europe. It has been found in several localities between MN 6 and MN 9, including Arroyo del Val, Can Llobateres, Höwenegg, Atzelsdorf (as “*Sansanosmilus vallesiensis*”), La Grive-Saint Alban and Rudabánya (Viret, 1951; de Beaumont, 1986; Fraile et al., 1997; Werdelin, 2005; Nagel, 2009; Alba et al., 2011; Robles et al., 2013b). Robles et al. (2013b) provided an emended diagnosis for this species: “Mid-sized barbourofelin with dental formula 3I1C2P1M/3I1C2P1M. Brachycephalic cranium with short and broad muzzle. Palate broadest at the level of P4. Broad and robust zygomatic arches. Orbital closure with complete postorbital bars. Large infraorbital foramen above P3. Large postcanine fossa. High sagittal crest and robust occipital crests. Large frontal sinus. Mastoid process located at the level of the inflated bullae. Comma-shaped condylar foramen under the occipital condyle. Foramen ovale situated next to the foramen rotundum at the base of the bulla, close to the well-developed retroarticular process. Auditory bulla invading the mastoid. Shallow and long mandible, with a very high and verticalized symphysis. Sinuous and high mandibular corpus (highest at the level of p4), with a shallow, large and a U-shaped genial flange at the level of the postcanine diastema (only well developed in adults). Two mental foramina on the upper part of the flange. Posteriorly curved angular process. Posteriorly directed condyloid process that does not surpass the alveolar level. Slightly lingually curved coronoid process. Very deep masseteric fossa. Dentition characterized by sabre-like upper canines, with mesial and distal crenulated borders, and labial and lingual vertical grooves, as well as incisor-like lower canines. Labiolingually compressed cheek-teeth with crenulated borders. Tetracuspid P3. P4 with preparastyle and without protocone, with two main roots and a variously developed or fused vestigial mesiolabial root. M1 vestigial and partially hidden by P4. All lower teeth distolingually oriented relative to the mandibular corpus. Reduced p3 with two fused roots or a single root. Tetracuspid p4. m1 with two main asymmetric cusps and without metaconid.”

The second species, *Barbourofelis piveteaui* (OZANSOY, 1965), has been found in Kalfa (MN 10; Lungu, 1978) and the Anatolian locality of Yassiören (Middle Sinap, MN 9; Ozansoy, 1964; Geraads & Güleç, 1997). Geraads & Güleç (1997) provided an emended diagnosis for this species: “A species of *Barbourofelis* of medium size, comparable to that of *B. morrisi*. Maxilla very deep vertically, anterior root of zygomatic arch deeply excavated for masseter insertion; blade of P4 very long and high; M1 much reduced, largely hidden by P4 in labial view; mandibular symphysis thin, with deep and low genial fossa; p3 sometimes absent.”

Finally, the genus *Sansanosmilus* includes only its type species, *Sansanosmilus palmidens* (DE BLAINVILLE, 1843), which has been reported from Savigné-sur-Lathan (MN 5; Ginsburg, 2001) and Sansan (MN6; de Blainville, 1843; Filhol, 1890; Ginsburg, 1961a; Peigné, 2012). It is notable that Chen & Wu (1976) report this species from Jiulongkou in China.

Fig. 1.9: *Sansanosmilus palmidens*. Source: Antón (2013). Artist: M. Antón.

Prionodontidae HORSFIELD, 1822

The family Prionodontidae HORSFIELD, 1822, consists of a very small group that is today represented by two species of the genus *Prionodon* HORSFIELD, 1822. This is a small-sized feliform that lives in Southeast Asia (Jennings & Veron, 2015). No fossil representatives of this genus have been found. However, the fossil genus *Palaeoprionodon* FILHOL, 1880, has been considered as being very close to *Prionodon* and possibly belong to the Prionodontidae (Gaubert & Veron, 2003). This genus has also been attributed to the family Stenoplesictidae SCHLOSSER, 1923 (see below). It has been described only from the Oligocene of France and with a possible specimen from Mongolia (Filhol, 1880; Karl et al., 2007). Therefore, no Miocene representatives of this group have been found in Europe or anywhere else.

Fig. 1.10: *Prionodon linsang*. Source: flickr.dot.

Eupleridae CHENU, 1850

This family includes 10 species divided in seven genera, all of them being small- to medium-sized and endemic to Madagascar (also named Malagasy carnivorans) (e.g. Veron & Goodman, 2018). Impressively, no fossil members of the family have been found up to now. The only sub-fossil species is the subfossil *Cryptoprocta spelaea* GRANDIDIER, 1902, which got extinct approximately 2000 years ago (Meador et al., 2019 and references therein). Therefore, no representatives of this family are present in the Miocene of Europe or anywhere else.

Fig. 1.11: *Cryptoprocta ferox*. Source: dreamstime.com.

Herpestidae BONAPARTE, 1845

Today, this family is relatively diverse, including 34 species (divided in 14 genera) os small-sized carnivorans that live in Africa and Asia (e.g. Patou et al., 2009). However, the fossil record of this family is relatively scarce, probably because of the small size and the fragility of its skeletal elements. Though, a fossil herpestid genus has been present in the Miocene of Europe. The genus *Leptoplesictis* FORSYTH MAJOR, 1903 is represented by three species: *Leptoplesictis aurelianensis* (SCHLOSSER, 1888) (Pontlevoy, Petersbuch 2 and Hostalets de Pierola), *Leptoplesictis atavus* DE BEAUMONT, 1973a (Vieux-Collonges and Sansan) and *Leptoplesictis filholi* (GAILLARD, 1899) (La Grive-Saint Alban and Stein am Rhein; type species), (Roth, 1988; Ginsburg, 1999; Grohé et al., 2020). The diagnosis of the genus based on Werdelin & Peigné (2010) and Grohé et al. (2020) is: Small-sized carnivoran; dental formula (lower dentition only) I 3, C 1, P 4, M 2; premolars with tall cusps; p4 posterior accessory cusp very large; m1 postvallid notch less deep than in Herpestes; m2 trigonid and talonid distinct.

Roth (1988) provided diagnoses for all three species (translated from German):

Leptoplesictis aurelianensis: “Viverrid of the size of *Herpestes sanguineus* (Rüppell, 1835). Lowe carnassial with sharp-edged trigonid cuspids, protoconid with triangular base, metaconid small, on a rounded base, without front ridge; entoconid flat. The m2 is single-rooted with almost circular alveolus, crown circumference elongated-oval, crown with strong relief, protoconid high; talonid shallow, the rear margin smooth and without points. The p4 with strong distal accessory cuspid on a rounded base; Edges of the main cuspid sharp-edged, mesial accessory cuspid smaller than in *L. filholi* with a short, slightly sloping cutting edge and a lingual, steeply sloping rounded ridge. The p3 as p3, features only weaker and less prominent distal accessory cuspid.”

Leptoplesictis filholi: “The m2 alveolus with fused roots, tooth crown longer than at *L. aurelianensis*. Protoconid of m1 in relation to metaconid and paraconid higher than in *L. aurelianensis*; Metaconid bent somewhat distally and slightly curved backwards. Mesial accessory tip of the p4 stronger and higher than in *L. aurelianensis* with an additional basal cingulum in front. The p3 is the smaller version of the p4. The lower carnassial with a narrow, triangular outline, length short, wide mesially and distally.”

Leptoplesictis atavus: “The m1metaconid is straight and further forward than in *L. aurelianensis* and *L. filholi*, not visible from buccal view; the two talonid cuspids are higher than in *L. aurelianensis* and *L. filholi*; Hypoconid strong with a pronounced rear edge, clearly separated from the remaining talonid margin; Talonid distal margin flat; Trigonid wider and shorter in relation to the talonid than in *L. aurelianensis* and *L. filholi*. The m2 alveolus elongated-oval. The m1 is plumper than that of *L. filholi*, narrower mesially and distally, paraconid and metaconid with a broader base than that of *L. filholi*.”

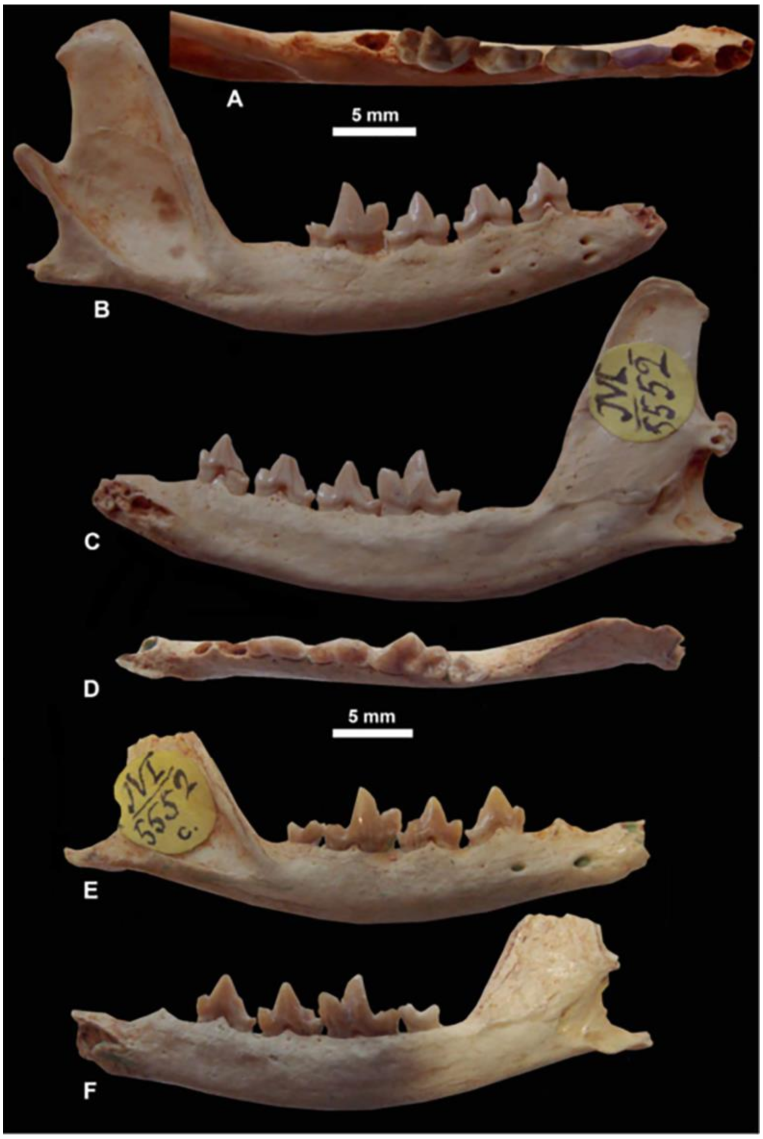

Fig. 1.12: *Leptoplesictis filholi* from La Grive-Saint Alban. Source: Morales & Pickford (2021).

Hyaenidae GRAY, 1821

Today the family Hyaenidae includes only four species, but during the Miocene members of this group covered a very wide range of different niches. Specifically, the Miocene has been considered as the period during which the hyenas originated, diversified and dominated throughout the Old World (Werdelin, 1991; Werdelin & Solounias, 1991; Turner et al., 2008). Unfortunately, despite the important progress that has been made in the study of fossil hyenas during the past decades, the taxonomic status of many genera/species is doubtful. The absence of diagnoses, the existence of many taxonomic names and the (usually) restricted nature of many type specimens have created a problematic image. However, a rough synopsis of our current knowledge concerning the Miocene hyenas will be attempted here. The following pages are based mostly on Werdelin & Solounias (1991), Ginsburg (1999), Semenov (2008) and Turner et al. (2008), but also in Viranta & Werdelin (2003), Kaya et al. (2005) and Koufos (2012b).

The most basal hyaenid genus is *Protictitherium* KRETZOI, 1938. Six well-defined species of this genus are known, including a doubtful one. The type species, *Protictitherium crassum* (DEPÉRET, 1892) is known from several Miocene localities such as La Grive-Saint Alban (type locality), Montredon, Can Llobateres, Hostalets de Pierola Inferior, Dorn-Dürkheim, Eppelsheim, Kalfa and several others. However, no diagnosis is known. *Protictitherium llopisi* (CRUSAFONT PAIRÓ & PETTER, 1969) from Can Bayona (Spain) was considered as a synonym of *P. crassum*, but Werdelin & Solounias (1991) suggested that it should be considered as a separate species. Another well-known species is *Protictitherium gaillardi* (FORSYTH MAJOR, 1903), which is known from La Grive-Saint Alban (type locality), Vieux-Collonges, Pontlevoy, Can Llobateres, Can Ponsic, Castell de Barberà, Hostalets de Pierola etc. Again, no diagnosis is known. The species *Protictitherium intermedium* SCHMIDT-KITTLER, 1976, *Protictitherium cingulatum* SCHMIDT-KITTLER, 1976, and *Protictitherium aegaeum* KAYA, GERAADS & TUNA, 2005, have been described from Anatolia, whereas *Protictitherium thessalonikensis* KOUFOS, 2012b, has been described from Greece. The diagnoses of these four species are given below.

Protictitherium intermedium: “Intermediate between *Plioviverrops gervaisi* and *Protictitherium gaillardi* in terms of size and morphology; m1 talonid/trigonid length comparable to that of *P. gaillardi*, but slightly higher; m1 metaconid as high as the paraconid and lingually bent; m1 entoconid lower than in *P. gervaisi*; m1 mesial root larger than the distal root” (translated from German from Schmidt-Kittler, 1976).

Protictitherium cingulatum: “Slightly smaller than *Protictitherium gaillardi*; m1 with longer talonid and lower trigonid than in *P. gaillardi* and *P. crassum*; m1 metaconid and entoconid strong; p4 as in *P. crassum* with a very strong mesial accessory cuspid; m1, p4 and mostly also p3 with a strong buccal cingulum” (translated from German from Schmidt-Kittler, 1976).

Protictitherium aegaeum: “A species of *Protictitherium* of large size; P3 narrow, mesial cusp on slightly shifted lingually; P4 with large protocone; upper molars large, with crescent-shape protocone, mesio-buccal angle much expanded; p4 with strong mesial cuspid, main cuspid very high; m1 with high trigonid, paraconid almost as high as the protoconid, metaconid high, talonid long, with entoconid the highest cuspid; m2 large, with high metaconid; differs mainly from the closely related *P. crassum* by its high p4, very high trigonid of m1 with paraconid almost as high as protoconid" from Kaya et al. (2005).

Protictitherium thessalonikensis: "Small size; low cusps(-ids) in the teeth; protocone of the P4 in line with the mesial border of the parastyle; large molars, especially M2; slight buccal projection of the paracone in the M1; strongly molarized p4; strong metaconid and large talonid with high entoconid in the m1." from Koufos (2012b).


Fig. 1.13: Skeleton and skull of *Protictitherium crassum* from Batallones-1. Source: Fraile (2017).

The second small-sized basal hyaenid genus is *Plioviverrops* KRETZOI, 1938, which is known from 5 species. The type species, *Plioviverrops orbignyi* (GAUDRY & LARTET, 1856) is known from several Turolian localities, such as Pikermi, Samos, Perivolaki and Los Aljezares. *Plioviverrops gervaisi* DE BEAUMONT & MEIN, 1972 and *Plioviverrops gaudryi* DE BEAUMONT & MEIN, 1972 were described based on material from Vieux-Collonges and La Grive-Saint Alban respectively, but some authors have suggested that they could represent the same form (Werdelin & Solounias, 1991). The species *Plioviverrops guerini* (VILLALTA COMELLA & CRUSAFONT PAIRÓ, 1945a) is known from Crevillente, Los Mansuetos, Concud and other Spanish localities. Finally, *Plioviverrops faventinus* TORRE, 1989, is known from Monticino in Italy.

The genus *Thalassictis* GERVAIS, 1850, EX VON NORDMANN, is the oldest true ictithere genus. The ictitheres constitute of a group of hyenas that occupied the ecological niche of canids during the Miocene. This genus (as nearly all the fossil hyenas) is in need of a revision. However, the current point of view distinguishes six species of this genus: *Thalassictis robusta* GERVAIS, 1850, EX VON NORDMANN (based on material from Kishinev), *Thalassictis certa* (FORSYTH MAJOR, 1903) (based on material from La Grive-Saint Alban), *Thalassictis montadai* (VILLALTA COMELLA &

CRUSAFONT PAIRÓ, 1943a) (based on material from Hostalets de Pierola), *Thalassictis proava* (PILGRIM, 1910) (based on material from Chinji, Pakistan), *Thalassictis sarmatica* (PAVLOW, 1908) (based on material from Kishinev) and *Thalassictis spelaea* (SEMENOV, 1988) (based on material from Gritsev). The latter is considered as a species of *Ictitherium* WAGNER, 1848 by Semenov (1988, 1989, 2008).

The genus *Ictitherium* WAGNER, 1848, includes two species: the type species *Ictitherium viverrinum*, ROTH & WAGNER, 1854 (smaller; very common in the Turolian; Pikermi, Samos, Montredon, Grebeniki, Chobruchi, Titov Veles and many Chinese localities) and *Ictitherium pannonicum* KRETZOI, 1952 (larger; mostly present in northeastern Europe; Polgardi, Chobruchi etc. with possible occurrences in the south like in Valdecebro and Kerassia).

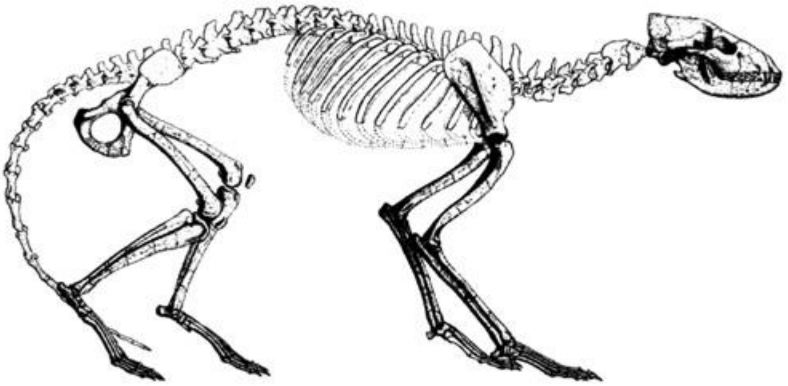

Fig. 1.14: Skeleton and skull of *Ictitherium viverrinum* from Pikermi. Source: Gaudry (1862–1867).

The contents of the genus *Hyaenictitherium* KRETZOI, 1938, have not been resolved. Semenov (1989, 2008), followed by several scholars, splits this genus in two, attributing some forms to the new genus *Hyaenotherium* SEMENOV, 1989. On the other hand, erection of taxonomic groups in non-peer-reviewed manuscripts are not considered valid, even more if the diagnoses and descriptions are not in English. The most common species is *Hyaenictitherium* (*Hyaenotherium*) *wongii* (ZDANSKY, 1924), which is present in several Turolian localities (Samos, Pikermi, Axios Valley, Grebeniki, Kemiklitepe, Maragheh etc.). However, based on the approach of Semenov (1989, 2008) there are three more species present in the Miocene of Europe: *Hyaenictitherium* (*Hyaenotherium*) *magnum* SEMENOV, 1989 (from Cherevichnoe and Maragheh), *Hyaenictitherium* (*Hyaenotherium*) *hyaenoides orlovi* SEMENOV, 1989 (from Kalmakpay) and *Hyaenictitherium venator* SEMENOV, 1989 (from Novoelisavetovka, Pavlodar, Taraklia and Tydurovo). A more comprehensive review of the material is considered vital for the clarification of this groups' taxonomy.

The species *Miohyaenotherium bessarabicum* SEMENOV, 1989, is the only species of its genus. It was described by Semenov (1989) based on material from Belka (Ukraine).

The only European species of *Lycyaena* HENSEL, 1862 is *Lycyaena chaeretis* (GAUDRY, 1861). This form is known from several localities, such as Pikermi, Samos, El Arquillo and Taraklia. Together with the following two genera, they constitute of cursorial/transitional forms in terms of ecology.

The genus *Hyaenictis* GAUDRY, 1861, includes two species in Europe: *Hyaenictis graeca* GAUDRY, 1861 (type species; found only in Pikermi) and *Hyaenictis almerai* VILLALTA COMELLA & CRUSAFONT PAIRÓ, 1948 (found only in Sant Miquel de Toudell and Ronda Oest Sabadell Sector D). Therefore, this is a very rare Turolian genus. A translation of the diagnosis of *H. almerai* was given in Vinuesa et al. (2017) as: "Relatively evolved *Hyaenictis*, having lost the p1, diastema very reduced; relatively robust mandible; shortened face, and canine in a more vertical position; m1 without metaconid; p2 long, slightly pointed and with a developed anterior cusp".

The only Miocene species of the genus *Chasmaporthetes* HAY, 1821, is *Chasmaporthetes bonisi* KOUFOS, 1987, described based on material from Dytiko (Greece). The diagnosis of Koufos (1987) for this species is: "Curved and shallow horizontal mandibular ramus; double mental foramen; curved and imbricated toothrow; oval posterior border in the premolars; more robust premolars than the known species of *Chasmaporthetes*; p1 present; very rudimentary or absent anterior accessory cusp in p2; no anterior accessory cusp in p3; no metaconid in m1; small and bicuspid talonid of m1 with reduced entoconid". The validity of this form was doubted by Werdelin & Solounias (1991), but it was re-established in Turner et al. (2008) retaining doubts only for the type specimen.

The rare genus *Allohyaena* KRETZOI, 1938 includes two species: *Allohyaena kadici* KRETZOI, 1938 (Csakvar, MN 10; Dorn-Dürkheim, MN 11) and *Allohyaena sarmatica* SEMENOV, 1994 (Gritsev, MN 9). It has been considered as closely related to the percrocutids (e.g. Semenov, 1994). The diagnosis of the genus based on Werdelin & Kurtén (1999) is the following: "Very large Hyaenidae; p2–3/P2–3 elongate, compressed, low crowned; P3 two- or three-rooted, with small lingual cusp; P4 large and massive with elongate blade, strong, medially directed protocone and well developed preparastyle; p4 short and broad with large anterior cusp; ml relatively short, broad, with high-crowned trigonid and short, broad talonid without distinct cusps, metaconid present but confluent with protoconid; small m2 present; dp4 with tall metaconid closely attached to posterolingual side of protoconid, tall, posteriorly situated entoconid, very low hypoconid and hypoconulid".

The species *Metahyaena confector* VIRANTA & WERDELIN, 2003 (the only species of the genus) was described based on material from Sinap (Turkey). This genus is characterized by narrow premolars with convex mesial faces in their main cuspids.

The species *Belbus beaumonti* (QIU, 1987) is the only species of its genus. It has been found only in Samos (Greece) and Çobanpinar (Turkey). The affinities of this genus are controversial, as some scholars place it in the Hyaenidae, while other place it in Percrocutidae.

Finally, the species *Adcrocuta eximia* (ROTH & WAGNER, 1854) (the only species of the genus) is the oldest crocutoid hyena. Its first appearance is in Xirochori (late Vallesian) and it dominates the Greco-Iranian and Chinese localities during the Turolian.

Fig. 1.15: Complete skeleton of *Adcrocuta eximia* from Hadjidimovo published by Kovachev (2012). Source: commons.wikimedia.org.

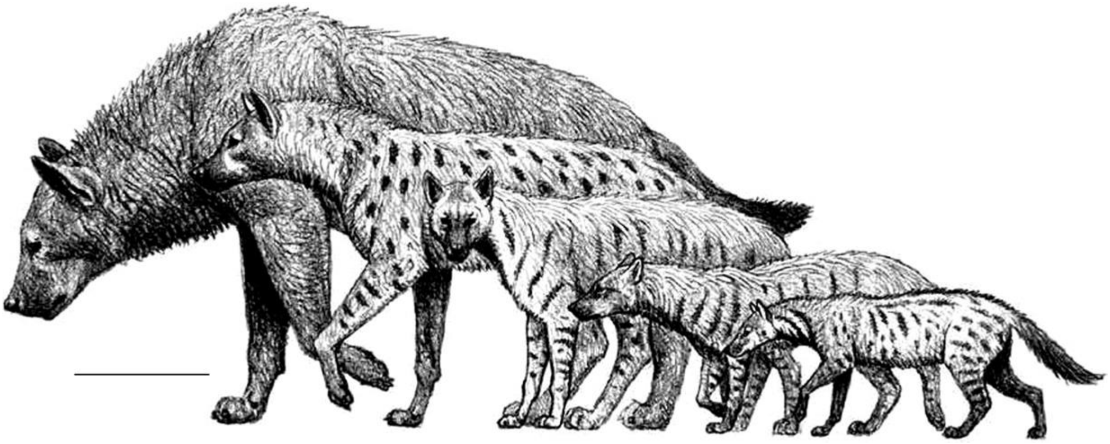

Fig. 1.16: Late Miocene hyaenids: *Adcrocuta eximia*, *Hyaenictitherium wongii*, *Ictitherium viverrinum*, *Protictitherium crassum* and *Plioviverrops orbignyi*. Source: Turner et al. (2008). Artist: M. Antón.

Percrocutidae Werdelin & Solounias, 1991

The family Percrocutidae WERDELIN & SOLOUNIAS, 1991, includes extinct, large-sized bone-crushing hyenas from the Miocene of Old World. The relationships of this group to the family Hyaenidae *sensu stricto* have been discussed above. For the purposes of the present study, this group is here analyzed separately.

Only two genera of percrocutids have been widely accepted today: *Percrocuta* KRETZOI, 1938 and *Dinocrocuta* SCHMIDT-KITTLER, 1976. The genera *Allohyaena* Kretzoi, 1938, and *Belbus* WERDELIN & SOLOUNIAS, 1991, have also been added to this family (Werdelin & Solounias, 1991), but further studies re-included it to the hyaenids (Turner et al., 2008; Coca-Ortega & Pérez-Claros, 2019, 2020).

Based on the reviews of Howell & Petter (1985) and Radović et al. (2021), the genus *Percrocuta* has been found mainly in the Middle Miocene of Eurasia, whereas its African record is extended into the base of the Late Miocene. Only two species have been found in Europe: *Percrocuta miocenica* (PAVLOVIĆ & THENIUS, 1965) (Serravalian of Balkans and Anatolia) and *Percrocuta abessalomi* (GABUNIA, 1973) (Langhian of Georgia). Radović et al. (2021) provided an emended diagnosis for the genus *Percrocuta*: “Percrocutids of relatively small size. Last molars (M2/m2) lost; m1 lacking a metaconid or with a vestigial metaconid; tendency toward shortening of the talonid and elongation of the trigonid, accentuated in more derived representatives; P3 with or without an internal root; P4 with a reduced protocone, situated more or less posterior to the anterior margin of the parastyle; p2 and p3 short (relative to p4 and m1) and broad with high robusticity indices”. They also provided a diagnosis for *P. miocenica*: “Strong, robust mandible, with a deep and large masseteric fossa, and strong masseteric crests. Strong canine, absent p1. Primitive-looking premolars, showing p2 < p3 < p4 size sequence. Relatively long m1, with a very reduced metaconid and short talonid with only a single, laterally extended cusp”.

In contrast to the limited occurrences of *Percrocuta* in the fossil record of Europe and Anatolia, the genus *Dinocrocuta* has been found in more abundance. In Europe and Anatolia, this genus has been described based on the following forms*: Dinocrocuta gigantea* (SCHLOSSER, 1903) (Balkans and Moldova), *Dinocrocuta robusta* (LUNGU, 1978) (Moldova), *Dinocrocuta senyureki* (OZANSOY, 1957) (Anatolia), *Dinocrocuta minor* (OZANSOY, 1965) (Anatolia) and *Dinocrocuta salonicae* (Andrews, 1918) (Greece). Outside Europe and Anatolia, this genus has been found in India (with the species *Dinocrocuta grandis* (KURTÉN, 1957)), in Algeria (with the species *Dinocrocuta algeriensis* (ARAMBOURG, 1959)) and in China and Mongolia (as *D. gigantea*). All these appearances correspond to Vallesian and early-middle Turolian faunas. The species *D. senyureki* has been tentatively reported (as. “*Percrocuta* aff. *senyureki*”) in Sahabi, based on a fragmentary right mandible and a P2 (Howell, 1987, fig. 4). If this attribution is correct, this would be the last appearance of *Percrocuta* (and the family Percrocutidae in general) in the fossil record. However, it is herein considered that this material is very fragmentary to be securely identified as a percrocutid. Its large size differentiates it from *A. eximia* (which has also been reported in the locality), but this is not enough to identify it in a generic level. Therefore, it is here suggested to refer to this form as “Hyaenidae indet.” and to restrict the stratigraphical range of *Percrocuta* in the Vallesian and early Turolian.

Fig. 1.17: Skull of *Dinocrocuta gigantea* from Fugu, Shaanxi. Source: Xiong (2019).

Fig. 1.18: *Dinocrocuta* hunting *Hipparion*. Source: sciencephoto.com. Artist: M. Witton.

Lophocyonidae FEJFAR, SCHMIDT-KITTLER & ZACHAROV, 1987

The family Lophocyonidae FEJFAR, SCHMIDT-KITTLER & ZACHAROV, 1987, includes four genera that range through the Early and Middle Miocene of Europe and Anatolia. The diagnosis of the family based on Morales et al. (2019b) is: “Feliformia with dental formula (permanent teeth) 3142/3142; large molars, the upper molars exhibiting dilambdodont morphology, lower molars lophodont with height of the talonid as well developed as that of the trigonid; molarized premolars, incipient in primitive forms, p4 always with metaconid and P3 with metacone; in the most derived forms the dentition is hypsodont and the molarization affects all of the anterior premolars”.

The genus *Sivanasua* PILGRIM, 1932 includes the species *Sivanasua viverroides* (SCHLOSSER, 1916) from Rothenstein 1 (Germany), Chêne de Navère and Pellecahus (France); and *Sivanasua moravica* FEJFAR & SCHMIDT-KITTLER, 1984 from Dolnice (Czech Republic) and La Grive-Saint Alban (France).

The genus *Euboictis* FEJFAR & SCHMIDT-KITTLER, 1984 only includes the species *Euboictis aliverensis* SCHMIDT-KITTLER, 1983 from the locality of Aliveri (Euboea, Greece).

The genus *Lophocyon* FEJFAR, SCHMIDT-KITTLER & ZACHAROV, 1987, includes *Lophocyon carpathicus* FEJFAR, SCHMIDT-KITTLER & ZACHAROV, 1987, from Košice-Bankov (MN 7/8; Slovakia) and *Lophocyon paraskevaidisi* KOUFOS, DE BONIS & SEN, 1995 from Thymiana (Chios, Greece). The diagnosis for the latter species based on Koufos et al. (1995) includes: “*Lophocyon* with strongly projected metastyle and shallow groove between the metastyle and parastyle of P3 and P4; protocone of P3 and P4 without lingual basal cingulum; across the mesial border of P3 and P4 there is a developed shelf between the protocone and the parastyle consisted of small cuspids; the lower teeth are high crowned, the premolars are molarized, with wide talonid; m2 with strong hypoconulid situated far backwards”.

Finally, the genus *Izmirictis* MORALES et al., 2019b, includes only *Izmirictis cani* MORALES et al., 2019b from the locality of Sabuncubeli (MN 3) in Turkey. The diagnosis for the species and genus includes: “Lophocyonid with moderately lophodont lower molars, m1 talonid cuspids high and well differentiated; M1 with paracone and metacone in buccal position and strong lingual cingulum; P4 with conservative carnassial morphology; anterior premolars (P3 and p4) robust and moderately molarized”. It is considered the most basal lophocyonid.

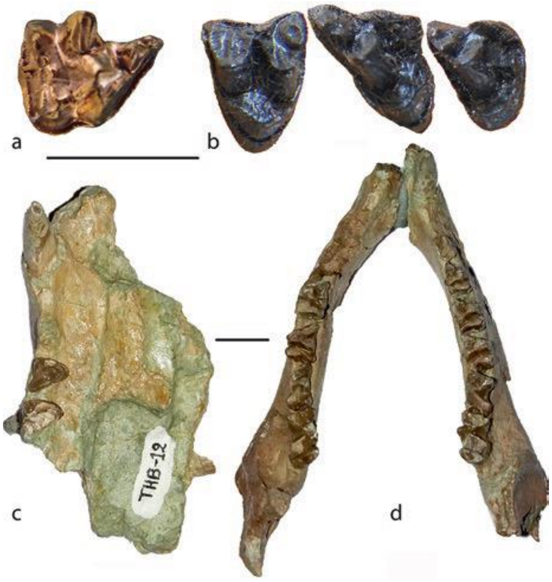

Fig. 1.19: Lophocyonidae from Greece: (a–b) *Euboictis aliverensis* and (c–d) *Lophocyon paraskevaidisi*. Source: Koufos (2021).

Viverridae GRAY, 1821

The family Viverridae GRAY, 1987, includes small- to medium-sized feliforms that today inhabit Africa and Southeastern Asia. However, the fossil record of the family includes some representatives in the Miocene of Europe. Several groups have been attributed to this family, but are now considered to be distinct. Semenov (1989) (also following the traditional approach of Gaudry, 1862–1867) considered the ictitheres to belong to the viverrids, whereas they are now considered to belong to the Hyaenidae (e.g. Turner et al., 2008). The traditional sense of the family (e.g. sensu Simpson, 1945) included also the Stenoplesictidae, Prionodontidae, Eupleridae and Herpestidae, which are today considered to be distinct families.

The most common and widespread viverrid in the Miocene of Europe is the genus *Semigenetta* HELBING, 1927 (Fig. 1.20). Based on the review of Kargopoulos et al. (2021a), the diagnosis for this form is "genus of the Genettinae with M2 absent; m1 talonid much reduced; m1 hypoconid present; m1 entoconid and hypoconulid absent, replaced by a lingual talonid ridge; m2 reduced". The species of this genus are differentiated mainly based on body size, which is reflected in the length of the lower carnassial. The most common species is *Semigenetta sansaniensis* (LARTET, 1851) (MN 4–MN 10), which (based on Kargopoulos et al., 2021a) is diagnosed as follows: "species of *Semigenetta* of moderate size (m1L = 8.5–11.5 mm); m1 talonid lingual ridge without distinct cuspids; slender mandibular ramus; moderately trenchant premolars and m1 trigonid". A more primitive form is *Semigenetta laugnacensis* (DE BONIS, 1973) (MN 2 and MN 3) from France. The diagnosis for this species is: "Species of *Semigenetta* of very small size (m1L = 7.1–7.5 mm); slender mandibular ramus; moderately trenchant premolars and m1 trigonid". A doubtful additional species is *Semigenetta cadeoti* ROMAN & VIRET, 1934 from the MN 4 of France, which is described as "Species of *Semigenetta* of exceptionally small size (m1L ≈ 6 mm); slender mandibular ramus; moderately trenchant premolars and m1 trigonid". The second most common form is *Semigenetta elegans* DEHM, 1950 from the MN 3 and MN 4 of Europe, Anatolia and China. This is the only species of the genus that is known outside Europe. Its diagnosis is "species of *Semigenetta* of small size (m1L = 7.5–9.0 mm); m1 lingual talonid ridge usually with distinct cuspids; slender mandibular ramus; moderately trenchant premolars and m1 trigonid". Finally, the large species *Semigenetta grandis* CRUSAFONT PAIRÓ & GOLPE POSSE, 1981, is known from only a handful of European localities. Its diagnosis is "species of *Semigenetta* of large size (m1L = 12.5–15.5 mm); m1 talonid lingual ridge without distinct cuspids; robust mandibular ramus; considerably trenchant premolars and m1 trigonid".

Another common viverrid from the Miocene of Europe is *Viverrictis* DE BEAUMONT, 1973a. Two species of this genus have been identified: the MN 5 and MN 6 *Viverrictis vetusta* DE BEAUMONT, 1973a, and the MN 7/8 *Viverrictis modica* DE BEAUMONT, 1973a.

An additional enigmatic form is *Jourdanictis grivensis* VIRET, 1951, from La Grive-Saint Alban. Based on the re-appraisal of the described maxilla as *Plioviverrops gaudryi* by de Beaumont & Mein, 1972, only the lower dentition of this genus is known.

Finally, a short reference will be made to *Herpestides antiquus* (DE BLAINVILLE, 1842), which has been reported from Saint-Gérand-le-Puy (MN 2). This species is considered to be a stem feliform, so it is not considered as a viverrid sensu stricto. However, it was preferred to be added in this chapter due to its resemblance to the Miocene viverrids.

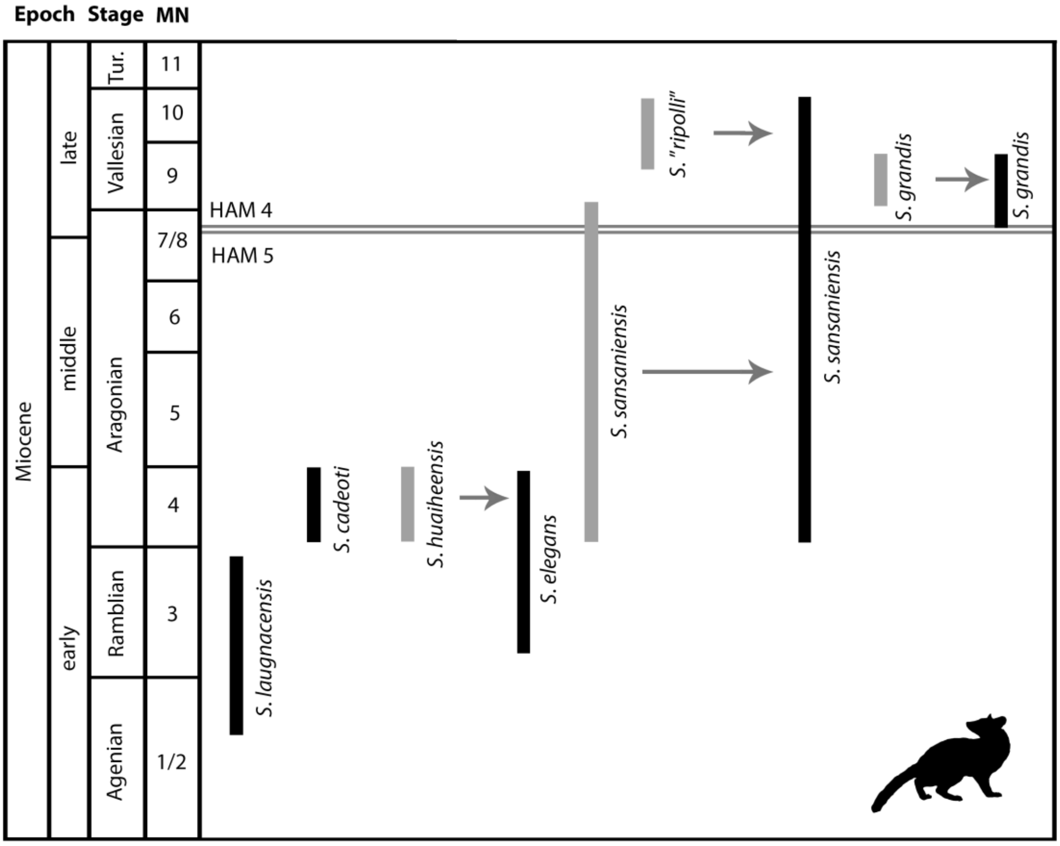

Fig. 1.20: Biochronological distribution of the species of *Semigenetta*. Source: Kargopoulos et al. (2021a).

Stenoplesictidae SCHLOSSER, 1923

No certain reports of the family Stenoplesictidae SCHLOSSER, 1923, have been made in the Miocene of Europe. This group is present in the Oligocene of Europe (e.g. Peigné & de Bonis, 1999; Fig. 1.21), but also to the Miocene of Africa (e.g. Werdelin & Peigné, 2010). However, based on the unresolved taxonomic status of the family and the small size of its representatives (which is disadvantageous for the discovery of complete specimens), future reports of this group in Europe don't seem improbable.

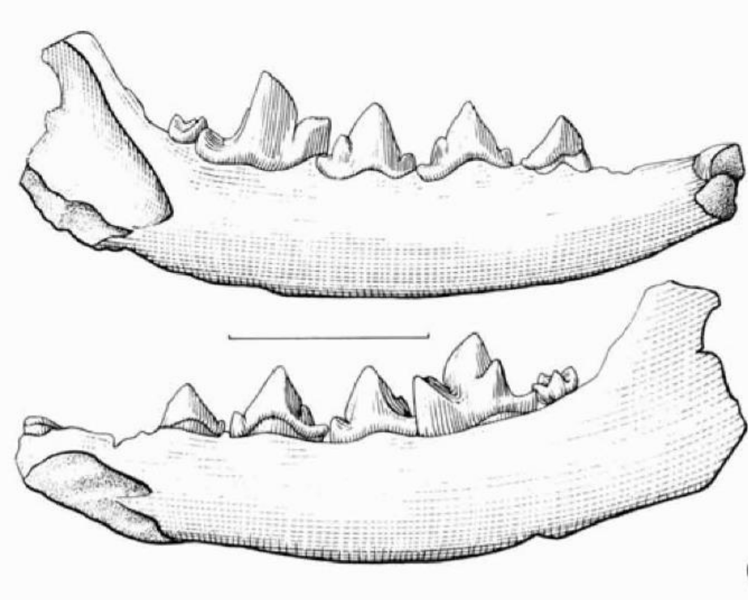

Fig. 1.21: Lectotype of *Stenoplesictis minor*. Source: Peigné & de Bonis (1999).

Nandiniidae POCOCK, 1929

The family Nandiniidae POCOCK, 1929, includes only the genus *Nandinia* GRAY, 1843, which today inhabits Central Africa. Very few fossil remains have been attributed to this lineage. Morales et al. (2005) reported the presence of one lower carnassial from the Lukeino Formation of Tugen Hills, Kenya (6.1–5.7 Ma). There are no reports of the genus outside Africa.

Fig. 1.22: *Nandinia binotata*. Source: biolib.cz.

Nimravidae Cope, 1880b

The family Nimravidae Cope, 1880b (in its strict sense, excluding the barbourofelids) has been reported in the fossil record from the Late Eocene until the Late Oligocene (Peigné, 2003; Antón, 2013). Therefore, there are no findings of this group in the Miocene of Europe.

Fig. 1.23: The nimravid *Hoplophoneus mentalis* in the Late Eocene of N. America. Source: Antón (2013). Artist: M. Antón.

Palaeogalidae MARTIN & LIM, 2001

The oldest report of the genus *Palaeogale* VON MEYER, 1846 (which is the sole genus of the family Palaeogalidae MARTIN & LIM, 2001) is in the Late Eocene of North America (Martin & Lim, 2001; Famoso & Orcutt, In Press). During the Oligocene it is reported in Asia, North America and Europe, while it has been found in the Early Miocene of the two latter continents. The European Miocene representatives of the family based on de Bonis (1981) and Ginsburg (1999) are: *Palaeogale praehyaenoides* MORLO, 1996 (Steinbruch Wiesbaden, Germany, MN2; Morlo, 1996), *Palaeogale minuta* GERVAIS, 1848–1852 (several MN1–MN4 localities; Morlo, 1996 and references therein) and *Palaeogale hyaenoides* DEHM, 1950 (several MN3–MN4 localities; Roth, 1989 and references therein). Therefore, there are no certain reports of this family after the Early Miocene.

Fig. 1.24: The holotype of *Palaeogale hyaenoides* from Wintershof-West (SNSB-BSPG 1937-II-13111).

Canidae FISCHER DE WALDHEIM, 1817

The largest part of the evolutionary history of canids took place in North America. This is the continent in which their first appearance takes place at the Late Eocene (e.g. Wang et al., 2004; Wang & Tedford, 2008). However, during the Late Miocene, some representatives of this group are present in the fossil record of Europe. All of them are attributed to the genus *Eucyon* TEDFORD & QIU, 1996, which was erected in order to described all the primitive (Late Miocene and early Pliocene) *Canis*-like canids. The original diagnosis of this form (based on material from China) is the following: "The new genus is distinguished from the fossil (*Leptocyon*) and living Vulpini (*Vulpes* s. l., *Urocyon* and *Otocyon*) by possession of three synapomorphies also possessed by all other members of the Canini (South American canines and *Canis*, *Cuon*, and *Lycaon*): A frontal sinus is present; it invades the base of the post-orbital process usually removing the "vulpine-crease" or depression on the dorsal surface of the process; the paroccipital process is expanded posteriorly and usually has a salient tip and the mastoid process is enlarged into a knob or ridge-like prominence. The Chinese material shows that *Eucyon*, like other Canini, has lost the fox-like lateral flare and eversion of the dorsal border of the orbital part of the zygoma. *Eucyon* lacks a feature characteristic of all other Canini, namely development of a transverse cristid connecting the hypoconid and entoconid of the m1 talonid. On the other hand *Eucyon* species have, as an autapomorphy, a second posterior cusplet on the p4 possessed only by the wolf group among the Canini".

Possibly the oldest canid in Europe is "*Canis*" *cipio* CRUSAFONT PAIRÓ, 1950a, from the Spanish locality of Concud. However, Crusafont Pairó & Kurten (1976) had reported some canid postcranial remains from Can Ponsic. However, this attribution is doubtful. Other European members of this group are *Eucyon debonisi* MORALES, MONTOYA & ABELLA, 2009, from Venta del Moro (Spain) and *Eucyon monticinensis* (ROOK, 1992) from Monticino (Italy). The arrival of these forms is called the "*Eucyon*" event and it is suggested that it happened during the late Late Miocene (Wang et al., 2004; Wang & Tedford, 2008; Rook, 2009; Sotnikova & Rook, 2010; Bartolini-Lucenti & Rook, 2021; Böhme et al., 2021). Two additional canid species that have been found in Venta del Moro are *Vulpes adoxus* (MARTIN, 1973) and *Nyctereutes donnezani* (DEPÉRET, 1890) The possibility of discovering fossils of this family at the base of the Tortonian is considered relatively low.

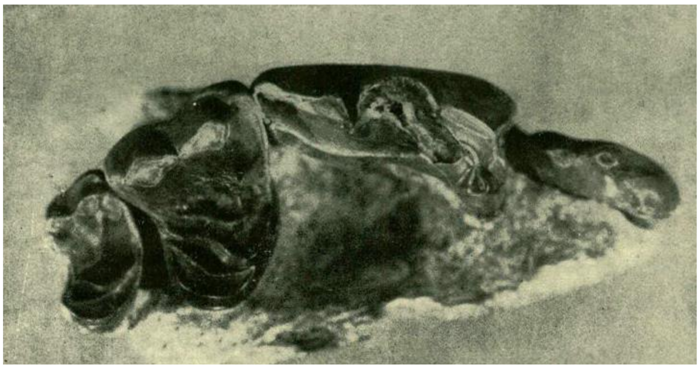

Fig. 1.25: The holotype of "*Canis*" *cipio* from Concud. Source: Crusafont Pairó (1950a).

Amphicyonidae TROUESSART, 1885

The family Amphicyonidae is one of the most diverse in the Miocene of Europe and a detailed review of this group is far beyond this Thesis' scope, especially given their infrequency in Hammerschmiede. However, a short overview will be attempted, in order to discuss this particular circumstance. During the past century there were some noteworthy reviews on the fossil record of the family, providing a solid ground in which comparisons are more and more clear (e.g. Kuss, 1965; Viranta, 1996; Hunt, 1998b, 2011; Ginsburg, 1999; Peigné & Heizmann, 2003; Peigné et al., 2006a, 2008; Morales et al., 2016, 2019a, 2021; Morlo et al., 2019a).

There are five distinct groups of amphicyonids that have been considered as different subfamilies: Amphicyoninae TROUESSART, 1885, Thaumastocyoninae HÜRZELER, 1940, Haplocyoninae DE BONIS, 1966, Temnocyoninae HUNT, 1998, and Daphoeninae HOUGH, 1948.

The subfamily Amphicyoninae is traditionally considered to be the most diverse amphicyonid group in the Miocene of Europe. Ginsburg (1999) distinguished four European groups of the genus *Amphicyon* LARTET, 1936, sensu lato: (1) the plesiomorfic group of *Amphicyon astrei* KUSS, 1962 (MN 1), *Amphicyon major* BLAINVILLE, 1841 (MN 4 to MN 8) and *Amphicyon eppelsheimensis* WEITZEL, 1930 (MN 9 to MN 11); (2) the large-sized *Amphicyon* (*Megamphicyon*) *laugnacensis* (GINSBURG, 1989) (MN 2 and MN 3) and *Amphicyon* (*Megamphicyon*) *giganteus* SCHINZ, 1825 (MN 4 to MN 6); (3) the group of *Amphicyon* (*Heizmannocyon*) *bohemicus* (SCHLOSSER, 1899a) (MN 3 to MN 5), *Amphicyon* (*Heizmannocyon*) *steinheimensis* FRAAS, 1885 (MN 6 and MN 7; Fig. 1.26); (4) and the more carnivorous *Amphicyon lactorensis* ASTRE, 1928 (MN 4 and 5), *Amphicyon* (*Euroamphicyon*) *olisiponensis* ANTUNES & GINSBURG, 1977 (MN 4) and *Amphicyon castellanus* GINSBURG et al., 1981 (MN 9 and MN 10). However, this scheme is not accepted by all other scholars. For instance, Morales et al. (2021b) attribute the species *A. bohemicus* to the genus *Paludocyon* MORALES et al., 2021b. This subfamily also includes *Magericyon anceps* PEIGNÉ et al., 2008 (from the locality of Batallones, MN 10) and these authors considered that *A. castellanus* should be included to this genus. Though, the phylogenetic analysis they performed suggested that these two species are closer to the thaumastocyonines.

Fig. 1.26: The holotype of *Amphicyon steinheimensis* from Steinheim (SMNS-4808).

The amphicyonine genus *Cynelos* JOURDAN, 1862, according to Ginsburg (1999) includes two lineages in the Miocene: the small-sized lineage includes *Cynelos rugosidens* (SCHLOSSER, 1899) (MN 2) and *Cynelos schlosseri* (DEHM, 1950) (MN 3), whereas the large-sized lineage includes *Cynelos lemanensis* (POMEL, 1846) (MN 1 and MN 2) and *Cynelos helbingi* (DEHM, 1950) (MN 3 and MN 4; Fig. 1.27). Recent reviews on this genus can be found in Peigné & Heizmann (2003), Hunt & Stepleton (2015) and Hunt & Yatkola (2020). It must be mentioned that Morales et al. (2021b) attribute the species *C. schlosseri* to the genus *Dehmicyon* MORALES et al., 2021b. The genus *Pseudocyon* LARTET, 1851, includes only one species in the Miocene of Europe: *Pseudocyon sansaniensis* LARTET, 1851 (MN 3 to MN 9). Schlosser (1899), Viranta (1996) and Peigné et al. (2008) considered *Amphicyon steinheimensis* to also belong to this genus, but this attribution is still doubtful as Heizmann (1973) and Ginsburg (1999) considered it to belong to *Amphicyon*, whereas Hunt (1998) considered it as a species of *Cynelos*. Finally, the subfamily is represented by *Pseudarctos bavaricus* SCHLOSSER, 1899 (MN 4 to MN 9) and *Ictiocyon socialis* (SCHLOSSER, 1904) (MN 3 to MN 4).

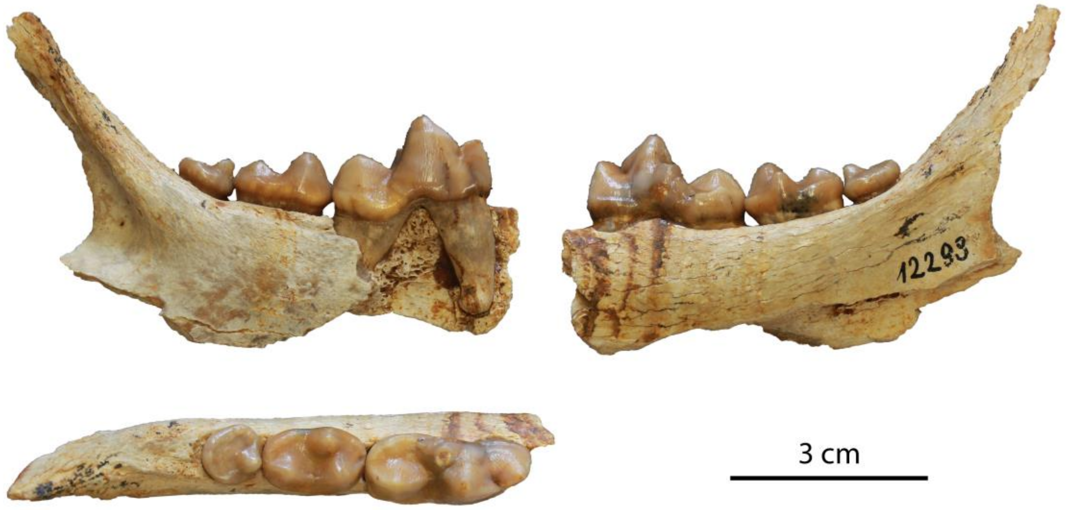

Fig. 1.27: The holotype of *Cynelos helbingi* from Wintershof-West (SNSB-BSPG-1937-II-12293).

The tribe Ysengrinini HEIZMANN & KORDIKOVA, 2000, contains the genera *Ysengrinia* GINSBURG, 1965, *Crassidia* HEIZMANN & KORDIKOVA, 2000, and *Amphicyonopsis* VIRET, 1951. The position of these forms is still debatable, as some authors consider them as amphicyonines (Ginsburg, 1999; Morlo et al., 2019a), whereas others consider them as thaumastocyonines (Morales et al., 2019a). The genus *Ysengrinia* contains the following species in chronological order: *Ysengrinia tolosana* (NOULET, 1876) (MP 30 and MN 1), *Ysengrinia gerandiana* (VIRET, 1929a) (MN 2), *Ysengrinia depereti* (MAYET, 1908) (MN 3) and *Ysengrinia valentiana* BELINCHÓN & MORALES, 1989 (MN 4). The genus *Crassidia* only includes *Crassidia intermedia* (VON MEYER, 1849) (MN 2) and the genus *Amphicyonopsis* includes only *Amphicyonopsis serus* (KUSS, 1965) (MN 7/8).

The subfamily Thaumastocyoninae has received a lot of attention the past decade with the description of new genera, the discovery of more material of the known forms and the discussion for the taxonomy and evolution of the group. In general, thaumastocyonines exhibit hypercarnivorous adaptations that resemble that of the felids. The first thaumastocyonine that was reported was *Agnotherium antiquum* KAUP, 1833, which has been found in the MN 9 and MN 10 of Europe and possibly North Africa. The genus *Thaumastocyon* STEHLIN & HELBING, 1925, includes 2 species: the smaller *Thaumastocyon bourgeoisi* STEHLIN & HELBING, 1925, from MN 5 and the larger *Thaumastocyon dirus* GINSBURG et al., 1981, from Los Valles de Fuentidueña (MN 9). Viret (1929b) erected the species *Tomocyon grivense* VIRET, 1929b, based on material from La Grive (MN 7/8). Recently, the species *Peignecyon felinoides* MORALES et al., 2019 (Tuchořice, MN 3) and *Ammitocyon kainos* MORALES et al., 2021a (Batallones, MN 10) were described for the first time.

The last European amphicyonid subfamily is Haplocyoninae. This group includes four genera: *Haplocyon* SCHLOSSER, 1901, *Gobicyon* COLBERT, 1939, *Haplocyonopsis* DE BONIS, 1973, and *Haplocyonoides* HÜRZELER, 1940. The genus *Haplocyon* includes two species: *Haplocyon elegans* DE BONIS, 1966 (MN 2) and *Haplocyon crucians* (FILHOL, 1879) (MN 2). The species *Gobicyon serbiae* GINSBURG, 1999 (Prebreza, MN

6) and *Haplocyonopsis crassidens* DE BONIS, 1973 (MN 1) are the only members of their respective genera in Europe. A recent review of the genus *Gobicyon* was made in Jiangzuo et al. (2019b). Finally, the genus *Haplocyonoides* includes three species: *Haplocyonoides mordax* HÜRZELER, 1940 (MN 2 and MN 3), *Haplocyonoides suevicus* PEIGNÉ & HEIZMANN, 2003 (Ulm-Westtangente, MN 2) and *Haplocyonoides ponticus* KUSS, 1960 (Melchingen, MN 9).

Temnocyoninae is a group that occurred only in North America, so it is not going to be discussed here. A thorough review of this subfamily was made by Hunt (2011). They exhibit dental similarities to the Haplocyoninae.

Finally, Daphoeninae is another North American subfamily that will not be discussed here. A review of this group can be found in Hunt (1998b).

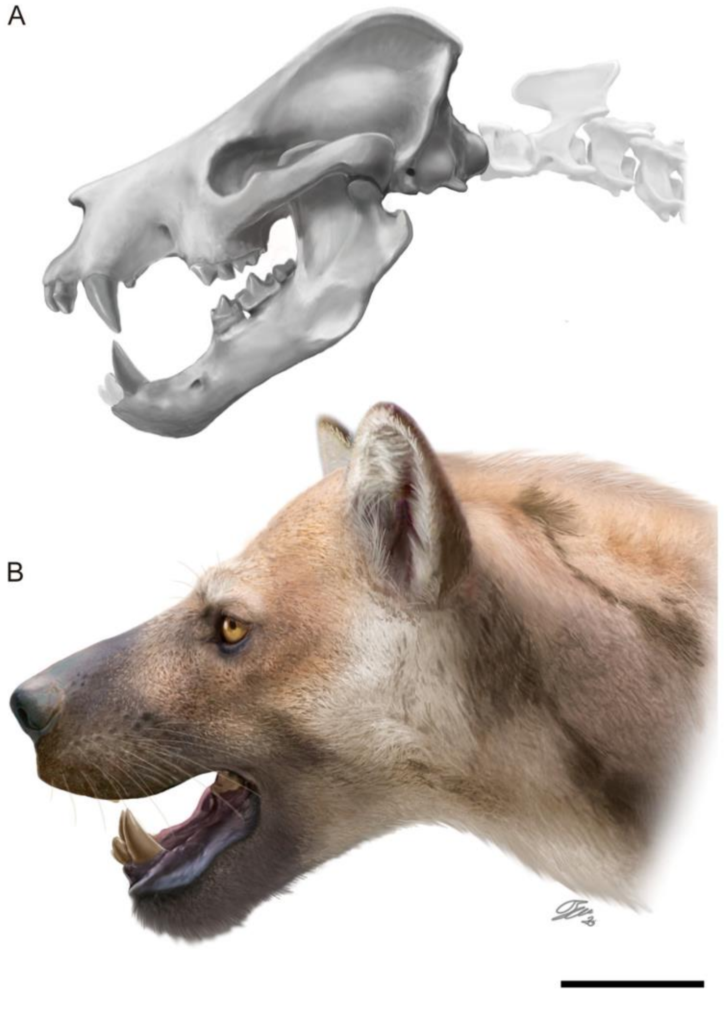

Fig. 1.28: Reconstruction of *Ammitocyon kainos*. Source: Morales et al. (2021a). Artist: O. Sanisidro.

Amphicynodontidae SIMPSON, 1945

This family is represented mostly by North American and Asian forms. However, some species have been found in Europe. These forms are attributed to the genera *Amphicynodon* FILHOL, 1881, *Pachycynodon* SCHLOSSER, 1888, and *Wangictis* DE BONIS et al., 2019, and all of them are of Oligocene age, so a more detail discussion on them seems irrelevant. A detailed review of these species can be found in Cirot & de Bonis (1992).

Fig. 1.29: Mandible of *Amphicynodon typicus* from the Phosphorites de Quercy. Source: de Bonis et al. (2019).

Hemicyonidae Frick, 1926

As aforementioned, this group has been considered as a subfamily of the ursids for several decades. However, herein it is preferred to follow the approaches of de Bonis (2013) and Hontecillas (2019) as the most recent and thorough reviews of the family. There are two distinct subfamilies of hemicyonids: Hemicyoninae Frick, 1926, and Phoberocyoninae Ginsburg & Morales, 1995. The latter are mainly differentiated by the enlargement of their upper and lower carnassials.

A number of Oligocene hemicyonines is present during the Oligocene of Europe, among the genera *Adelpharctos* de Bonis, 1971, *Filholictis* de Bonis, 2013, *Cyonarctos* de Bonis, 2013 and *Cephalogale* Jourdan, 1862. However, the latter also has three Miocene representatives: *Cephalogale ursinus* de Bonis, 1973, from Paulhiac (MN 1), *Cephalogale ginesticus* Kuss, 1962 (MN 1) and *Cephalogale gracilis* (Pomel, 1853) (MN 2). Another early Miocene form is the species *Zaragocyon daamsi* Ginsburg & Morales, 1995 from the MN 2 of Spain. The genus *Hemicyon* Lartet (1851) exhibits a relatively extended range in the Miocene record of Europe, represented by four consequent species: *Hemicyon gargan* Ginsburg & Morales, 1998 (MN 3), *Hemicyon stehlini* Hürzeler, 1944 (MN 4 and MN 5), *Hemicyon sansaniensis* Lartet, 1851 (MN 5 and MN 6) and *Hemicyon goeriachensis* (Toula, 1884a) (MN 6 and MN 7/8). The genus *Dinocyon* Jourdan, 1861 is represented by two species: *Dinocyon mayorali* (Astibia et al., 2000) from MN 5 and *Dinocyon thenardi* Jourdan, 1861, from La Grive (MN 7/8). Finally, the genus *Agriotherium* Wagner, 1837 is the youngest member of the hemicyonid lineage. Its only European Miocene representative is *Agriotherium roblesi* Morales & Aguirre, 1976 (Venta del Moro, MN 13), which is followed by other forms of the same genus in the Pliocene.

The subfamily Phoberocyoninae includes three genera: *Phoberocyon* Ginsburg, 1955, *Plithocyon* Ginsburg, 1955, and *Phoberogale* Ginsburg & Morales, 1995. The genus *Phoberocyon* includes three species of the same age (MN 3): *Phoberocyon hispanicus* Ginsburg & Morales, 1998, *Phoberocyon dehmi* (Ginsburg, 1955) and *Phoberocyon aurelianensis* (Mayet, 1908). On the other side, the genus *Plithocyon* is represented throughout the Early-Middle Miocene by four species: *Plithocyon bruneti* Ginsburg, 1980 (MN 3), *Plithocyon conquense* Ginsburg & Morales, 1998 (MN 4), *Plithocyon antunesi* Ginsburg & Morales, 1995 (MN 4 and MN 5), *Plithocyon armagnacensis* Ginsburg, 1955 (MN 5 to MN 7/8). Finally, the genus *Phoberogale* only includes the type species *Phoberogale depereti* (Viret, 1929a) (MN 2).

Fig. 1.30: Reconstruction of *Hemicyon* sp. Source: sciencephoto.com. Artist: M. Antón.

Ursidae FISCHER DE WALDHEIM, 1817

The family Ursidae includes the extant bears and their fossil relatives. Two subfamilies are present in the European Miocene fossil record: Ursinae FISCHER DE WALDHEIM, 1817, and Ailuropodinae GREVÉ, 1894.

The oldest (MN 3) and most basal members of this family are attributed to the genus *Ballusia* GINSBURG & MORALES, 1998, which is represented by the smaller-sized *Ballusia elmensis* (STEHLIN, 1917) and the larger-sized *Ballusia hareni* (GINSBURG, 1989). A translation of the original diagnosis of Ginsburg & Morales (1998) is herein attempted: "Primitive ursid of small size, close to *Ursavus* and *Hemicyon*, but distinguishable from *Hemicyon* by the distinctly longer upper molars; on M1 the lingual crest (which passes through the protocone and the metaconule) is more distant from the paracone-metacone line, while the lingual cingulum is wider, shorter and draws more or less an arc in occlusal view. M2 is distinctly elliptical, with a wide lingual cingulum (as in M1) and more separated from the medial crest than in *Ursavus*, while the posterior chewing area, located between the metacone and the metaconule, is shorter and wider. The m1 looks more like those of *Hemicyon* and *Plithocyon* than those of *Ursavus*, with a trigonid still quite high".

The subfamily Ursinae is represented by the genus *Ursavus* Schlosser, 1899, which is the most diverse of the Miocene bears of Europe, including at least five different species: *Ursavus isorei* GINSBURG & MORALES, 1998 (MN 3), *Ursavus brevirhinus* (HOFMANN, 1887) (MN 4 to MN 6), *Ursavus intermedius* VON KOENIGSWALD, 1925 (MN 6 to MN 7/8), *Ursavus primaevus* (GAILLARD, 1899) La Grive (MN 7/8) and *Ursavus ehrenbergi* (BRUNNER, 1942) Halmyropotamos (MN 12; Fig. 1.31).

Fig. 1.31: The holotype of *Ursavus ehrenbergi* from Halmyropotamos (AMPG-1883).

The subfamily Ailuropodinae is also diverse, including more genera. The genus *Agriarctos* Kretzoi, 1942 includes three species: *Agriarctos depereti* (SCHLOSSER, 1902) (MN 9), *Agriarctos gaali* KRETZOI, 1942 (MN 12 or MN 13) and *Agriarctos vighi* KRETZOI, 1942 (MN 12 or MN 13). The species *Kretzoiarctos beatrix* (ABELLA et al., 2011) has been found in the late Aragonian of Spain. The diagnosis of the genus based on Abella et al. (2012) is the following: “Small-sized ailuropodine species. P4 with a well-developed protocone situated opposite to the paracone, and parastyle of moderate size but well-individualized from the protocone. M1 with a highly-developed metastyle and lingual cingulum poorly differentiated from the protocone and hypocone. Robust mandibular corpus, deepest under the m1 and m2. Low-crowned and curved lower canine. Lower premolars (p2–p4) with a single, duniform main cusp, and reduced mesial and distal accessory cusps, not separated by any diastema. Long and low-crowned m1, with the metaconid and protoconid of similar height, long and shallow talonid basin, and no cusp at the paraconid-hypoconid valley. Relatively long m2 with well-developed trigonid and talonid basins”.

Another ailuropodine from the Vallesian of Rudabánya (MN 9) is *Miomaci pannonicum* DE BONIS et al., 2017. The diagnosis provided by de Bonis et al. (2017) is the following: “medium-sized ursid, primitive by the anteriorly situated protocone of P4 and the short talon of M2; vertical ascending ramus of the mandible; lower p1-p3 reduced but p2 and p3 two-rooted; p4 with a well-developed posterior accessory cuspid; low trigonid of m1 with blunt cuspids, mesio-distally oriented paraconid, gentle mesial and distal slopes of the protoconid, distally situated metaconid, talonid wider than trigonid; oval m3; low upper canine, small but two-rooted P3; P4 with very tiny parastyle, protocone at the same level than paracone; M2 with a small talon”.

Finally, the genus *Indarctos* includes three derived ailuropodines from the Late Miocene: *Indarctos vireti* VILLALTA & CRUSAFONT, 1943b (MN 10), *Indarctos arctoides* (DEPÉRET, 1895) (MN 10) and *Indarctos punjabensis* (LYDEKKER, 1884) (Turolian; Fig. 1.32).

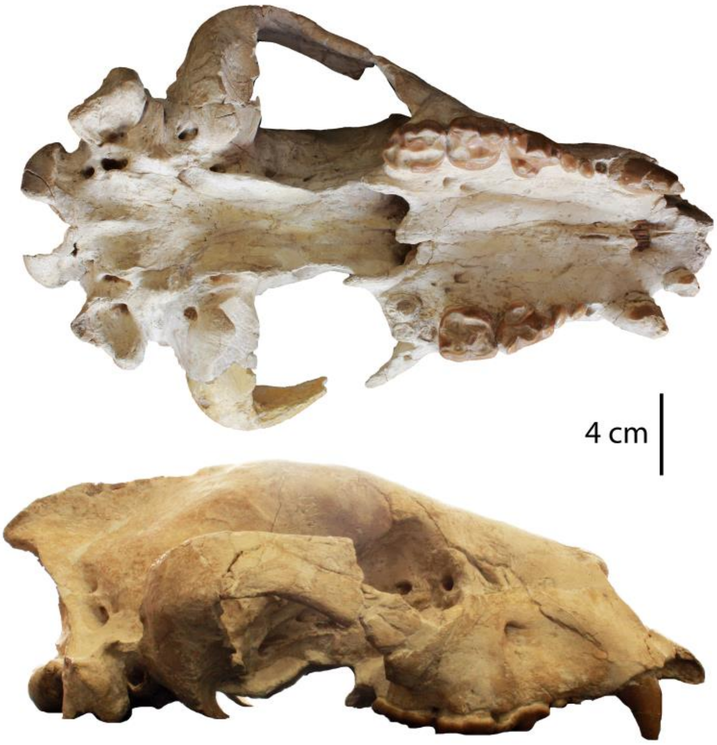

Fig. 1.32: Skull of *Indarctos punjabensis* from Samos (NHMW-1912/0004/0001).

Enaliarctidae MITCHEL & TEDFORD, 1973

This group has only been found in Oligocene and Early Miocene fossiliferous sediments of North America (California and Oregon). Therefore, it will not be discussed further here. Detailed descriptions and discussions over this group can be found in Mitchel & Tedford (1973), Berta (1991) and Poust & Boessenecker (2018).

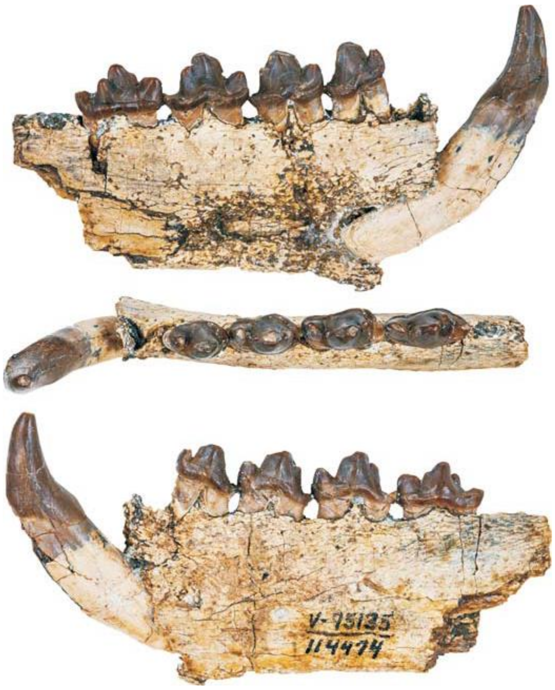

Fig. 1.33: Mandible of *Enaliarctos mealsi* from Schooner Gulch, Mendocino County, California. Source: Poust & Boessenecker (2018).

Otariidae GRAY, 1825

Similarly to the enaliarctids, this group has not been found in Europe. It has been discovered only in North America and Asia, so it will not be discussed further. Recent reviews on the fossil representatives of this family can be found in Barnes et al. (2006), Boessenecker & Churchill (2015) and Veles-Juarbe (2017).

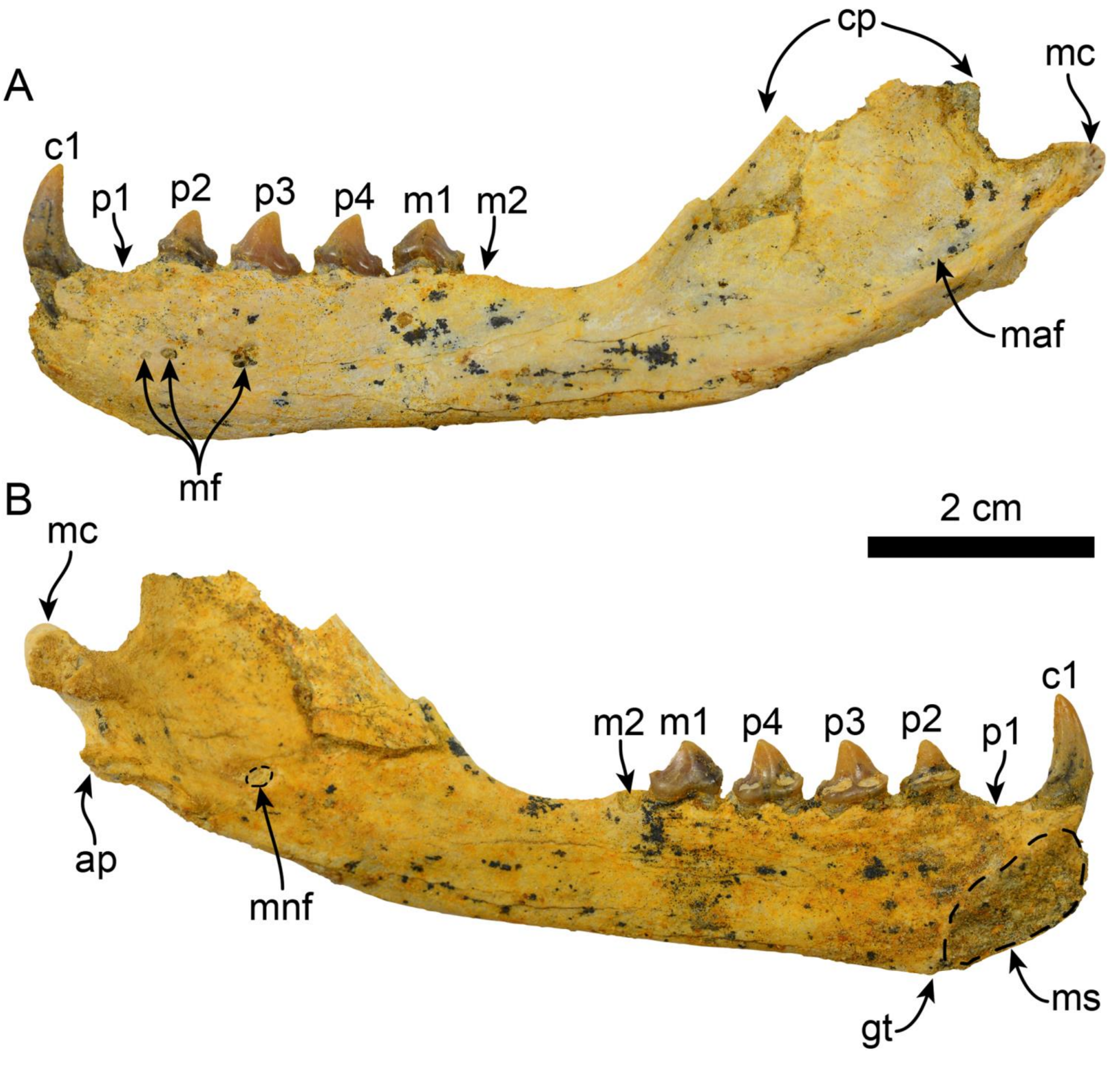

Fig. 1.34: Mandible of *Eotaria crypta* from Mission Viejo, Orange County, Cailfornia. Source: Velez-Juarbe (2017).

Odobenidae ALLEN, 1880

The family of odobenids is also not found in the fossil record of Europe, as it has been restricted to the northwest Pacific (mostly California). Today, its only representative is the walrus *Odobenus rosmarus* (LINNAEUS, 1758).

Fig. 1.34: Skull of the extant walrus *Odobenus rosmarus* (NHMBA-1420).

Phocidae GRAY, 1821

In contrast to all the other pinniped groups, the European fossil record of the phocids is considerably rich. A thorough review of these representatives was made by Koretsky (2001), but several more discoveries have been published since then. Herein, a summary of the current knowledge Miocene phocids of Europe will be presented. The evolution of Paratethys has been a core aspect on the phocid distribution.

The most widely accepted taxonomic scheme defines that the family Phocidae is divided in four subfamilies: Devinophocinae KORETSKY & HOLEC, 2002, Cystophorinae GRAY, 1866, Phocinae GRAY, 1821, and Monachinae TROUESSART, 1897.

The subfamily Devinophocinae includes only the genus *Devinophoca* KORETSKY & HOLEC, 2002, which is known only from the early Middle Miocene of Slovakia. The most recent emended diagnosis for this form given by Rahmat & Koretsky (2018) is the following: “mandibular body low in height (as in Monachinae and Phocinae); symphyseal part of mandible thick and straight (similar to Monachinae); diastemata between teeth absent (as opposed to Cystophorinae, Monachinae and Phocinae); unique incisor combination I3/1 (as opposed to Cystophorinae, Monachinae and Phocinae); p4 alveolar width and length greater than those of m1 (similar to some Monachinae and Phocinae)”. Only two species have been described: *Devinophoca claytoni* KORETSKY & HOLEC, 2002 (type species) and *Devinophoca emryi* KORETSKY & RAHMAT, 2015.

The subfamily Cystophorinae also has a relatively limited fossil record. The emended diagnosis for the subfamily by Koretsky & Rahmat (2013) is the following: “Large seals (length up to 5 m) with six incisors (I=2/1; in contrast to Monachinae with 8 incisors and Phocinae with 10 incisors); paroccipital process of skull poorly developed (in contrast to Desmatophocinae); anteroposterior length of auditory bulla less than distance between the bullae (in contrast to Phocinae and Desmatophocinae); infraorbital process present; interorbital space wide; interorbital width less than 30%, but equal to or greater than 25% of mastoid width (as in Devinophocinae); anterior palatal foramina oval (as in Devinophocinae) and shallow; preorbital part of maxilla with narrow concavity (similar to Lobodontini; in contrast to Monachinae, Phocinae, and Devinophocinae). Upper second incisors tend to enlarge rather than first incisors. Mandibular chin prominence absent; alveoli of p4 bigger than alveoli of m1; coronoid proves very narrow and turned caudally, especially in male; condyloid process not well marked; symphysis reaches posterior alveolus of p1; mandibular notch very narrow; retromandibular space elongated (≈3.5 cm in females and ≈3 cm in males). Middle of internal crest of humeral trochlea rises wave-like over coronoid fossa; widths of distal and proximal epiphyses almost equal. Medial and lateral femoral condyles almost equal in size; lesser trochanter present in males; minimum width of femoral shaft 1.4–1.9 times width of proximal epiphysis.” The species *Miophoca vetusta* ZAPFE, 1937, is known from the early Middle Miocene of Slovakia. Additionally, the species *Pachyphoca ukrainica* KORETSKY & RAHMAT, 2013, is known from the Bessarabian of Ukraine.

The subfamily Phocinae includes several Miocene forms in the fossil record of Europe. The species *Histriophoca alekseevi* KORETSKY, 2001 has been found in Kishinev (Middle Sarmatian, Moldavia). The original diagnosis is the following: “Alveoli of second and third upper incisors of equal length; alveolus of first incisor is half as wide as and shorter than either external alveolus; distance from posterior palatal fossa to lateral notch of palatine is 3mm; palatal process of maxilla swollen; diastemata between all teeth large and similar in size; length of alveolus Ml/ml larger than that of P4/p4; shallow chin prominence of mandible located under ml”.

Another form of similar temporospatial range in *Monachopsis pontica* (EICHWALD, 1850) from the Late Miocene of Ukraine, Romania and Turkey. The emended diagnosis by Koretsky (2001) includes: “Phocinae of very small size; P4-M1 single-rooted; diastemata between teeth absent; palatal process of maxilla highly swollen; infraorbital foramen visible in dorsal view. Lesser tubercle of humerus located on same level as proximal part of deltoid crest, higher than head. Ratio of head’s width to its height near 103%. Deltoid crest strongly developed, reaches coronoid fossa; epicondyloid crest weakly developed. Greater trochanter of femur slightly higher than head, its proximal part narrower than distal; trochanteric fossa shallow, located transversely relative to bone’s axis; head strongly bent distally; neck short; minimal width of diaphysis shifted proximally; greatest breadth across condyles 49.9-58.9% of bone length”.

The genus *Praepusa* KRETZOI, 1941, includes four species: *Praepusa pannonica* KRETZOI, 1941 (Middle Sarmatian of Hungary and Moldavia), *Praepusa vindobonensis* TOULA, 1898 (Early Sarmatian of Austria and Middle Sarmatian of Moldavia and Ukraine), *Praepusa magyaricus* KORETSKY, 2003 (from the Middle Miocene of Hungary) and *Praepusa boeska* KORETSKY, PETERS & RAHMAT, 2015 (from the Late Miocene of Netherlands). The emended diagnosis for this genus made by Koretsky et al. (2015) is the following: “Cranial diagnosis the same as for *Praepusa vindobonensis*; mandibular diagnosis the same as for *Pr. pannonica*. Deltoid crest of humerus has shape of sharp blade; lesser tubercle elongated along axis of bone; head width to height ratio greater than 0.964; lateral epicondyle reaches distal part of deltoid crest. Greater trochanter of femur considerably higher than head; its proximal and distal parts approximately of equal width; trochanteric fossa wide and medially open, but deep; head slightly deflected distally and seated on narrow, long neck; minimal width of diaphysis in middle part of bone; maximal intercondylar distance 12.0–15.8 % of femoral length. Sacrum consists of three fused short vertebrae with smaller alas, and narrower bases than in *Phocanella*; cranial articular processes (processus articularis cranialis) shorter, flattened with square bases; foramina smaller, wider and shorter, base not round, but rectangular shape; lateral sacral crests oblong in shape, more elongated and reaching above second dorsal foramina, in contrast to *Phocanella pumilla* where crests reach only lower (distal) part of foramina”.

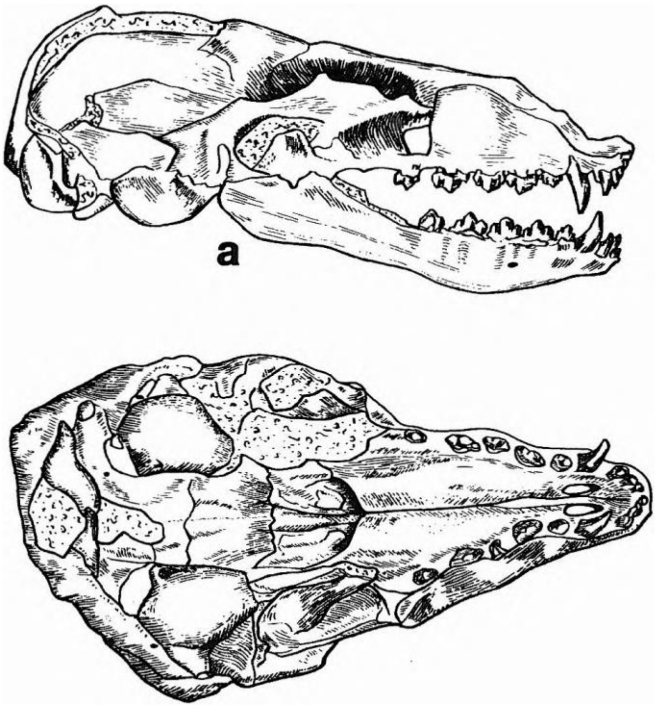

Fig. 1.35: Skull *Praepusa vindobonensis*. Source: Koretsky (2001).

The species *Cryptophoca maeotica* (VON NORDMANN, 1860,) is also known from Kishinev (Middle Sarmatian, Moldavia). The emended diagnosis in Koretsky (2001) is the following: "Lower canine and p1 very large (Tables 5a, b), p1 single-rooted; symphysis straight, its inner part enlarged from anterior alveolus p2 to canine; mental protuberance located between p3 and p4. Deltoid crest up to 1/4 of humeral length, not reaching coronoid fossa; proximal border of deltoid crest is its widest part; lesser tubercle of humerus located on same level as proximal border of deltoid crest; head round. Femur with almost rectangular greater trochanter; trochanteric fossa deep and open; head of femur large (Table 7a), situated on relatively narrow, short neck; minimal width of diaphysis shifted toward proximal epiphysis; greatest breadth across condyles 20-21% of bone length; proximal epiphysis narrower than the distal by 2-8%".

The species *Sarmatonectes sintsovi* KORETSKY, 2001, was described based on material from Kishinev (Middle Sarmatian, Moldavia). The original diagnosis is the following: "Deltoid crest extends more than 2/3 of humeral length; maximal width of deltoid crest located in its proximal portion; lesser tubercle of humerus located distal to proximal border of deltoid crest; head compressed craniocaudally; lateral epicondyle reaches middle of diaphysis. Proximal and distal parts of greater trochanter of femur approximately of equal width; trochanteric fossa shallow and opened medioproximally; lesser trochanter small, located at same level as distal border of greater trochanter; head small, situated on relatively wide, short neck; minimum width of diaphysis located in middle part of bone; maximum intercondylar distance 12.3-14.3% of bone's length".

The species *Prophoca proxima* VAN BENEDEN, 1877, has been described from the Middle Miocene of Borderhout (Belgium). The diagnosis provided by Koretsky (2001) for this form includes: "Deltoid crest extends distally more than 2/3 of humeral length, not reaching coronoid fossa; lesser tubercle of humerus located distally to the head but on same level as proximal border of deltoid crest; head compressed mediolaterally; lateral epicondyle reaches distal end of deltoid crest".

The species *Leptophoca amphiatlantica* KORETSKY, RAY & PETERS, 2012 has been described based on material from the Middle Miocene of the Netherlands and the Lower-Middle Miocene of USA). The original diagnosis includes: "New species of *Leptophoca* of smaller body size than *L. lenis*. The femur is having a short intertrochanteric crest which does not reach lesser trochanter; the head is small and seated on a narrow, long neck; the smallest width of the diaphysis is shifted toward the proximal half of the femur; maximum intercondyloid width is 14-15% of the bone's length".

The species *Gryphoca nordica* KORETSKY, RAHMAT & PETERS, 2014, has been described from the Late Miocene of Belgium and Denmark. The diagnosis for the genus by Koretsky et al. (2014) is the following: "Phocine of medium size similar to modern *Halichoerus grypus*. Deltoid crest of humerus short, narrow, and thin, terminating about 1/2 length of bone; its distal end gently broadening and somewhat overhanging the bone; lesser tubercle located slightly above head and proximal part of deltoid crest; intertubercular groove narrow and deep; medial epicondyle reaches distal end of deltoid crest; entepicondylar foramen present. Femoral greater trochanter higher than head; minimal width of shaft located in middle part of femur; epicondyles very thin".

The species *Platyphoca danica* KORETSKY, RAHMAT & PETERS, 2014, was discovered in the Late Miocene of Denmark. The diagnosis for the genus by Koretsky et al. (2014) includes: "Deltoid crest of humerus very short and terminating at less than 1/2 of length of bone; from base of lesser tubercle, along medial surface of bone, passes a crest that is only slightly shorter than deltoid crest; maximal enlargement of deltoid crest in its proximal part; intertubercular groove very shallow and not well defined; both epicondyles well developed and very wide; distal part of each epicondyle flat.".

Additionally, the species *Planopusa semenovi* KORETSKY & RAHMAT, 2021, was recently described from the MN 9 of Gritsev. The diagnosis for this form includes: "Small seal with extremely short rostrum (table 1), differing from all other fossil and extant phocines by: 1) flattened palatal process of maxilla; 2) P4 longer than M1; 3) alveoli form a straight line; 4) wider rostrum across canines compared to other small Phocinae (but narrower than in *Monachopsis pontica*)".

Finally, the subfamily Monachinae includes some doubtful species and a handful of better determined ones.

Three closely related species have been described from the Late Miocene of Belgium: *Monotherium delognii* VAN BENEDEN, 1876, *Monotherium aberratum* VAN BENEDEN, 1876, *Monotherium affine* VAN BENEDEN, 1876. However, their taxonomic validity is considered uncertain (Koretsky, 2001). Another species found in Belgium is "*Prophoca*" *rousseaui* VAN BENEDEN, 1876, which is considered to be Middle Miocene (Koretsky, 2001).

The genus *Pontophoca* MCLAREN, 1960 has been described by two species: *Pontophoca sarmatica* (ALEKSEEV, 1924) (from Kishinev) and *Pontophoca jutlandica* KORETSKY, RAHMAT & PETERS, 2014 (from the Late Miocene of Denmark). The diagnosis of the genus based on Koretsky et al. (2014) includes: "Lower premolars p1 and p2 double-rooted, placed parallel to tooth row axis; protoconid on p2 triangular; diastemata present; metaconid and basal cingulum weakly developed. Deltoid crest of humerus terminates in middle of diaphysis, its proximal part averted in dorsal direction; distal epiphysis considerably inflated compared to proximal epiphysis; lesser tubercle located higher than proximal end of deltoid crest and head; index of head's height (ratio of head width/head height) near 100 %; supracondylar crest strongly developed. Height of femoral greater trochanter slightly exceeds that of head; its distal end narrower than its proximal end; head very small compared with the otherwise massive bone and seated on narrow neck; minimal width of diaphysis located in proximal part of bone between neck and distal part of greater trochanter; distal end of femur 1.4–1.5 times broader than proximal end; condyles widely separated; maximal distance between epicondyles about or more than 70 % of bone's length".

Desmatophocidae Hay, 1930

Similar to several other pinniped groups, the desmatophocids are not present in the Miocene of Europe. In particular, they have been found only in North America and Japan. More information about this group can be found in Boessenecker & Churchill (2018).

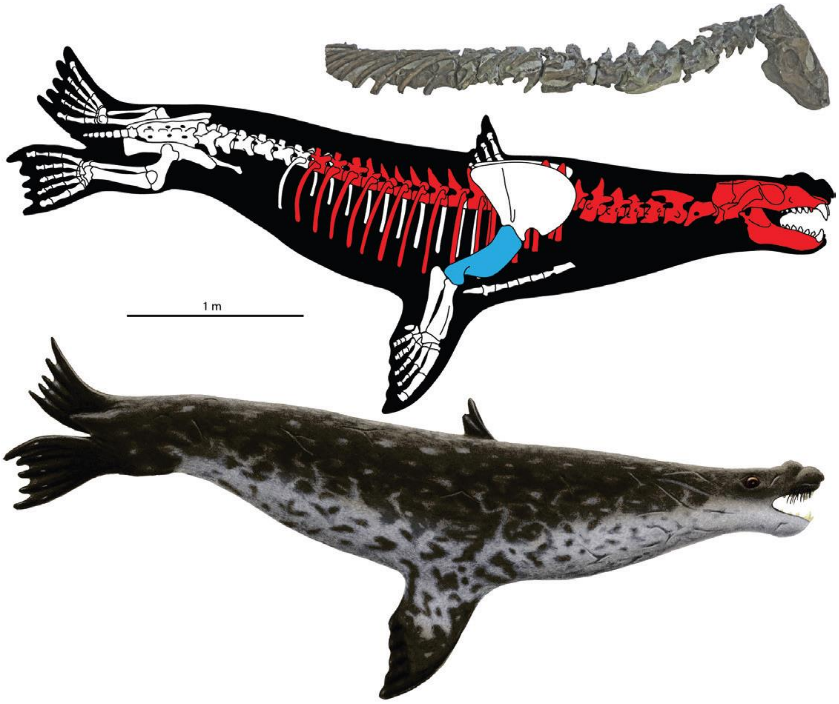

Fig. 1.36: Reconstruction of *Allodesmus demerei*. Source: Boessenecker & Churchill (2018).

Ailuridae GRAY, 1843

Today, the family Ailuridae GRAY, 1843, includes only the red panda *Ailurus fulgens*. This is a small (≈5 kg) hypocarnivorous species that lives in south-east Asia (Roberts and Gittleman, 1984). The exact phylogenetic relationships of this family have been a matter of debate for several decades. The remarkable convergent adaptations of the red panda and the giant panda have been interpreted as indicators of common ancestry, connecting the genera *Ailurus* CUVIER, 1825, and *Ailuropoda* (Cserhati, 2021 and references therein). Other scholars pointed towards the common traits between ailurids and the procyonids (e.g. Roussiakis, 2002). Today, their status as a distinct family is not doubted, but there is still debate on their exact position in the caniform phylogenetic tree.

The oldest genus that has been attributed to the family Ailuridae is *Amphictis* POMEL, 1853, from the Late Oligocene to Early Miocene (MP 28 to MN 4) of Europe (Ginsburg, 1999; Peigné & Morlo, 2010). This genus belongs to a basal line, which is often called Amphictinae WINGE, 1895 (e.g. Ginsburg, 1999). This genus has relatively small M2 and m2 and its morphology mostly resembles that of the mustelids. Four species of *Amphictis* are present in the Miocene of Europe, but they are restricted to its early stages, so they will not be discussed further.

The other known fossil ailurids are divided in two subfamilies: Ailurinae GRAY, 1843, and Simocyoninae DAWKINS, 1868. The former subfamily includes the extant panda (*Ailurus fulgens*) and some other hypocarnivorous forms. The genus *Parailurus* SCHLOSSER, 1899, includes the species *Parailurus anglicus* (DAWKINS, 1888), *Parailurus hungaricus* KORMOS, 1935, *Parailurus baikalicus* SOTNIKOVA, 2008 and some isolated teeth from North America and Japan (Peigné & Morlo, 2010). All known specimens come from the Pliocene and most of them have been found in Europe. The species *Pristinailurus bristoli* WALLACE & WANG, 2004 (only species of *Pristinailurus* WALLACE & WANG, 2004) is also included in the Ailurinae (Wallace & Wang, 2004, 2007). It has been found in the latest Miocene to Early Pliocene of USA (Wallace & Wang, 2004). Finally, The species *Magerictis imperialensis* GINSBURG, MORALES, SORIA & HERRAEZ, 1997 (the only species of the genus *Magerictis* GINSBURG, MORALES, SORIA & HERRAEZ, 1997) is known from the early Middle Miocene of Madrid only from one m2. This is the only Miocene ailurine of Europe. Finally, some unidentified ailurine remains (named as “Ailurinae indet.”) were published by Ginsburg et al. (2001) from the late Middle Miocene of Four (France).

The simocyonines are the most common ailurids in the Miocene of Europe. The oldest species is *Alopecocyon goeriachensis* TOULA, 1884b, originally described from Göriach. This is also the most common and most widespread form, since it is known from many localities from MN 5 to MN 7/8 (Ginsburg, 1999). Similarly to Magerictis imperialensis, the species *Protursus simpsoni* Crusafont Pairó & Kurtén, 1976, is also known only from one m2, from the locality of Can Llobateres. Recently, Kargopoulos et al. (In Press) suggested that this species is also present in Rudabánya.

The remaining four ailurid species are included in the genus *Simocyon* WAGNER, 1858. This genus has been found exclusively in Late Miocene localities, spreading from

MN 9 to MN 12. It is relatively larger in size and it exhibits gradual adaptations to durophagy. The oldest species is *Simocyon diaphorus* (KAUP, 1832), which was originally described from Eppelsheim. Another mandible of this species from the type locality was published by Kullmer et al. (2008) and it has also been found in Rudabánya (Werdelin, 2005). Another member of the genus is *Simocyon batalleri* (VIRET, 1929c), which has been found only in Batallones and Sabadell (Peigné et al., 2005). However, the locality of Batallones has provided a lot of cranial and postcranial material (Peigné et al., 2005; Salesa et al., 2008; Fabre et al., 2015), so this is probably the most well-known Miocene ailurid of Europe. Another *Simocyon* species is *Simocyon hungaricus* KADIC & KRETZOI, 1927, which is only known from the type locality of Csakvar. Finally, the last Miocene simocyonine (and ailurid) of Europe is *Simocyon primigenius* ROTH & WAGNER, 1954, which has been found in several Turolian localities of the Balkans and China (e.g. Zdansky, 1924; Pilgrim, 1931; Wang, 1997; Roussiakis, 2002).

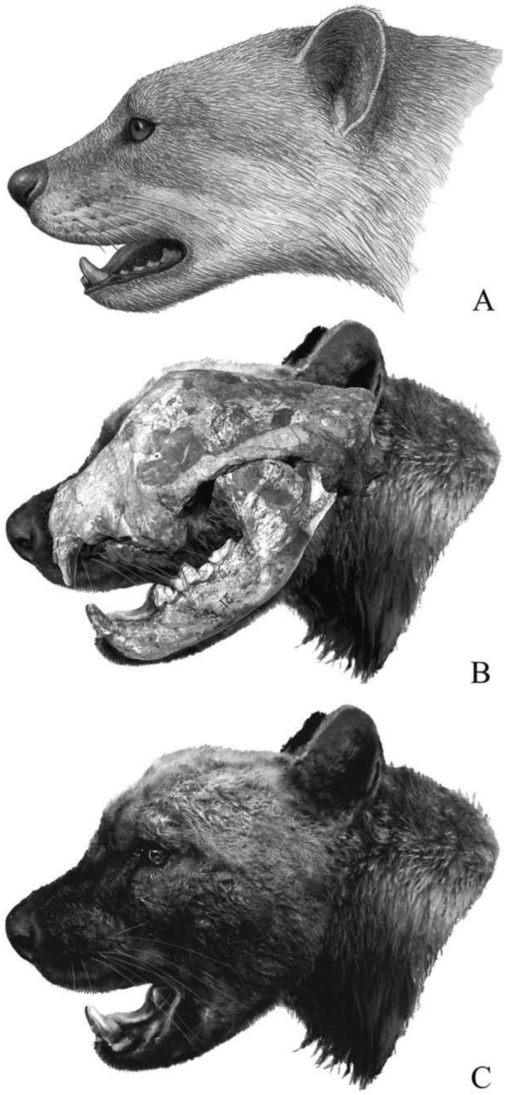

Fig. 1.37: Reconstruction of *Simocyon batalleri* (upper figure; source: Peigné et al. 2005; artist: M. Antón) and *Simocyon primigenius* (middle and lower figure; source: Spassov & Geraads, 2011; artist: V. Simeonovski).

Mephitidae BONAPARTE, 1845

As already noted in several other groups, the exact phylogenetic position and the exact contents of the mephitids are still doubtful. They are characterized by developed grinding dental areas (P4 protocone region, M1 lingual platform and m1 talonid), which have led to a convergence to the melines. Especially considering the Miocene forms, there are several genera that are considered as possible mephitids, but contradictions are still present. Herein, an oversimplified approach of including all discussed forms into Mephitinae BONAPARTE, 1845, is followed. This is preferred only for the sake of equal demonstration and not to suggest any phylogenetic content.

The oldest possible mephitid of Europe is *Miomephitis pilgrimi* DEHM, 1950, from the locality of Wintershof-West. A translation of the original diagnosis is here attempted: "mephitine, similar to *Promephitis*, but with more blunt cusps and flat grinding surfaces; m1 short in relation to p3 and p4; m1 paraconid short and oblique; m1 talonid short; P4 without a parastyle with a not well-developed protocone and a small metastyle". Unfortunately this form is known only based on dental and mandibular material.

Fig. 1.38: Holotype of *Miomephitis pilgrimi* from Wintershof-West (SNSB-BSPG-1937-II-13324).

The genus *Proputorius* FILHOL, 1890, is known from two species: *Proputorius sansaniensis* FILHOL, 1890 (larger; type locality is Sansan) and *Proputorius pusillus* (VIRET, 1951) (smaller; type locality is La Grive-Saint-Alban). This genus is characterized by a hollow m1 talonid basin and an M1 without a metaconule (Ginsburg, 1999). Both forms are relatively common and have been found in several Middle Miocene localities.

The genus *Grivamephitis* DE BEAUMONT, 1973b, is known from two species, which have been found only in the locality of La Grive-Saint-Alban: *Grivamephitis pusilla* (FORSYTH MAJOR, 1903) (smaller and older) and *Grivamephitis meini* DE BEAUMONT, 1973b (larger and younger) (Mein & Ginsburg, 2002).

Two forms, originally described from the locality of Steinheim, have been considered to be junior synonyms and to possibly have mephitid affinities. These are *Palaeomephitis steinheimensis* JÄGER, 1839, and *Trochotherium cyamoides* FRAAS, 1870. The former was described based on a partial cranium, whereas the latter based on dental material. Based on their similar dimensions, their relevant apomorphies and their coexistence in Steinheim, Wolsan (1999) suggested argued that the two forms must be considered conspecific. Therefore, only the former is considered valid. Even though this approach seems reasonable, it is herein preferred to retain the name *Trochotherium cyamoides*, until a complete skull verifies this synonymy. The dental material of this form exhibits extreme characteristics with the lower carnassial consisting mostly of the protoconid.

Two more mephitids have been described from the Vallesian of Spain. The species *Mesomephitis medius* (Petter, 1963) (originally described as *Proputorius medius* Petter, 1963, based on material from Can Llobateres) has been found in several localities of Spain (Robles, 2014). The other species is *Palaeomeles pachecoi* VILLALTA COMELLA & CRUSAFONT PAIRÓ, 1943a, which was originally reported based on material from Castell de Barberà. The presence of the latter species to Hammerschmiede (Kargopoulos et al., In Press) consists of the first report of the genus outside Spain.

Finally, the family is represented by the genus *Promephitis* GAUDRY, 1861, which includes at least 5 species in the Late Miocene of Europe, while several others have been published in a wider temporospatial range. This genus was reviewed extensively by Wang & Qiu (2004) and Geraads & Spassov (2016). The oldest species of the genus is *Promephitis pristinidens* PETTER, 1963, which is known from the Vallesian locality of Viladecaballs. However, Geraads & Spassov (2016) suggested that this species probably shouldn’t be placed to this genus. Three Turolian forms have been described: *Promephitis lartetii* GAUDRY, 1861 (type species; from Pikermi, Samos, Perivolaki, Küçükyozgat, Akkaşdağı, Hadjidimovo and Kalimantsi), *Promephitis majori* PILGRIM, 1933 (from Samos and Hadjidimovo) and *Promephitis maeotica* ALEXEJEW, 1915 (from Novo Elisavetovka) (Geraads & Spassov, 2016). Finally, the species *Promephitis alexejewi* SCHLOSSER, 1924 (originally described from Chinese material) has been reported in the latest Miocene locality of Venta del Moro (Spain) (Montoya et al., 2011).

Fig. 1.39: Holotype of *Promephitis lartetii* from Pikermi (MNHN.F.PIK3019).

Procyonidae Gray, 1825

The family Procyonidae Gray, 1825, is represented in the Miocene fossil record of Europe by only three well-defined species that are divided in two genera. The locality that has yielded two of these species is Wintershof-West (Germany).

The species *Angustictis mayri* (Dehm, 1950) (originally described as a species of *Plesictis*) is the only species of the genus *Angustictis* Wolsan, 1993, and it has been described based on material from Wintershof-West. The diagnosis provided by Wolsan (1993) includes: “Procyonids of Clade B, distinguished by a combination of the following features: posterior border of the palate situated at level of the posterior-most upper teeth; P1 single-rooted (autapomorphy); P4 protocone conical: not formed by the cingulum entirely (autapomorphy); P4 hypocone absent; anterior and posterior cingula of M1 continuous around the lingual base of the protocone; M2 two-rooted (autapomorphy)”.

Fig. 1.40: Holotype of *Angustictis mayri* from Wintershof-West (SNSB-BSPG-1937-II-13281).

The second procyonids genus from the Miocene of Europe is *Broiliana* Dehm, 1950. The diagnosis of this genus based on Wolsan (1993) includes: “Procyonids of Clade B, distinguished by a combination of the following features: posterior border of the palate situated at level of the posterior-most upper teeth; P1 two-rooted; P4 hypocone considerably smaller than the protocone or not differentiated; anterior and posterior cingula of M1 continuous around the lingual base of the protocone; M2 three-rooted and distinctly smaller than P4; m1 metaconid distinctly higher than the paraconid”. Two different species belonging to this genus have been described: *Broiliana nobilis* Dehm, 1950 (type species; Wintershof-West) and *Broiliana dehmi* de Beaumont & Mein, 1973 (Serre de Verges). Additionally, Morlo (1996) reported a new unnamed form from Weisenau.

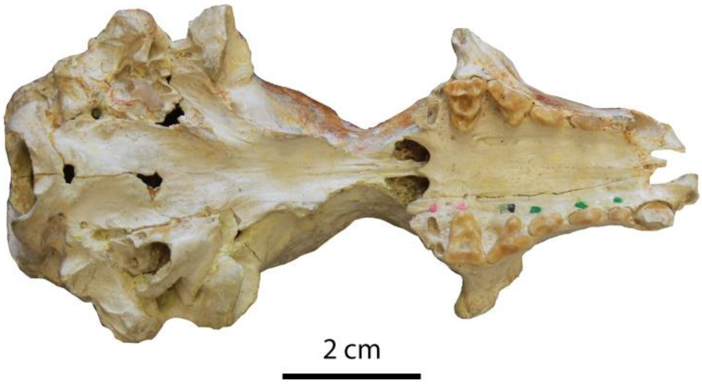

Fig. 1.41: Holotype of *Broiliana nobilis* from Wintershof-West (SNSB-BSPG-1937-II-13524).

Mustelidae FISCHER DE WALDHEIM, 1817

The family Mustelidae FISCHER DE WALDHEIM, 1817 is the most diverse of the order Carnivora, included more than 50 extant species. It has been similarly diverse through the Miocene, as it includes almost 80 species during this time. A thorough review of all these forms will require a considerable number of pages and it is far from the scope of this introduction. However, the main groups are going to be presented.

The subfamily Guloninae GRAY, 1825, is one of the most diverse mustelid groups during the Miocene. It contains several marten-like and wolverine-like genera. Many of the marten-like species have been referred to as "*Martes*" spp. A morphological and metrical review of these forms can be found in Kargopoulos et al. (In Press). The species that belong to this group are: "*Martes*" *sansaniensis* (LARTET, 1851), "*Martes*" *munki* ROGER, 1900, "*Martes*" *laevidens* DEHM, 1950, "*Martes*" *sainjoni* (MAYET, 1908), "*Martes*" *delphinensis* DEPÉRET, 1892, "*Martes*" *burdigalensis* DE BEAUMONT, 1974, "*Martes*" *collongensis* ROTH & MEIN, 1987, "*Martes*" *cadeoti* MEIN, 1958, "*Martes*" *filholi* (DEPÉRET, 1887), "*Martes*" *woodwardi* PILGRIM, 1931, "*Martes*" *jaegeri* (SCHLOSSER, 1902), "*Martes*" *lefkonensis* SCHMIDT-KITTLER, 1995, "*Martes*" *anderssoni* SCHLOSSER, 1924, "*Martes*" *melibulla* PETTER, 1963, "*Martes*" *basilii* PETTER, 1964, "*Martes*" *leporinum* (KHOMENKO, 1914), "*Martes*" *ginsburgi* MONTOYA et al., 2011. As discussed in Kargopoulos et al. (In Press) these forms are probably not congeneric to the extant martens and a revision of their taxonomic status is needed.

Other weasel- or marten-like species from the Miocene of Europe include: *Sinictis pentelici* (GAUDRY, 1862) from Pikermi, *Aragonictis araid* VALENCIANO et al., 2022 from the Aragonian of Spain, *Baranogale adroveri* PETTER, 1964 from the Late Miocene of Spain, *Heterictis oppoliensis* (WEGNER, 1913) from Oppeln, *Paramartes pococki* KRETZOI, 1952 from Polgardi and finally, the genus Circamustela Petter, 1967, including three species *Circamustela hartmanni* KARGOPOULOS et al., 2022 from Hammerschmiede, *Circamustela dechaseauxi* PETTER, 1967 from Can Llobateres and Los Valles de Fuentidueña, and *Circamustela peignei* VALENCIANO et al., 2020a from Batallones.

Fig. 1.42: Lower dentition including the holotype (A) of *Circamustela hartmanni* from Hammerschmiede. Source: Kargopoulos et al. (In Press).

The wolverine-like Miocene gulonines of Europe are less diverse and frequent than the marten-like forms. However, they still exhibit a noteworthy number of species. Possibly the oldest members of this lineage are *Dehmictis vorax* (DEHM, 1950) and *Laphyctis comitans* DEHM, 1950 from Wintershof-West. The latter genus is mainly known from the species *Laphyctis mustelinus* VIRET, 1933, which has been found in several Aragonian localities of Europe. The genus *Laphyctis* VIRET, 1933, has been considered to be closely related to the genus *Ischyrictis* HELBING, 1930. This genus is represented by two species: *Ischyrictis bezianensis* GINSBURG & BULOT, 1982, from MN 4 and MN 5 of France, and *Ischyrictis zibethoides* (BLAINVILLE, 1842) from several Aragonian localities of Europe. These species have been attributed to the tribe Ischyrictini PIA, 1939, by Valenciano et al. (2020c).

Ginsburg & Morales (1992) erected the new species *Iberictis* GINSBURG & MORALES, 1992, including two species: *Iberictis azanzae* GINSBURG & MORALES, 1992, *Iberictis buloti* GINSBURG & MORALES, 1992 from the MN 4 of Spain and France. Finally, the genus *Plesiogulo* Zdansky, 1924, includes the following species: *Plesiogulo crassa* (TEILHARD & LEROY, 1945) and *Plesiogulo brachygnathus* (SCHLOSSER, 1903) from several Vallesian and Turolian localities of Eurasia, and *Plesiogulo monspessulanus* VIRET, 1939, from the Late Miocene and Early Pliocene of Europe and South Africa. Based on the phylogenetic scheme of Valenciano et al. (2020c) these forms together with the extant wolverine are attributed to the tribe Gulonini GRAY, 1825.

Fig. 1.43: The holotype of *Dehmictis vorax* from Wintershof-West (BSPG-SNSB-1937-II-13298).

The subfamily Mellivorinae GRAY, 1865, is mainly represented in the Miocene of Europe by the genus *Eomellivora* ZDANSKY, 1924. The species included in this genus are: *Eomellivora wimani* ZDANSKY, 1924, *Eomellivora fricki* PIA, 1939, *Eomellivora moralesi* ALBA et al., 2022, *Eomellivora ursogulo* (ORLOV, 1948), *Eomellivora hungarica* KRETZOI, 1942, and *Eomellivora piveteaui* OZANSOY, 1965. A detailed revision of these forms can be found in Valenciano et al. (2015) and Alba et al. (2022). Another species that has been found in the latest Miocene of Europe is *Mellivora benfieldi* HENDEY, 1978.

The genus *Hoplictis* GINSBURG, 1961a, has been considered either as a gulonine (Ginsburg, 1999) or as a mellivorine (Valenciano et al., 2020c). It includes the species *Hoplictis noueli* (MAYET, 1908), *Hoplictis florancei* (MAYET, 1908), and *Hoplictis helbingi* (VIRET, 1951). The species *Hoplictis petteri* CRUSAFONT PAIRÓ, 1972, is now considered to be a junior synonym of *Eomellivora fricki* (Valenciano et al., 2019).

Another genus that has been considered to be closely related to the gulonines is *Trochictis* VON MEYER, 1842. This genus includes the following species: *Trochictis carbonaria* VON MEYER, 1842, *Trochictis depereti* Forsyth Major, 1903, *Trochictis artenensis* (GINSBURG, 1968), *Trochictis narcisoi* PETTER, 1976 and *Trochictis peignei* MORLO et al., 2019b. The most recent review of Morlo et al. (2019b) tentatively attributed these forms to the subfamily Ictonychinae Pocock, 1921, and provided the following emended diagnosis for the genus: "*Trochictis* is a small mustelid with the tooth formula 3132/3132, with p1/P1 and m3/M3 lacking. Premolars are unicuspid, except p4 of late Middle to Late Miocene species, which has a distal accessory cuspid. No diastemas are present in the mandible. The m1 is elongated, widest at the trigonid, with a buccal cingulid reaching to the anteriormost point of the tooth, a postmetacristid (= metastylid in Wang et al. 2017) that slopes down in a flat angle and is connected to the lingual talonid edge (= entocristid), an elongated and low talonid with the hypoconid being the highest cusp, a small hypoconulid present at the labio-distal corner, and the lingual edge of the talonid smooth or with minute cuspules. In Late Miocene species, the length/width index exceeds 2.5. The m2 is highly reduced due to a very small talonid and reaches between 40% and 46% of the length of m1." The genus ranges from MN 3 to MN 9.

An enigmatic group of mustelids is the subfamily Stromeriellinae GINSBURG, 1999. It is based on two forms that have been discovered in Wintershof-West: *Franconictis humilidens* (DEHM, 1950) and *Stromeriella franconica* DEHM, 1950. The latter genus also includes *Stromeriella depressa* MORLO, 1996, and *Stromeriella aginensis* (DE BONIS, 1973). The original diagnosis of Ginsburg (1999) at family-level is the following: "Musteloidea with postlateral sulcus of brain present, M2 small but present, elongated talonid of m1–m2".

The subfamily Melinae BONAPARTE, 1838, includes forms that are similar to the extant badgers, including several Miocene genera. However, the monophyly of this group is highly doubted. The oldest member of this group is the species *Taxodon sansaniensis* LARTET, 1851, which has been found in the Middle Miocene of Europe. Another species of the same genus is *Taxodon hessicum* GINSBURG, 1999, from the Turolian of Dorn-Dürkheim. The locality of Can Llobateres has yielded the species *Sabadellictis crusafonti* PETTER, 1963, which is known only from the type locality. The species *Plesiomeles cajali* VIRET & CRUSAFONT PAIRÓ, 1955, has been found in the Spanish Vallesian locality of Viladecaballs. The Turolian includes more badger-like species. The species *Adroverictis ginsburgi*, ALCALÁ et al., 1994, has been described based on material from Spain. *Parataxidea maraghana* (KITTL, 1887) was originally described based on material from Maragheh, but it has been discovered also in Samos (Koufos et al., 2011). The genus *Promeles* ZITTEL, 1890, includes two species: *Promeles palaeattica* WEITHOFER, 1888, from MN11 and MN12, and *Promeles macedonicus* SCHMIDT-KITTLER, 1995 from the latest Miocene. Finally, the species *Polgardia pannonica* KRETZOI, 1951, has been found in the latest Miocene locality of Polgardi.

Another mustelid group that is usually considered as a subfamily is Leptarctinae GAZIN, 1936. This group only contains three species in the Miocene of Europe. The species *Trochotherium cyamoides* FRAAS, 1870, has been originally described based on material from Steinheim, but it has also been found in La Grive-Saint-Alban (Viret, 1951). The latter locality has also yielded the only known remains of the species *Gaillardina transitoria* (Gaillard, 1899). Finally, the most common leptarctine in the Miocene of Europe is *Trocharion albanense* Forsyth Major, 1903, which was also originally described based on material from La Grive-Saint-Alban. A recent review of this group can be found in Robles et al. (2010).

The subfamily Lutrinae Bonaparte, 1845, includes the extant otters and their fossil relatives. Two species are present during the Middle Miocene of Europe: *Lartetictis dubia* (Blainville, 1842) and *Paralutra jaegeri* (Fraas, 1862). These forms are very common and they have been suggested to occupy similar niches (e.g. Heizmann & Morlo, 1998). An additional species has been originally attributed to the latter genus, named *Paralutra garganensis* Willemsen, 1983, from the latest Miocene of Gargano. However, this species has been suggested to be considerably different from the type species and it should be included to a different genus (Wang et al., 2018). The locality of Hammerschmiede has recently yielded material of the new species *Vishnuonyx neptuni* Kargopoulos et al., 2021b.

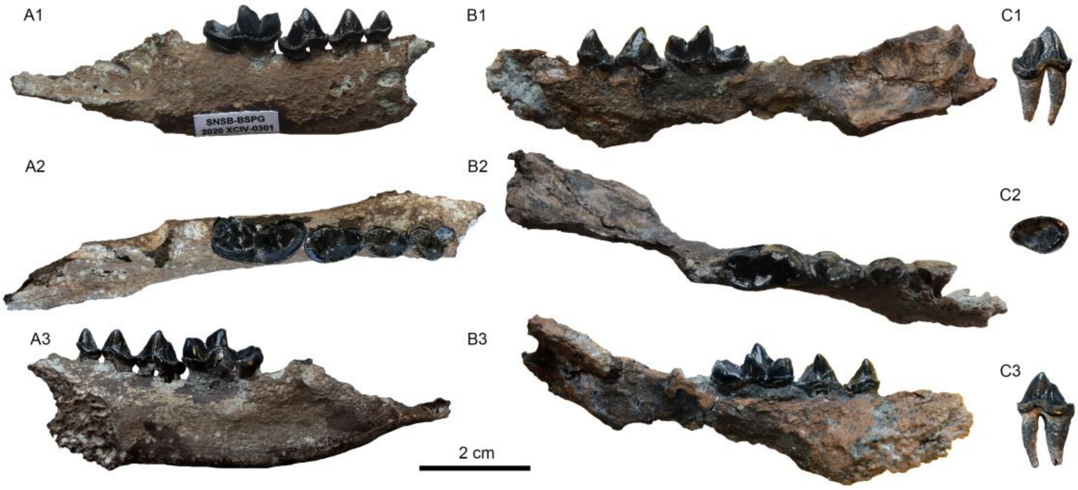

Fig. 1.44: The holotype and paratypes of *Vishnuonyx neptuni* from Hammerschmiede. Modified from Kargopoulos et al. (2021b).

The Late Miocene displays a higher diversity of lutrine species. The genus *Limnonyx* Crusafont Pairó, 1950b, has been found in the early Vallesian of Europe with two species: *Limnonyx sinerizi* Crusafont Pairó, 1950b, from Spain and *Limnonyx pontica* (von Nordmann, 1858) from Kishinev and Eppelsheim. Eppelsheim has also been the type locality for the species *Sivaonyx hessicus* (Lydekker, 1890). A late Vallesian form named *Teruelictis riparius* Salesa et al., 2013, was reported recently in the locality of La Roma 2 with a nearly complete skeleton. The Turolian of Italy has provided holotypic material for three contemporary lutrines: *Tyrrhenolutra helbingi* Hürzeler, 1987, *Paludolutra maremmana* Hürzeler, 1987, and *Paludolutra campanii* (Meneghini, 1862). The latter genus has also been reported during the same time in Spain with the species *Paludolutra lluecai* (Villalta Comella & Crusafont Pairó, 1945b). In the Balkan Peninsula, the species *Enhydriodon latipes* Pilgrim, 1931, is known only from some postcranial material from Pikermi. Finally, the species *Lutra affinis* GERVAIS, 1859 has been reported from the latest Miocene localities of Maramena and Venta del Moro.

A genus that has been considered to have similar ecological niche to the lutrines is the genus *Potamotherium* GEOFFROY SAINT-HILAIRE, 1883. This form is known from the Late Oligocene until the latest Aragonian. Two species have been described: *Potamotherium valletoni* GEOFFROY SAINT-HILAIRE, 1883, and *Potamotherium miocenicum* (PETERS, 1868). The latter is considered to be a younger form of this genus. Its affinities to the pinnipeds have been discussed in detail by several researchers (e.g. Savage, 1957; de Muizon, 1982; Rybczynski et al., 2009; Patterson et al., 2020).

Finally, another group with uncertain affinities is Plesictinae containing several Early Miocene small-sized forms. The genus *Plesictis* POMEL, 1846, includes the following species: *Plesictis pygmaeus* SCHLOSSER, 1888, *Plesictis sicaulensis* (VIRET, 1929a), *Plesictis palustris* POMEL, 1853, *Plesictis croizeti* POMEL, 1846, *Plesictis solidus* DE BONIS, 1973, *Plesictis cultellatus* DE BONIS, 1973, *Plesictis stenoplesictoides* HELBING, 1917, *Plesictis julieni* VIRET, 1929a, and *Plesictis vireti* DEHM, 1950. However, it must be mentioned that Wolsan & Morlo (1997) suggested that the species *Plesictis croizeti* is a synonym to *Herpestides antiquus*. Other members of this lineage are: *Bathygale lemanensis* (POMEL, 1853), *Paragale huerzeleri* PETTER, 1967, *Plesiogale angustifrons* POMEL, 1853, and *Plesiogale postfelina* DEHM, 1950.

Concluding, a reviewed version of the list of Miocene carnivorans of Europe published Ginsburg (1999, table 1) is herein provided:

Table 1.2: List of the carnivoran species in the Miocene of Europe

Family	**Subfamily**	**Species**	**Type Locality**
Amphicyonidae	Amphicyoninae	*Amphicyon astrei*	Garrouch (France)
		Amphicyon major	Sansan (France)
		Amphicyon eppelsheimensis	Eppelsheim (Germany)
		Amphicyon giganteus	Avaray (France)
		Paludocyon bohemicus	Tuchořice (Czech R.)
		“Amphicyon” steinheimensis	Steinheim (Germany)
		Amphicyon lactorensis	Le Mas d’Auvignon (France)
		Amphicyon olisiponensis	Lisbon (Portugal)
		Magericyon castellanus	Los Valles de Fuentidueña (Spain)
		Magericyon anceps	Batallones (Spain)
		Cynelos rugosidens	Haslach (Germany)
		Cynelos schlosseri	Wintershof-West (Germany)
		Cynelos lemanensis	Saint-Gérand-le-Puy (France)
		Cynelos helbingi	Wintershof-West (Germany)
		Pseudocyon sansaniensis	Sansan (France)
		Pseudarctos bavaricus	Tutzing (Germany)
		Ictiocyon socialis	Solnhofen (Germany)
	“Ysengrinini”	*Ysengrinia gerandiana*	Saint-Gérand-le-Puy (France)
		Ysengrinia depereti	Chilleurs-aux-bois (France)
		Ysengrinia valentiana	Buñol (Spain)
		Amphicyonopsis serus	La Grive-Saint-Alban (France)
		Crassidia intermedia	Michelsberg (Germany)
	Thaumastocyoninae	*Thaumastocyon bourgeoisi*	Pontlevoy (France)
		Thaumastocyon dirus	Los Valles de Fuentidueña (Spain)
		Tomocyon grivense	La Grive-Saint-Alban (France)
		Peignecyon felinoides	Tuchořice (Czech R.)
		Ammitocyon kainos	Batallones (Spain)
		Agnotherium antiquum	Eppelsheim (Germany)
	Haplocyoninae	*Haplocyon elegans*	Saint-Gérand-le-Puy (France)
		Haplocyon crucians	Saint-Gérand-le-Puy (France)
		Haplocyonopsis crassidens	Paulhiac (France)
		Gobicyon serbiae	Prebreza (Serbia)
		Haplocyonoides mordax	Hessler (Germany)
		Haplocyonoides suevicus	Ulm-Westtangente (Germany)
		Haplocyonoides ponticus	Melchingen (Germany)
Canidae	Caninae	“*Canis*” *cipio*	Concud (Spain)
		Eucyon debonisi	Venta del Moro (Spain)
		Eucyon monticinensis	Monticino (Italy)
Hemicyonidae	Phoberocyoninae	*Phoberogale depereti*	Montaigu-le-Blin (France)
		Phoberocyon hispanicus	Loranca (Spain)
		Phoberocyon dehmi	Wintershof-West (Germany)
		Phoberocyon aurelianensis	Orléanais Sands (France)

		Plithocyon bruneti	Pontigné (France)
		Plithocyon conquense	La Retama (Spain)
		Plithocyon antunesi	Olival de Susana (Portugal)
		Plithocyon armagnacensis	Sansan (France)
	Hemicyoninae	*Cephalogale ursinus*	Paulhiac (France)
		Cephalogale gracilis	Saint-Gérand-le-Puy (France)
		Cephalogale ginesticus	Ginestous (France)
		Zaragocyon daamsi	Cetina de Aragon (Spain)
		Hemicyon gargan	Noyant-sous-le-Lude (France)
		Hemicyon stehlini	Pontlevoy (France)
		Hemicyon sansaniensis	Sansan (France)
		Hemicyon goeriachensis	Göriach (Austria)
		Dinocyon thenardi	La Grive-Saint-Alban (France)
		Dinocyon mayorali	Tarazona de Aragon (Spain)
Ursidae	Ursinae	*Ballusia elmensis*	Elm (Germany)
		Ballusia hareni	Savigné-sur-Lathan (France)
		Ursavus isorei	Dénezé-sous-le-Lude (France)
		Ursavus brevirhinus	Steyregg (Austria)
		Ursavus primaevus	La Grive-Saint-Alban (France)
		Ursavus ehrenbergi	Halmyropotamos (Greece)
		Ursavus intermedius	Engelwies (Germany)
	Ailuropodinae	*Agriarctos depereti*	Melchingen (Germany)
		Agriarctos gaali	Hatvan (Hungary)
		Agriarctos vighi	Rózsaszentmárton (Hungary)
		Kretzoiarctos beatrix	Nombrevilla-2 (Spain)
		Miomaci pannonicum	Rudabánya (Hungary)
		Indarctos vireti	Viladecaballs (Spain)
		Indarctos arctoides	Montredon (France)
		Indarctos punjabensis	Pikermi (Greece)
		Agriotherium roblesi	Venta del Moro (Spain)
Phocidae	Devinophocinae	*Devinophoca claytoni*	Stokerau (Slovakia)
		Devinophoca emryi	Stokerau (Slovakia)
	Cystophorinae	*Miophoca vetusta*	Devínska Nová Ves (Slovakia)
		Pachyphoca ukrainica	Khomutovo (Ukraine)
	Phocinae	*Histriophoca alekseevi*	Kishinev (Moldavia)
		Monachopsis pontica	Kerch (Ukraine)
		Praepusa pannonica	Érd (Hungary)
		Praepusa vindobonensis	Neussdorf (Austria)
		Praepusa magyaricus	Pècs-Danicz (Hungary)
		Praepusa boeska	Antwerp (Belgium)
		Cryptophoca maeotica	Kishinev (Moldavia)
		Sarmatonectes sintsovi	Kishinev (Moldavia)
		Prophoca proxima	Borderhout (Belgium)
		Platyphoca danica	Skærum Mølle (Denmark)
		Leptophoca amphiatlantica	Parker’s Creek (USA)
		Gryphoca nordica	de Kuilen (Denmark)
		Planopusa semenovi	Gritsev (Ukraine)
	Monachinae	*Monotherium delognii*	(Belgium)

		Monotherium aberratum	(Belgium)
		Monotherium affine	(Belgium)
		“*Prophoca*” *rousseaui*	(Belgium)
		Pontophoca sarmatica	Kishinev (Moldavia)
		Pontophoca jutlandica	Gram (Denmark)
Ailuridae	Ailurinae	*Magerictis imperialensis*	Madrid (Spain)
	Simocyoninae	*Simocyon primigenius*	Pikermi (Greece)
		Simocyon diaphorus	Eppelsheim (Germany)
		Simocyon batalleri	Sabadell (Spain)
		Simocyon hungaricus	Csakvar (Hungary)
		Protursus simpsoni	Can Llobateres (Spain)
		Alopecocyon goeriachensis	Göriach (Austria)
	“Amphictinae”	*Amphictis antiquus*	Langy (France)
		Amphictis schlosseri	Weisenau (Germany)
		Amphictis wintershofensis	Wintershof-West (Germany)
		Amphictis prolongata	Steinbruch (Germany)
Mephitidae	Mephitinae	*Miomephitis pilgrimi*	Wintershof-West (Germany)
		Proputorius sansaniensis	Sansan (France)
		Proputorius pusillus	La Grive-Saint-Alban (France)
		Grivamephitis pusillus	La Grive-Saint-Alban (France)
		Grivamephitis meini	La Grive-Saint-Alban (France)
		Trochotherium cyamoides	Steinheim (Germany)
		Palaeomephitis steinheimensis	Steinheim (Germany)
		Mesomephitis medius	Can Llobateres (Spain)
		Palaeomeles pachecoi	Castell de Barberà (Spain)
		Promephitis pristinidens	Viladecaballs (Spain)
		Promephitis lartetii	Pikermi (Greece)
		Promephitis majori	Samos (Greece)
		Promephitis maeotica	Novo Elisavetovka (Ukraine)
		Promephitis alexejewi	Ertemte (China)
Procyonidae	Broilianinae	*Broiliana nobilis*	Wintershof-West (Germany)
		Broiliana dehmi	Serre de Verges (France)
		Angustictis mayri	Wintershof-West (Germany)
Mustelidae	Guloninae	“*Martes*” *sansaniensis*	Sansan (France)
		“*Martes*” *munki*	Häder (Germany)
		“*Martes*” *laevidens*	Wintershof-West (Germany)
		“*Martes*” *sainjoni*	Artenay (France)
		“*Martes*” *delphinensis*	La Grive-Saint-Alban (France)
		“*Martes*” *burdigalensis*	Vieux-Collonges (France)
		“*Martes*” *collongensis*	Vieux-Collonges (France)
		“*Martes*” *cadeoti*	Vieux-Collonges (France)
		“*Martes*” *filholi*	La Grive-Saint-Alban (France)
		“*Martes*” *woodwardi*	Pikermi (Greece)
		“*Martes*” *jaegeri*	Salmendingen (Germany)
		“*Martes*” *lefkonensis*	Maramena (Greece)
		“*Martes*” *melibulla*	Can Llobateres (Spain)
		“*Martes*” *basilii*	Los Aljezares (Spain)
		“*Martes*” *leporinum*	Taraklia (Moldavia)

		"Martes" ginsburgi	Venta del Moro (Spain)
		Aragonictis araid	Andurriales (Spain)
		Heterictis oppoliensis	Opole (Poland)
		Circamustela dechaseauxi	Can Llobateres (Spain)
		Circamustela peignei	Batallones (Spain)
		Circamustela hartmanni	Hammerschmiede (Germany)
		Sinictis pentelici	Pikermi (Greece)
		Baranogale adroveri	Los Mansuetos (Spain)
		Paramartes pococki	Polgardi (Hungary)
		Dehmictis vorax	Wintershof-West (Germany)
		Laphyctis commitans	Wintershof-West (Germany)
		Iberictis azanzae	Artesilla (Spain)
		Iberictis buloti	Pellecahus (France)
		Ischyrictis zibethoides	Sansan (France)
		Ischyrictis bezianensis	Bézian (France)
		Laphyctis mustelinus	La Grive-Saint-Alban (France)
		Plesiogulo monspessulanus	Montpellier (France)
		Plesiogulo crassa	Yushe (China)
		Plesiogulo brachygnathus	North China (China)
	indet.	*Hoplictis noueli*	Artenay (France)
		Hoplictis florancei	Pontlevoy (France)
		Hoplictis helbingi	La Grive-Saint-Alban (France)
	Mellivorinae	*Eomellivora wimani*	North China (China)
		Eomellivora fricki	Wien XII-Altmannsdorf (Austria)
		Eomellivora moralesi	Abocador de Can Mata (Spain)
		Eomellivora ursogulo	Grebeniki (Ukraine)
		Eomellivora hungarica	Polgardi (Hungary)
		Eomellivora pivetaui	Yassiören (Turkey)
		Mellivora benfieldi	Langebaanweg (South Africa)
	Ictonychinae?	*Trochictis artenensis*	Artenay (France)
		Trochictis carbonaria	Käpfnach (Czech Republic)
		Trochictis narcisoi	Can Llobateres (Spain)
		Trochictis depereti	La Grive-Saint-Alban (France)
		Trochictis peignei	Eppelsheim (Germany)
	Stromeriellinae	*Stromeriella franconica*	Wintershof-West (Germany)
		Stromeriella depressa	Amöneburg (Germany)
		Stromeriella aginensis	Laugnac (France)
		Franconictis humilidens	Wintershof-West (Germany)
	Melinae	*Taxodon sansaniensis*	Sansan (France)
		Taxodon hessicus	Dorn-Dürkheim (Germany)
		Promeles palaeattica	Pikermi (Greece)
		Promeles macedonicus	Maramena (Greece)
		Plesiomeles cajali	Viladecaballs (Spain)
		Sabadellictis crusafonti	Can Llobateres (Spain)
		Adroverictis ginsburgi	Ademuz (Spain)
		Adroverictis schmidtkittleri	Yeni Eskihisar (Turkey)
		Polgardia pannonica	Polgardi (Hungary)
	Leptarctinae	*Trocharion albanense*	La Grive-Saint-Alban (France)

		Trochotherium cyamoides	Steinheim (Germany)
		Gaillardina transitoria	La Grive-Saint-Alban (France)
	Lutrinae	*Paralutra jaegeri*	Steinheim (Germany)
		“*Paralutra*” *garganensis*	Gargano (Italy)
		Lartetictis dubia	Sansan (France)
		Limnonyx sinerizi	Can Ponsic (Spain)
		Limnonyx pontica	Kishinev (Moldavia)
		Sivaonyx hessicus	Eppelsheim (Germany)
		Enhydriodon latipes	Pikermi (Greece)
		Tyrrhenolutra helbingi	Baccinello V1 (Italy)
		Teruelictis riparius	La Roma 2 (Spain)
		Paludolutra lluecai	Los Aljezares (Spain)
		Paludolutra maremmana	Monte Bamboli (Italy)
		Paludolutra campanii	Monte Bamboli (Italy)
		Lutra affinis	Montpellier (France)
		Vishnuonyx neptuni	Hammerschmiede (Germany)
indet.	Potamotheriinae	*Potamotherium valletoni*	Saint-Gérand-le-Puy (France)
indet.		*Potamotherium miocenicum*	Eibiswald (Austria)
indet.	Plesictinae	*Plesictis pygmaeus*	Mouillac (France)
indet.		*Plesictis sicaulensis*	Coderet (France)
indet.		*Plesictis palustris*	Saint-Gérand-le-Puy (France)
indet.		*Plesictis croizeti*	Saint-Gérand-le-Puy (France)
indet.		*Plesictis solidus*	Paulhiac (France)
indet.		*Plesictis cultellatus*	Paulhiac (France)
indet.		*Plesictis stenoplesictoides*	Chavroches (France)
indet.		*Plesictis julieni*	Saint-Gérand-le-Puy (France)
indet.		*Plesictis vireti*	Wintershof-West (Germany)
indet.		*Bathygale lemanensis*	Saint-Gérand-le-Puy (France)
indet.	indet.	*Paragale huerzeleri*	Montaigu-le-Blin (France)
indet.	indet.	*Plesiogale angustifrons*	Montaigu-le-Blin (France)
indet.	indet.	*Plesiogale postfelina*	Wintershof-West (Germany)
indet.	indet.	*Herpestides antiquus*	Saint-Gérand-le-Puy (France)
Felidae	Felinae	*Stenogale brevidens*	Haslach (Germany)
		Stenogale julieni	Chavroches (France)
		Stenogale aurelianensis	Orleanais (France)
		Pseudictis guntianus	Günzburg (Germany)
		Proailurus lemanensis	Saint-Gérand-le-Puy (France)
		Leptofelis vallesiensis	Batallones (Spain)
		Pristifelis attica	Pikermi (Greece)
		Felis christoli	Montpellier (France)
		Felis zitteli	La Grive-Saint-Alban (France)
		Styriofelis lorteti	La Grive-Saint-Alban (France)
	Pantherinae	*Miopanthera turnauensis*	Göriach (Austria)
	Machairodontinae	*Pseudaelurus romieviensis*	La Romieu (France)
		Pseudaelurus quadridentatus	Sansan (France)
		Yoshi garevskii	Karaslari (North Macedonia)
		Yoshi minor	Shang-Yin-Kou (China)
		“*Metailurus parvulus*”	Pikermi (Greece)

		Metailurus major	Tai-Chia-Kou (China)
		Metailurus boodon	Grebeniki (Ukraine)
		Promegantereon ogygia	Eppelsheim (Germany)
		Paramachairodus orientalis	Maragheh (Iran)
		Paramachaerodus maximiliani	Shang-Yin-Kou (China)
		Stenailurus teilhardi	Piera (Spain)
		Fortunictis acerensis	Casa del Acero (Spain)
		Machairodus aphanistus	Eppelsheim (Germany)
		Machairodus alberdiae	Los Valles de Fuentidueña (Spain)
		Amphimachairodus giganteus	Pikermi (Greece)
Barbourofelidae	Barbourofelinae	*Albanosmilus jourdani*	La Grive-Saint-Alban (France)
		Afrosmilus hispanicus	La Artesilla (Spain)
		Prosansanosmilus peregrinus	Langenau (Germany)
		Prosansanosmilus eggeri	Sandelzhausen (Austria)
		Sansanosmilus palmidens	Sansan (France)
Herpestidae	Herpestinae	*Leptoplesictis aurelianensis*	Pontlevoy (France)
		Leptoplesictis atavus	Vieux-Collonges (France)
		Leptoplesictis filholi	La Grive-Saint-Alban (France)
Viverridae	Genettinae	*Semigenetta laugnacensis*	Laugnac (France)
		Semigenetta elegans	Wintershof-West (Germany)
		Semigenetta sansaniensis	Sansan (France)
		Semigenetta grandis	Castell de Barberà (Spain)
		Semigenetta cadeoti	La Romieu (France)
	Viverrinae	*Viverrictis vetusta*	Vieux-Collonges (France)
		Viverrictis modica	La Grive-Saint-Alban (France)
	indet.	*Jourdanictis grivensis*	La Grive-Saint-Alban (France)
Lophocyonidae	Lophocyoninae	*Sivanasua viverroides*	Rothenstein (Germany)
		Sivanasua moravica	Dolnice (Czech R.)
		Euboictis aliverensis	Aliveri (Greece)
		Lophocyon carpathicus	Košice-Bankov (Slovakia)
		Lophocyon paraskevaidisi	Thymiana (Greece)
Hyaenidae	Ictitheriinae	*Plioviverrops collectus*	Laugnac (France)
		Plioviverrops gervaisi	Vieux-Collonges (France)
		Plioviverrops gaudryi	La Grive-Saint-Alban (France)
		Plioviverrops orbignyi	Pikermi (Greece)
		Plioviverrops guerini	Piera (Spain)
		Plioviverrops faventinus	Monticino (Italy)
		Protictitherium gaillardi	La Grive-Saint-Alban (France)
		Protictitherium crassum	La Grive-Saint-Alban (France)
		Protictitherium llopisi	Can Bayona (Spain)
		Protictitherium thessalonikensis	Ravin de la Pluie (Greece)
		Thalassictis certa	La Grive-Saint-Alban (France)
		Thalassictis montadai	Hostalets de Pierola (Spain)
		Thalassictis robusta	Kishinev (Moldavia)
		“Hyaenictitherium parvum”	Belka (Ukraine)
		Hyaenictitherium hyaenoides	North China (China)
		Hyaenictitherium magnum	Cherevichnoe (Ukraine)
		Hyaenictitherium venator	Novoelisavetovka (Ukraine)

		Hyaenictitherium wongii	North China (China)
		Ictitherium spelaeum	Gritsev (Ukraine)
		Ictitherium viverrinum	Pikermi (Greece)
		Ictitherium ibericum	Bazalethi (Georgia)
		Ictitherium pannonicum	Polgardi (Hungary)
		Miohyaenotherium bessarabicum	Belka (Ukraine)
	Hyaeninae	*Lycyaena chaeretis*	Pikermi (Greece)
		Hyaenictis almerai	San Miguel del Toudell (Spain)
		Hyaenictis graeca	Pikermi (Greece)
		Chasmaporthetes bonisi	Dytiko (Greece)
		Belbus beaumonti	Samos (Greece)
		Allohyaena kadici	Csakvar (Hungary)
		Allohyaena sarmatica	Gritsev (Ukraine)
		Adcrocuta eximia	Pikermi (Greece)
Percrocutidae	Percrocutinae	*Percrocuta miocenica*	Prebreza (Serbia)
		Percrocuta abessalomi	Belomechs (Georgia)
		Dinocrocuta gigantea	North China (China)
		Dinocrocuta robusta	Kalfa (Moldova)
		Dinocrocuta salonicae	Thessaloniki (Greece)

Chapter 2

The Miocene of Europe: Faunas, Palaeogeography and Palaeoclimate

Fig. 2.1: Wildlife of the Miocene era. Artist: M. Antón.

Faunas

The following pages are focusing on the carnivoran faunas of the most well-known Miocene localities of Europe. This approach is helpful in providing a temporospatial frame for the study of evolution, taxonomy and ecology of fossil carnivorans. Some Asian and African localities are also discussed, because of their affinities with the European ones. This section is organized based on the age of the localities. However, it must be noted that usually the exact age of the studied localities is not known. Greater detail is given in late Middle and early Late Miocene localities, as they exhibit the most noteworthy resemblances with Hammerschmiede.

The discussed localities are studied using the Mammals from the Mediterranean Neogene units (MN units). This is a system originally developed during the 1960s–70s (Thaller, 1965, 1966, 1972; Mein, 1975, 1979; Fahlbusch, 1976) that has been used in order to divide mammalian assemblages and to correlate them with stratigraphic periods. In this sense, such a system is interpreted as a biochronologic tool and not as a biostratigraphic one (Gradstein, 2012). Thirteen zones have been established for the Miocene and each one of them is defined based on the faunal assemblage of one type locality. The most widely used systems are those of Mein (1989), de Bruijn et al. (1992) and Agustí et al. (2001). Since many members of these assemblages have been discovered in a restricted geographical range, the MN system must also be used in a relatively regional scale. It must be noted that these MN units are not biozones in the traditional sense, because they are not formed by the ranges of taxa, but by the evolutionary stage of characteristic lineages in mammalian assemblages (Fahlbusch, 1991). The latter paper includes a comprehensive discussion on the theoretical background and the practical problems of the MN system. A detailed historical overview of this matter can also be found in van Dam (2003).

Not all of the discussed localities are characterized by similar deposition environments. Some of them correspond to stratified deposits, whereas others represent fissure fillings (e.g., La Grive and Wintershof-West). Therefore, the chronologic framework for the latter localities is not that clear. A detailed review concerning the formation, stratigraphy and wider use of fissure fillings can be found in Bolliger & Rummel (1994). Additionally, many localities are composites of several individual sites in a broader region and longer stratigraphic time (e.g., Samos, Pontlevoy, Eppelsheim etc.). Thus, it is possible that not all the discussed carnivoran species have been sympatric and that the locality (as a whole) spans through a long time period. However, even though such inconsistencies exist, the relevant comparisons are still considered useful, if these notes are taken into account.

Early Miocene

MN 1

Paulhiac: The locality of Paulhiac is situated a few miles north of the village of Monflanquin in Lot-et-Garonne (France) (de Bonis, 1973, fig. 1). It is possibly the oldest Miocene locality that has yielded a considerable amount of carnivoran remains. It has been considered as the typical MN 1 locality (Mein, 1989; de Bruijn et al., 1992).

Therefore, the age of the locality is estimated to be between 23.8 and 22.1 Ma (Agustí et al., 2001). The carnivoran list of the locality based on de Bonis (1973) includes: *Cephalogale ursinus*, *Cephalogale ginesticus*, *Haplocyon elegans*, *Haplocyon crucianus*, *Haplocyonopsis crassidens* (type locality for species and genus), *Amphicyon* cf. *astrei*, *Ysengrinia tolosana*, Amphicyonidae indet. (2 species), *Plesictis solidus* (type locality), *Plesictis palustris*, *Plesictis cultellatus* (type locality), *Plesictis* sp. (2 species) and *Proailurus lemanensis*. Therefore, the guild of Paulhiac includes 14 carnivorans.

MN 2

Laugnac: This locality is situated slightly more south than Paulhiac, standing between the small cities of Agen and Villeneuve-sur-Lot in Lot-et-Garonne (France) (de Bonis, 1973, fig. 1). The fauna of Laugnac is considered the most typical for the younger half of MN 2 (Mein, 1989; de Bruijn et al., 1992). Therefore, the age of the locality is slightly older than 20.0 Ma. The carnivoran species of the locality according to de Bonis (1973) are: *Haplocyon elegans*, *Haplocyonoides mordax*, *Cynelos rugosidens*, *Cynelos lemanensis*, *Amphicyon astrei*, *Ysengrinia* sp., *Plesictis* aff. *solidus*, *Semigenetta laugnacensis* (as “*Plesictis laugnacensis*”; type locality), *Palaeogale minuta*, *Plesiogale angustifrons*, *Amphictis aginensis* (type locality), *Herpestides collectus* (type locality) and *Proailurus lemanensis*. Therefore, 13 carnivoran species in total are present in the locality.

MN 3

Estrepouy: The locality of Estrepouy is situated very close to the village of La Romieu (Gers, France) (Roman & Viret, 1934, fig. 1). However, the age of this fauna is considered to be older than that of La Romieu (Roman & Viret, 1934) and slightly older than that of Wintershof-West (Mein, 1989; de Bruijn et al., 1992; Ginsburg, 2011; Hugueney & Bulot, 2011). Therefore, an age slightly older than 17.4 Ma can be suggested. Ginsburg (2011) published the presence of the following carnivorans in the locality: *Amphicyon lanthanicus*, *Cynelos helbingi*, *Plithocyon bruneti*, *Hemicyon gargan*, *Palaeogale hyaenoides*, *Semigenetta elegans* and *Styriofelis turnauensis* (as “*Pseudaelurus turnauensis*”). Therefore, the Estrepouy fauna includes 7 species of carnivorans.

Wintershof-West: This fissure-filling locality is situated a few miles north of the city of Eichstätt in Bavaria (Germany). The age of the locality has been estimated to be slightly younger than that of Beaulieu (17.5 Ma; Aguilar et al., 2003), so approximately 17.4 Ma. However, Böhme et al. (2012, fig. 5) consider it as approximately 18.5 Ma. It has been considered by de Bruijn et al. (1992) as the most typical MN 3 locality. The carnivorans of this locality were studied in detail by Dehm (1950). The carnivoran list includes: *Amphicyon socialis*, *Amphicyon acutidens* (type locality), *Amphicyon* *dietrichi* (type locality), *Amphicyon* aff. *crassidens*, *Amphicyon* aff. *giganteus*, *Cynelos schlosseri* (as "*Amphicyon schlosseri*"; type locality), *Cynelos helbingi* (as "*Amphicyon helbingi*" type locality), aff. *Pseudocyon sansaniensis*, *Hemicyon* sp. (two species), *Ursavus elmensis*, *Plesictis vireti* (type locality), *Plesictis* aff. *pygmaeus*, *Plesictis* aff. *sicaulensis*, *Angustictis mayri* (as *Plesictis mayri*; type locality), *Franconictis humilidens* (as "*Plesictis humilidens*"; type locality), *Amphictis* aff. *antiquus*, "*Martes*" *laevidens* (type locality), *Dehmictis vorax* (as "*Laphyctis vorax*"; type locality), *Laphyctis comitans* (type locality), *Palaeogale minuta*, *Palaeogale hyaenoides* (type locality), *Plesiogale postfelina* (type locality), *Broiliana nobilis* (type locality for species and genus), *Stromeriella franconica* (type locality for species and genus), Melinae indet., *Miomephitis pilgrimi* (type locality for species and genus), *Semigenetta elegans* (type locality), Plioviverrops gervaisi (as "*Progenetta praecurrens*") and *Styriofelis turnauensis* (as "*Pseudaelurus transitorius*"). Obviously, the carnivoran datum from Wintershof-West is very rich, including 30 species, while for 16 of them it is their type locality. Therefore, it is reasonable to state that this is one of the most important localities in the Early Miocene of Europe concerning the mammalian carnivores.

MN 4

Artenay: This locality is situated near the small village of Artenay in Loiret (France). The age of Artenay is estimated to be near the base of MN 4, so approximately 17.0 Ma (Mein, 1989; de Bruijn et al., 1992; Agustí et al., 2001). The carnivoran list published by Mayet (1908) and Ginsburg (1990, 2002) includes: *Amphicyon giganteus*, *Cynelos schlosseri*, *Ictiocyon socialis*, *Pseudocyon sansaniensis*, *Ursavus brevirhinus*, *Hemicyon stehlini*, *Palaeogale hyaenoides*, *Palaeogale minuta*, "*Martes*" *sainjoni* (type locality), "*Martes*" *munki*, "*Martes*" *burdigaliensis*, *Ischyrictis zibethoides*, *Hoplictis noueli*, *Trochictis artenensis* (type locality), *Potamotherium miocenicum*, *Semigenetta elegans*, *Leptoplesictis aurelianensis* (as "*Herpestes aurelianensis*"), *Prosansanosmilus peregrinus*, *Miopanthera lorteti* (as "*Pseudaelurus lorteti*"), *Styriofelis lorteti* (as "*Pseudaelurus lorteti*") and the creodont *Hyaenailourus sulzeri*. Therefore, the fauna of the locality includes 21 carnivore species.

Pellecahus: This locality is very close to that of Estrepouy, La Romieu and Bézian in Gers (France) (Roman & Viret, 1934, fig. 1). The age of the locality has been suggested to be between that of Artenay and La Romieu (de Bruijn et al., 1992), so between 16.5 and 17.0 Ma. The carnivoran guild of Pellecahus based on Roman & Viret (1934) and Bulot & Ginsburg (1993) includes: *Hemicyon stehlini*, *Pseudarctos bavaricus*, *Ischyrictis bezianensis*, *Iberictis buloti*, "*Martes*" *burdigaliensis*, *Trochictis artenensis*, *Palaeogale minuta*, *Semigenetta* cf. *cadeoti* and *Pseudaelurus romieviensis*. Therefore, 11 species of carnivorans are present in this locality. It must be noted that Ginsburg (1999) doesn't mention the presence of "*Martes*" *burdigaliensis* in Pellecahus, but in Artenay.

La Romieu: This locality is situated at the small village of La Romieu in Gers (France). It is considered to be at the middle of MN 4, so its age is estimated to be approximately 16.5 Ma (Mein, 1989; de Bruijn et al., 1992; Agustí et al., 2001). The carnivoran fauna of this locality, based on Roman & Viret (1934) includes: *Amphicyon major* (including "*Amphicyon* aff. *steinheimensis*" and "*Amphicyon lactorensis*"), *Amphicyon giganteus*, *Pseudaelurus romieviensis* (type locality), *Semigenetta cadeoti* (type locality) and *Felis* sp. Therefore, only 5 species are included in this locality's fauna. However, La Romieu consists of the type locality for two of them, increasing the interest this fauna. The database of NOW also includes *Pseudocyon sansaniensis*, *Trochictis artenensis* and *Styriofelis turnauensis*. However, there is no actual report of these species in La Romieu. It is possible that there has been a misunderstanding with the locality of Bézian, as it is often called as "Bézian près de La Romieu". Additionally, Ginsburg (1999) mentions that *Paralutra jaegeri* is known from La Romieu. Again, it is a misconception, as the specimen described as "*Paralutra larteti*" by Roman & Viret (1934) comes from the locality of Pellecahus (Roman & Viret, 1934, p. 17). Possibly, the misunderstanding stems from the title of the publication of Roman & Viret (1934): "La faune de Mammiferes du Burdigalien de La Romieu (Gers)". Therefore, only the 5 aforementioned species are confirmed to be present in La Romieu.

Bézian: The locality of Bézian is situated very close to the locality of La Romieu (Gers, France) and it is suggested to have similar age (Ginsburg & Bulot, 1992; Ginsburg, 1999). The carnivoran fauna (studied by Ginsburg & Bulot, 1982) includes the following taxa: *Amphicyon giganteus*, *Pseudocyon sansaniensis*, *Cynelos schlosseri*, *Hemicyon stehlini*, *Palaeogale minuta*, "*Martes*" *sainjoni*, "*Martes*" *munki*, *Ischyrictis bezianensis* (type locality), *Trochictis artenensis* (as "*Mionictis artenensis*"), *Protictitherium gaillardi*, *Styriofelis turnauensis* (as "*Pseudaelurus transitorius*"), *Miopanthera lorteti* (as "*Pseudaelurus lorteti*") and *Prosansanosmilus peregrinus*. Therefore, the carnivoran guild of the locality includes 13 species.

Erkertshofen 2: This fissure-filling locality is situated extremely close to that of Wintershof-West (Bavaria, Germany) (Roth, 1989, fig. 1). Two fissures have been recognized: Erkertshofen 1 and Erkertshofen 2. The former has yielded only micromammalian remains, whereas the latter has also provided macromammals. The age of both layers is estimated to be typical of MN 4 and similar to La Romieu, so approximately 16.5 Ma (Mein, 1989; de Bruijn et al., 1992; Agustí et al., 2001). The carnivoran guild of Erkertshofen 2, based on Roth (1989), includes the following forms: *Hemicyon stehlini*, *Cynelos* cf. *helbingi*, *Laphyctis mustelinus*, *Hoplictis florancei*, cf. "*Martes*" *munki*, *Palaeogale hyaenoides*, *Semigenetta elegans* and cf. *Styriofelis turnauensis*. Therefore, this guild includes 8 species.

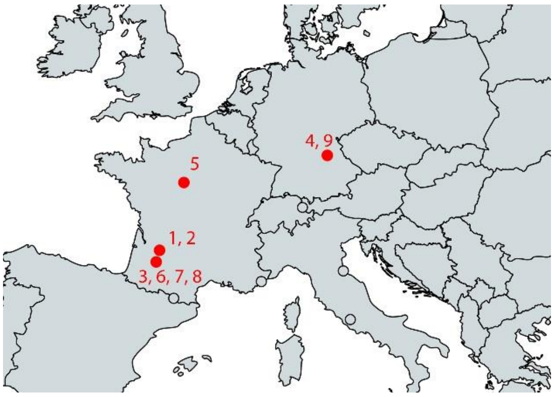

Fig. 2.2: Early Miocene localities of Europe. 1: Paulhiac, 2: Laugnac, 3: Estrepouy, 4: Wintershof-West, 5: Artenay, 6: Pellecahus, 7: La Romieu, 8: Bézian, 9: Erkertshofen.

Middle Miocene

MN 5

Sandelzhausen: This locality is situated near the small city of Mainburg (Bavaria, Germany) (Moser et al., 2009, fig. 1). Some years ago, it was thought to belong to MN 6 (Mein, 1989; de Bruijn et al., 1992). However, more recent approaches have revealed that in fact, it is position at the base of MN 5, having an age of approximately 16.0 Ma (Moser et al., 2009). Böhme et al. (2012, fig. 5) suggest a slightly older age, at 16.5 Ma. Another study, conducted by Abdul Azis et al. (2008) suggested an age of approximately 16.4 Ma (C5Cn.2n.). However, new approaches correlate these results to the base of C5C1n, at 15.15 Ma (Böhme, pers. commun.). The carnivoran guild of the locality based on Nagel et al. (2009) includes the following forms: *Amphicyon* cf. *major, Pseudarctos bavaricus*, *Hemicyon stehlini*, *Ischyrictis zibethoides*, "*Martes*" cf. *munki*, *Proputorius pusillus*, *Leptoplesictis* cf. *aurelianensis*, *Pseudaelurus romieviensis* and *Prosansanosmilus eggeri*. Therefore, the carnivoran fauna of Sandelzhausen includes 9 species.

Vieux Collonges: Vieux-Collonges is situated north of Lyon (Auvergne-Rhône-Alpes, France). This fissure-filling locality has been considered to be at the base of MN 5, possibly even entering the upper part of MN 4 (de Bruijn et al. 1992). Therefore, an age of approximately 16.0 Ma can be suggested (Agustí et al., 2001). The carnivoran fauna based on Mein (1958), de Beaumont & Mein (1972), de Beaumont (1973, 1974) and Roth & Mein (1987) includes: *Pseudarctos* sp., *Hemicyon vincenti* (type locality), *Ursavus elmensis*, Ursidae indet., *Ischyrictis zibethoides*, *Laphyctis mustelinus*, "*Martes*" *filholi*, "*Martes*" *delphinensis*, "*Martes*" *cadeoti*, "*Martes*" *munki*, "*Martes*" *collongensis*, "*Martes*" *burdigaliensis*, *Paralutra jaegeri*, *Trocharion albanense*, *Proputorius pusillus* (as "*Martes*" *pusilla*), *Alopecocyon getti* (possibly a junior synonym to *Alopecocyon goeriachensis*; if not, Vieux-Collonges is the type locality), *Plesiogale postfelina*, *Semigenetta sansaniensis* (as "*Semigenetta* aff. *repelini*"), *Viverrictis vetusta* (type locality), *Leptoplesictis aurelianensis* (as "*Herpestes aurelianensis*"), *Plioviverrops gervaisi*, *Protictitherium gaillardi* (as "*Progenetta gaillardi*"), *Protictitherium crassum* (as "*Progenetta* aff. *crassa*"), *Pseudaelurus* aff. *quadridentatus* and *Styriofelis turnauensis* (as "*Pseudaelurus*" *turnauensis*").

Therefore, the carnivoran guild of the locality includes 25 species, making it one of the richest in the Miocene fossil record.

Castelnau d'Arbieu: This locality is situated slightly west to the small village of Castelnau d'Arbieu (Gers, France). It has been considered as slightly younger than Vieux-Collonges, but older than Pontlevoy, so it stands at the middle-older part of MN 5 (de Bruijn et al., 1992). Therefore, an age of approximately 16.0–15.0 Ma can be suggested (Agustí et al., 2001). The carnivoran fauna of the locality according to Bulot et al. (1992) includes *Amphicyon steinheimensis*, *Pseudarctos bavaricus*, *Proputorius* cf. *pusillus*, *Semigenetta* cf. *sansaniensis* (as "*Semigenetta* cf. *repelini*") and *Protictitherium crassum*. Therefore, only 5 carnivorans have been found in this locality.

Mala Miliva: The locality of Mala Miliva is situated a few miles north to the village of Miliva in Serbia (Petronijevic, 1967). Based on de Bruijn et al. (1992, Table 2), this locality has similar age with Castelnau d'Arbieu and the upper part of Vieux-Collonges. Therefore, it belongs to the lower part of MN 5, which corresponds to an age of approximately 16.0–15.0 Ma (Agustí et al., 2001). The carnivoran fauna of Mala Miliva based on Petronijevic (1967) includes: *Lartetictis dubia* (as "*Mionictis dubia*"), "*Martes*" *munki* and *Semigenetta sansaniensis* (as "*Semigenetta mutata*"). This locality has been added mainly because of its geographical position.

Pontlevoy: This locality is situated a few miles west to the village of Pontlevoy (NOW database). Pontlevoy has been chosen as the reference locality for MN 5 (Mein, 1989; de Bruijn et al., 1992). Kälin & Kempf (2009) state that the locality of Pontlevoy is approximately 1.4 Ma older than that of Sansan. Therefore, if the age estimation of 15.0 Ma for Sansan by Sen (1997) is correct, then the age of Pontlevoy is approximately 16.4 Ma. The carnivoran fauna according to Stehlin & Helbing (1925) includes: *Amphicyon major*, *Amphicyon* sp. (2 species), *Thaumastocyon bourgeoisi* (type locality for genus and species), *Hemicyon* cf. *goeriachensis*, *Dinocyon* sp., Ursidae indet., "*Martes*" *munki*, *Ischyrictis zibethoides* (as "*Martes zibethoides*"), *Herpestes dissimilus*, *Leptoplesictis aurelianensis* (as "*Herpestes aurelianensis*"), *Semigenetta sansaniensis* (as "*Viverra* cf. *sansaniensis*"), *Pseudaelurus quadridentatus*, *Styriofelis turnauensis* (as "*Pseudaelurus transitorius*"), *Miopanthera lorteti* (as "*Pseudaelurus lorteti*"), Machairodontinae indet. (1 species) and Carnivora indet. (1 species). Therefore, 17 species are included in the Pontlevoy carnivoran guild.

Sibnica: This locality is situated in the village of Sibnica in Serbia (Petronijevic, 1967). It is considered younger than Mala Miliva by de Bruijn et al. (1992), being more similar to Pontlevoy. Therefore, it is considered as middle-late MN 5, corresponding to an age of approximately 15.0–13.8 Ma (Agustí et al., 2001). The carnivoran fauna of Sibnica based on Petronijevic (1967) includes: *Semigenetta sansaniensis* (as "*Semigenetta mutata*") and *Leptoplesictis aurelianensis* (as "*Herpestes aurelianensis*"). Therefore, only two carnivoran species are known in Sibnica. This locality is added because of its geographical position.

Paşalar: This locality is situated near the village of Paşalar in Bursa (Turkey) (Valenciano et al., 2020b, fig. 1). It has been considered as a basal MN 6 locality with similar age as that of Göriach (Mein, 1989; de Bruijn et al., 1992). However, new faunal data suggest a late MN 5 age (Alpagut et al., 2016). On the other hand, Böhme et al. (2011) have argued that biochronolocigal correlations with Europe in terms of rodents are irrelevant (based on the considerable differences between the regions) and suggested that an age of 13.8 Ma is highly possible. The carnivoran guild of the locality based on Schmidt-Kittler (1976), Alpagut et al. (2016) and Valenciano et al. (2020b) includes: *Amphicyon* cf. *major*, *Amphicyon* n. sp. (1 species), *Pseudarctos* sp. (1 species), *Gobicyon* sp. (1 species), *Hemicyon sansaniensis*, *Plithocyon* sp. (1 species), *Ursavus* cf. *primaevus*, *Ursavus* aff. *intermedius*, *Plesiogulo* n. sp. (1 species), *Anatolictis laevicaninus*, *Hoplictis anatolicus*, *Trocharion albanense*, *Proputorius* sp. (1 species), *Trochictis depereti*, *Lartetictis pasalarensis* (type locality), Lutrinae indet. (1 species), *Leptoplesictis* sp. (1 species), *Protictitherium intermedium*, *Protictitherium* aff. *gaillardi*, *Protictitherium cingulatum*, *Protictitherium* cf. *crassum*, *Protictitherium* sp. (1 species), *Percrocuta miocenica*, *Percrocuta* sp. (1 species), *Sansanosmilus* sp. (1 species), *Miopanthera lorteti* (as "*Pseudailurus lorteti*") and *Pseudaelurus* cf. *quadridentatus*. Therefore, the fauna of Paşalar includes 27 carnivoran species. However, a comprehensive review is required as many groups raise questions, e.g. the five different forms of *Protictitherium*.

MN 6

Sansan: Sansan is one of the most thoroughly studied Middle Miocene localities of Europe. It is situated a few miles west to the city of Toulouse (Ginsburg, 1961a, fig. 1). It is the most typical MN 6 locality (Mein, 1989; de Bruijn, 1992; Agustí et al., 2001). Sen (1997) estimated the age of Sansan at 15.0 Ma, which however is slightly old for an MN 6 locality. Peigné (2012) has provided the most recent review of the carnivorans of Sansan, including the following species: *Amphicyon major* (type locality), *Pseudocyon sansaniensis* (type locality), *Plithocyon armagnacensis* (type locality), *Hemicyon sansaniensis* (type locality), Ursidae indet., *Alopecocyon goeriachensis*, "*Martes*" *gaudryi* (as "*Martes sansaniensis*"; type locality), *Ischyrictis zibethoides* (type locality), *Taxodon sansaniensis* (type locality), *Proputorius sansaniensis* (type locality), *Lartetictis dubia* (type locality), Mustelidae indet. (2 species), *Sansanosmilus palmidens* (type locality), *Leptoplesictis atavus*, *Viverrictis modica*, *Semigenetta sansaniensis* (type locality), *Pseudaelurus quadridentatus* (type locality), *Miopanthera lorteti* (as "*Styriofelis lorteti*"), *Styriofelis turnauensis* and Carnivora indet. (1 species). The sum is 21 different species of carnivorans, and for 12 of them Sansan is the type locality.

Göriach: This locality is situated a few miles north of the small city of Bruck an der Mur (Styria, Austria). The age of the locality given by Aiglstorfer et al. (2014) (in agreement with Böhme et al. 2012, fig. 5) is approximately 14.5 Ma. The carnivoran fauna of the locality according to Thenius (1949) includes: *Amphicyon steinheimensis*, *Pseudarctos bavaricus*, *Hemicyon sansaniensis* (also as "*Harpaleocyon sansaniensis*"), *Ursavus brevirhinus*, *Lartetictis dubia* (as "*Mionictis dubia*"), *Trochictis depereti*, Mustelidae indet. (1 species), *Alopecocyon goeriachensis* (as "*Alopecodon leptorhynchus*" type locality), *Styriofelis turnauensis* (as "*Pseudaelurus turnauensis*"; type locality) and *Pseudaelurus quadridentatus* (as "*Pseudaelurus hyaenoides*"). Therefore, the guild of Göriach includes 10 carnivoran species.

Prebreza: This locality is situated a few miles northwest of the small town of Blace (Serbia) (Stefanović, 2004). The age of the fauna is estimated to be MN 6, but younger than Sansan, being more similar to Manchones (Mein, 1989; de Bruijn et al., 1992; Stefanović, 2004; Radović et al., 2021). Therefore, an age of approximately 14.0 Ma can be suggested. The carnivoran fauna of the locality according to Ginsburg (1999) and Stefanović (2004) includes: Mustelidae indet. (1 species), *Gobicyon serbiae* (type locality), *Tungurictis* sp. and *Percrocuta miocenica* (type locality). Therefore, it includes 4 species.

Arroyo del Val: This locality is situated a few miles north-east of the village of Murero in Zaragoza (Spain) (Peigné et al., 2006b, fig. 1). It is considered to belong to the upper part of MN 6, being younger than Sansan, Steinberg and Golderg (Mein, 1989; de Bruijn et al., 1992). Therefore, an age of approximately 14.0 Ma can be suggested (Sen, 1997). Of course, this estimation is based on the initial estimation for Sansan. The carnivoran fauna published by Fraile et al. (1997) and Peigné et al. (2006b) includes: *Amphicyon giganteus*, *Plithocyon armagnacensis*, *Protictitherium* aff. *crassum*, *Pseudaelurus quadridentatus* and *Sansanosmilus jourdani*. Therefore, the guild of Arroyo del Val includes 5 species.

La Barranca: This locality is situated very close to that of Arroyo del Val and is supposed to be of similar age (Peigné et al., 2006b, fig. 1). The carnivoran list published by Fraile et al. (1997) and Peigné et al. (2006b) includes: *Amphicyon giganteus*, *Plithocyon armagnacensis*, *Hemicyon* aff. *sansaniensis*, *Martes* sp., *Pseudaelurus quadridentatus*, *Miopanthera lorteti* (as "*Pseudaelurus lorteti*") and *Plioviverrops* sp. Therefore, it includes 7 carnivoran species.

Çandir: This locality is situated near the town of Çandir, north of Kayseri (Turkey) (Valenciano et al., 2020b, fig. 1). It has been considered as a late MN 6 fauna (Mein, 1989; de Bruijn et al., 1992). The carnivoran guild of the locality based on Schmidt-Kittler (1976) and Nagel (2003) includes: *Amphicyon major*, *Hemicyon sansaniensis*, *Amphictis cuspida* (type locality), *Ischyrictis anatolicus* (type locality), cf. *Trochictis depereti*, Lutrinae indet. (1 species), *Proputorius* sp. (1 species), *Protictitherium intermedium* (type locality), *Protictitherium* aff. *gaillardi*, *Percrocuta miocenica*, ?*Percrocuta* sp. (1 species) and *Pseudaelurus quadridentatus*. Therefore, the fauna of Çandir includes 12 carnivoran species.

MN 7/8

Steinheim: The locality of Steinheim is situated a few miles east of the city of Stuttgart and north of the city of Ulm (Tütken et al., 2006, fig. 1). It was initially chosen as the reference locality for MN 7 (Mein, 1989), but since the merging of MN 7 and MN 8, the reference locality for MN 7/8 is La Grive-Saint Alban (de Bruijn et al., 1992). The age of the locality has been assumed to be approximately 14.3–13.8 Ma (Tütken et al., 2006 and references therein). However, Böhme et al. (2012, fig. 5) suggest an age of 13.8 Ma. The carnivoran fauna of Steinheim based on Fraas (1862, 1870), Helbing (1929, 1936), Heizmann (1973) and Morlo et al. (2020) includes: *Amphicyon steinheimensis* (type locality), *Amphicyon* sp. (1 species), *Amphicyonopsis serus*, ?*Pseudarctos bavaricus*, *Ursavus* cf. *intermedius*, *Hemicyon goeriachensis*, *Laphictis mustelinus* (as "*Ischyrictis mustelinus*"), *Paralutra jaegeri* (type locality), *Trocharion albanense*, "*Martes*" cf. *filholi*, *Trochotherium cyamoides* (type locality), *Proputorius* sp., *Semigenetta sansaniensis*, *Pseudaelurus quadridentatus*, *Miopanthera lorteti* (as "*Styriofelis lorteti*") and *Albanosmilus jourdani* (as "*Sansanosmilus jourdani*"). Therefore, the carnivoran guild of Steinheim includes 16 species.

La Grive-Saint Alban: This locality is situated near the village of Saint-Alban-de-Roche (Isère, France) (Mein & Ginsburg, 2002, fig. 1). There are many distinct fissures in the locality and not all of them have the same age (de Bruijn et al., 1992; Mein & Ginsburg, 2002). However, the age of the locality spans through MN 7/8, of which it is the reference locality (de Bruijn et al., 1992; Mein & Ginsburg, 2002). The combined carnivoran fauna of these sites based on Viret (1933, 1951), Ginsburg (1999) and Mein & Ginsburg (2002) includes: *Amphicyon major*, *Amphicyon* aff. *steinheimensis*, *Agnotherium grivense* (type locality), *Pseudarctos* aff. *bavaricus* (including "*Pseudarctos albanensis*"), *Amphicyonopsis serus* (type locality), *Pseudocyon sansaniensis*, *Plithocyon armagnacensis*, *Hemicyon sansaniensis* (as "*Hemicyon goeriachensis*"), *Dinocyon thenardi* (type locality), Hemicyonidae indet. (1 species), *Ursavus primaevus* (type locality), *Alopecocyon goeriachensis* (as "*Viretius goeriachensis*"), "*Martes*" *filholi* (type locality), "*Martes*" *munki*, "*Martes*" *delphinensis* (type locality), *Laphictis mustelinus* (as "*Ischyrictis mustelinus*"; type locality), *Ischyrictis zibethoides*, *Hoplictis helbingi* (type locality), *Gaillardina transitoria* (type locality), *Trochictis depereti* (as "*Rhodanictis depereti*"), *Grivamephitis pusilla* (type locality), *Grivamephitis meini* (type locality), *Proputorius pusillus* (type locality), *Trochotherium cyamoides*, *Trocharion albanense* (type locality), *Paralutra jaegeri*, *Albanosmilus jourdani* (as "*Sansanosmilus jourdani*" type locality), *Semigenetta sansaniensis*, *Viverrictis modica* (type locality), *Jourdanictis grivensis* (type locality), *Sivanasua viverroides* (type locality), *Leptoplesictis filholi* (type locality), *Protictitherium crassum* (type locality), *Protictitherium gaillardi* (type locality), *Plioviverrops gaudryi* (type locality), *Thalassictis certa* (type locality), *Pseudaelurus quadridentatus*, *Miopanthera lorteti* (as "*Styriofelis lorteti*"; type locality), *Styriofelis turnauensis* (as "*Pseudaelurus turnauensis*"), "*Felis*" *zitteli* (type locality) and the creodont *Hyaenailourus* sp. (1 species). Therefore, the locality includes at least 41 species of carnivorans. This makes it the most speciose locality in terms of carnivorans in the European Miocene. However, it is obvious that this high number is affected by the inclusion of several different sites in this locality and not all of these forms are sympatric. For a detailed chart of their occurrences in the locality, see Mein & Ginsburg (2002).

Anwil: This locality is situated near the village of Anwil in the Canton of Basel (Switzerland) (Engesser, 2005). When the zones MN 7 and MN 8 were separate, Anwil was considered the reference locality for MN 8 (Mein, 1989). However, after the merging of these two zones, La Grive-Saint Alban is the reference locality for MN 7/8 (de Bruijn et al., 1992). However, it is clear that the fauna of Anwil is younger than that of Steinheim. The exact age of the locality is supposed to be closer to the former lower boundary of MN 8, approximately at 13.3 Ma (Kälin & Kempf, 2009). However, this age is considered to be too old in Agustí et al. (2001). Böhme et al. (2012, fig. 5) suggested a slightly younger age, at 13.1 Ma. The fauna published by Engesser (1972) includes the following carnivorans: *Pseudarctos* aff. *bavaricus*, *Ursavus brevirhinus*, *Trochotherium* sp., *Semigenetta sansaniensis* (as "*Semigenetta mutata*"), *Leptoplesictis filholi* (as "*Herpestes filholi*") and Carnivora indet. (1 species). Therefore, the guild of the fauna includes 6 carnivoran species.

Yeni Eskihisar: This locality is situated near the village of Eskihisar (Turkey) (Andrews et al., 1980, fig. 1). It has been considered as MN 7/8 (Mein, 1989; de Bruijn et al., 1992). The age of the locality is estimated between 13.2–11.1 (Andrews et al., 1980). The carnivoran guild of the locality based on Schmidt-Kittler (1976) includes: Mustelidae indet. (1 species), *Protictitherium cingulatum* (type locality), *Thalassictis montadai* (as "*Miohyaena montadai*") and *Miomachairodus pseudailuroides*. Therefore, the fauna of Yeni Eskihisar includes 4 carnivoran species.

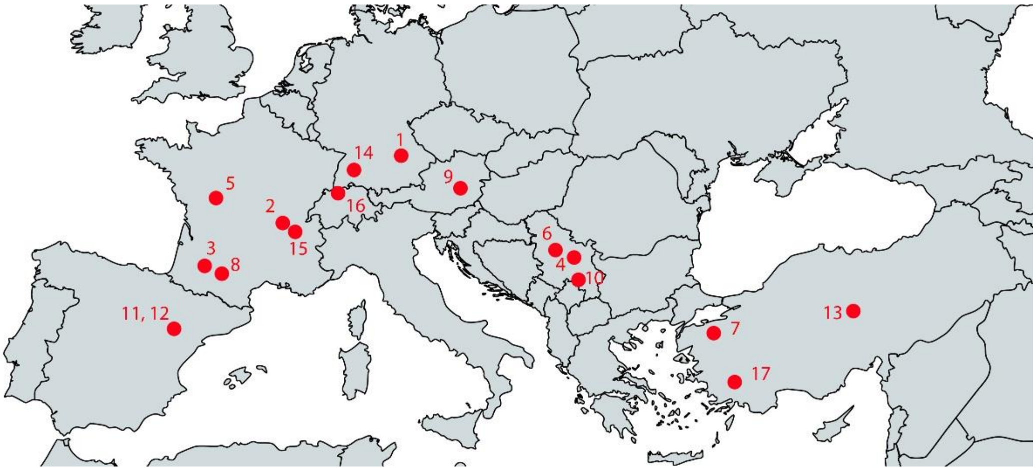

Fig. 2.3: Middle Miocene localities: 1 – Sandelzhausen, 2 – Vieux Collonges, 3 – Castelnau d'Arbieu, 4 – Mala Miliva, 5 – Pontlevoy, 6 – Sibnica, 7 – Paşalar, 8 – Sansan, 9 – Göriach, 10 – Prebreza, 11 – Arroyo del Val, 12 – La Barranca, 13 – Çandir, 14 – Steinheim, 15 – La Grive-Saint Alban, 16 – Anwil and 17 – Yeni Eskihisar.

Late Miocene

MN 9

Castell de Barberà: This locality is situated in the municipality of Barberà del Vallès near the city of Sabadell (Catalonia, Spain) (Alba et al., 2019, fig. 2). Its age has been considered to be near the base of the Vallesian, either slightly older (Agustí et al., 2001) or slightly younger than that (de Bruijn et al., 1992). Recently, Alba et al. (2019) calibrated the age of the locality at 11.19–11.15 Ma, placing it in the early stages of the Vallesian. Consequently, this is one of the localities that approach the age of Hammerschmiede. The carnivoran fauna based on Crusafont Pairó (1972), Golpe Posse (1974), Petter (1976), Crusafont Pairó & Golpe Posse (1981, 1982), Robles et al. (2013) and Robles (2014) includes: *Amphicyon major*, "*Martes*" sp., *Hoplictis helbingi* (the locality is mentioned as Santa Maria de Barberà in Crusafont, 1972), *Trocharion albanense*, *Palaeomeles pachecoi*, Melinae indet. (1 species), *Protictitherium gaillardi* (as "*Progenetta gaillardi*"), *Semigenetta grandis* (type locality), *Albanosmilus jourdani*, *Pseudaelurus quadridentatus*, *Styriofelis turnauensis* and Felidae indet (1 species). Therefore, the guild of the locality includes 12 species.

Eppelsheim: Eppelsheim is situated slightly south of the small city of Alzey (Mainz, Germany) (Böhme et al., 2012). The sediments of Eppelsheim were traditionally thought to be of early Vallesian age (Mein, 1989; de Bruijn et al., 1992). In fact, this area is part of the Eppelsheim Formation (also known as Dinotheriensande, due to the abundancy of dinotheres). However, Böhme et al. (2012) demonstrated that the age of Eppelsheim Formation spans from the early-middle Langhian (≈15.5 Ma) until the middle Tortonian (≈9.0 Ma). They differentiated three chronologic levels in the Dinotheriensande: an early Middle Miocene (MN 5 and MN 6), a late Middle Miocene (MN 7/8) and an early Late Miocene (MN 9), while some MN 10 or even MN 11 micromammalian indications are present. Therefore, the age of Eppelsheim is far from straightforward. However, it is interesting that none of the Middle Miocene species seen in the Formation is a carnivoran. All Carnivora from Eppelsheim are typical early Vallesian species. That is why it was chosen to place Eppelsheim at this point of the manuscript. The carnivoran guild of the locality based on Weitzel (1830), Kaup (1832), Lydekker (1890) and Morlo et al. (2019a, 2019b, 2020) includes: *Amphicyon eppelsheimensis* (type locality), *Pseudarctos bavaricus*, *Agnotherium antiquum* (type locality), *Amphicyonopsis serus*, *Simocyon diaphorus* (type locality), *Agriarctos depereti*, *Indarctos arctoides*, *Dinocyon teilhardi*, *Eomellivora piveteaui*, *Sivaonyx hessicus* (type locality), *Limnonyx ponticus*, cf. "*Martes*", "*Martes*" aff. *melibulla*, aff. *Circamustela*, *Trochictis peignei* (type locality), *Protictitherium crassum*, *Machairodus aphanistus* (type locality) and *Promegantereon ogygia* (type locality). Therefore, the Formation includes 18 species, and for 6 of them Eppelsheim is the type locality.

Höwenegg: The locality of Howenegg is situated a few kilometers west of the Bodensee Lake (Baden-Württemberg, Germany). Mein (1989) and de Bruijn et al. (1992) placed this locality in the lower part of MN 9. The absolute age of the locality has been radiometrically dated to 10.3 Ma (Swisher, 1996). Recalibration of this date results to 10.4 Ma (Böhme, pers. commun.). The carnivoran fauna published by de Beaumont (1986) includes: Amphicyonidae indet. (1 species), *Thalassictis robusta*, *Hyaenictitherium wongii* (as “*Thalassictis wongii*”), *Machairodus* cf. *aphanistus* and *Albanosmilus jourdani* (as “*Sansanosmilus jourdani*”). Therefore, the carnivoran guild of the locality includes 5 species.

Yassiören: This locality is situated at the Sinap Formation, north of Ankara (Turkey) (Sen, 2003, fig. 1). It has been considered as an MN 9 locality (Mein, 1989). However, the Sinap Formation includes dozens of sites divided in distinct composites and, unfortunately, it is not possible to discover exactly where the traditional specimens from Yassiören come from. However, it has been suggested that it belonged to the Sinap Tepe composite that has been dated to 10.9–9.3 Ma (Kappelman et al., 2003). The carnivoran guild of the locality based on Schmidt-Kittler (1976) includes: *Eomellivora piveteaui* (type locality), *Ictitherium intuberculatum* (type locality), *Protictitherium crassum* (as “*Ictitherium arambourgi*”), *Dinocrocuta senyureki* (as “*Hyaena senyüreki*” and “*Hyaenictis piveteaui*”), *Barbourofelis piveteaui* (as “*Megantereon piveteaui*”; type locality), *Miopanthera pamiri* (as “*Felis pamiri*”; type locality) and Felis sp. (1 species). Therefore, the locality includes 7 carnivoran species.

Kalfa: The locality of Kalfa is situated near the village of Kalfa (Anenii Noi, Moldova) (Lungu & Rzebik-Kowalska, 2011, fig. 1). It has been considered as a middle-MN 9 locality, being slightly younger than Höwenegg (Mein, 1989). However, this locality includes at least 5 fossiliferous levels (Lungu & Rzebik-Kowalska, 2011, fig. 5). The carnivoran assemblage of the locality based on Lungu & Rzebik-Kowalska (2011) includes: *Eomellivora piveteaui*, *Promeles* sp., *Protictitherium crassum* (including “*Ictitherium tauricum*”), *Thalassictis montadai* (as “*Miohyaena montadai* vallesiensis”), *Dinocrocuta robusta* (as “*Percrocuta robusta*”; type locality), *Barbourofelis piveteaui* (as “*Sansanosmilus piveteaui*”), *Machairodus laskarevi* (as “*Machairodus laskarevi*”; type locality; possibly a junior synonym of *Machairodus aphanistus*), *Styriofelis turnauensis* (as “*Pseudaelurus turnauensis*”) and cf. *Miopanthera pamiri* (as “*Pseudaelurus* cf. *pamiri*”). Therefore, the locality includes 9 carnivoran species.

Los Valles de Fuentidueña: This locality is situated slightly south to the small village of Fuentidueña (Segovia, Spain) (Alberdi Alonso, 1981, fig. 1). It is considered as a middle MN 9 locality (Mein, 1989; de Bruijn et al., 1992). Therefore, an age of approximately 10.5 Ma can be suggested (Agustí et al., 2001). The carnivorans of this locality based on Ginsburg et al. (1981) include: *Amphicyon major*, *Magericyon castellanus* (type locality), *Thaumastocyon dirus* (type locality), *Eomellivora wimani* (as “*Eomellivora liguritor*”), *Circamustela dechaseauxi*, “*Marcetia santigae*”, Mephitinae indet., Albanosmilus *jourdani* (as “*Sansanosmilus jourdani*”), *Pseudaelurus quadridentatus*, Felinae indet., *Machairodus aphanistus*, *Machairodus alberdiae* (type locality), *Protictitherium crassum*, *Plioviverrops* sp, *Lycyaena* aff. *chaeretis* and Carnivora indet. (1 species). Therefore, the guild of the locality includes 16 species.

Rudabánya: The locality of Rudabánya is situated at the north-eastern part of Hungary, near the border with Slovakia (Agustí et al., 2004, fig. 1). It is considered a typical MN 9 locality (Mein, 1989; de Bruijn et al., 1992). The age of the locality (based on biostratrigraphical data) is estimated to be approximately 10.0–9.7 Ma (Agustí et al., 2004). However, Böhme et al. (2012, fig. 5) suggest a 10.2 Ma age. The carnivoran guild based on Werdelin (2005) and de Bonis et al. (2017) includes: Amphicyonidae indet. (1 species), *Miomaci pannonicum* (type locality for species and genus), *Ursavus primaevus*, *Simocyon diaphorus*, *Protursus simpsoni* (as "*Viretius* sp." and "*Ursavus brevirhinus*"), *Taxodon* cf. *sansaniensis*, Melinae indet. (1 species), "*Martes* cf. *filholi*", *Paralutra jaegeri*, *Paralutra* sp. (second species), *Trochictis* sp. (1 species), *Proputorius* sp. (1 species), *Semigenetta grandis*, *Albanosmilus jourdani* (as "*Sansanosmilus jourdani*"), *Miopanthera lorteti* (as "*Pseudaelurus lorteti*"), *Styriofelis turnauensis* (as "*Pseudaelurus turnauensis*"), cf. *Thalassictis montadai*. Therefore, the locality includes 17 carnivoran species.

Can Ponsic: The locality of Can Ponsic is situated a few miles southwest of the city of Sabadell (Catalonia, Spain) (Robles et al., 2010, fig. 1). It is considered as a typical MN 9 locality (Mein, 1989; de Bruijn et al., 1992). The age of the locality based on Agustí et al. (1997) and Robles (2014) is approximately 10.4–10.0 Ma. The carnivoran guild of the locality based on Crusafont-Pairó & Kurtén (1976) and Robles (2014) includes: *Amphicyon major*, *Indarctos vireti*, Ailuropodinae indet. (1 species), "*Martes*" *basilii*, "*Martes*" aff. *andersoni*, *Limnonyx sinerizi* (type locality), *Mesomephitis medius*, *Promephitis pristinidens*, *Plesiomeles* aff. *cajali*, *Plesiomeles* sp. (1 species), *Protictitherium gaillardi*, *Thalassictis montadai*, Hyaenidae indet. (1 species), *Machairodus aphanistus*, *Pseudaelurus quadridentatus* and *Albanosmilus jourdani*. Therefore, the carnivoran guild of Can Ponsic includes 15 species.

Can Llobateres 1: The locality of Can Llobateres is southeast of the city of Sabadell (Agustí et al., 1996, fig. 1). It is considered the reference locality for MN 9 (Mein, 1989; de Bruijn et al., 1992). Macromammalian remains have been found only in Can Llobateres 1. The age of the Can Llobateres 1 was estimated by Agustí et al. (1996) as approximately 9.74–9.64 Ma. The carnivoran list of the locality based on Crusafont Pairó & Kurtén (1976) and Alba et al. (2011) includes: *Agnotherium antiquum*, *Amphicyon major*, *Pseudarctos* sp., *Thaumastocyon dirus*, *Indarctos vireti*, *Ursavus brevirhinus*, *Ursavus primaevus*, *Protursus simpsoni* (type locality for species and genus), *Circamustela dechaseauxi* (type locality for species and genus), *Hoplictis petteri* (type locality), *Paralutra jaegeri* (as "*Marcetia santigae*" and "*Paralutra* sp."), "*Martes*" *melibulla* (type locality), "*Martes*" *munki*, *Plesiogulo* sp., *Taxodon sansaniensis*, *Sabadellictis crusafonti* (type locality for species and genus), *Trocharion albanense*, *Trochictis narcisoi* (type locality), *Promephitis pristinidens*, *Mesomephitis medius* (type locality for species and genus), *Semigenetta sansaniensis* (as "*Semigenetta ripolli*"), *Protictitherium crassum*, *Protictitherium gaillardi*, *Albanosmilus jourdani* (as "*Sansanosmilus jourdani*") and *Machairodus aphanistus*. Therefore, the carnivoran guild of the locality includes 25 species, and for 7 of them Can Llobateres is the type locality.

MN 10

Batallones: The locality of Cerro de los Batallones is situated between the cities of Madrid and Toledo (Spain) (Domingo et al., 2016, fig. 1). Nine different sites have been discovered in this locality. From these, the majority of fossils has been found in BAT-1 and BAT-3. The age of the sites is ranging between 9.6 and 9.3 Ma (Peláez-Campomanes et al., 2017). The combined carnivoran fauna of Batallones based on Peigné et al. (2005), Martín Perea et al. (2017), Valenciano et al. (2020a) and Morales et al. (2021) includes: *Ammitocyon kainos* (type locality), *Magericyon anceps* (type locality), *Indarctos arctoides, Simocyon batalleri, Eomellivora piveteaui*, "*Martes*" *melibulla, Circamustela peignei* (type locality), aff. *Adroverictis ginsburgi, Promephitis* sp. (1 species), Mephitidae indet. (1 species), *Protictitherium crassum, Leptofelis vallesiensis*, *Pseudaelurus* sp. (1 species), *Promegantereon ogygia* and *Machairodus aphanistus*. Therefore, the guild of the locality includes 15 species.

Montredon: This locality is situated near the community of Bize-Minervois (Aude, France) (Depéret, 1895). It is considered as typical MN 10 locality of similar to or slightly younger age than Masia del Barbo (Mein, 1989; de Bruijn et al., 1992). Böhme et al. (2012) suggested an age for approximately 9.5 Ma for the locality, which fits quite well with the 9.3 Ma age of Masia del Barbo (van Dam, 1997). The carnivoran guild of the locality based on de Beaumont (1988) includes: Amphicyonidae indet. (1 species), *Indarctos arctoides* (type locality), *Simocyon* sp. (1 species), Mustelidae indet. (1 species), *Protictitherium crassum, Ictitherium viverrinum*, cf. "*Metailurus parvulus*" and *Machairodus* cf. *aphanistus*. Therefore, the fauna of Montredon includes 8 carnivoran species.

Ravin de la Pluie: This locality is situated in the Axios Valley, northwest of the town of Thessaloniki (Greece) (Koufos, 2000, fig. 1). It has been considered as a lower-middle MN 10 locality (Mein, 1989; de Bruijn et al., 1992). Sen et al. (2000) estimated an age of 9.3 Ma for the locality. The carnivoran fauna of Ravin de la Pluie based on Koufos (2000, 2012a, 2012b) includes: *Eomellivora wimani*, *Protictitherium thessalonikensis* (type locality), *Protictitherium* aff. *intermedium*, ?*Hyaenictis* sp. (1 species), *Adcrocuta eximia* and "*Metailurus parvulus*". Therefore, Ravin de la Pluie includes 6 carnivoran species.

Soblay: This locality is situated near the village of Saint-Martin-du-Mont (Ain, France) (Ménouret & Mein, 2008). It is considered a late MN 10 locality, being similar to Csakvar and Ravin des Zouaves (de Bruijn et al., 1992). However, Csakvar is now considered as early MN 11 locality (see below). Therefore, since no stratigraphic data exist, it is not possible to estimate an absolute age. The carnivoran guild of the locality based on Viret & Mazenot (1948) and Ménouret & Mein (2008) includes: *Agriarctos depereti* (as "*Ursavus depereti*"), *Indarctos* sp. (1 species), *Ursavus* cf. *brevirhinus*, "*Martes*" aff. *filholi, Ictitherium viverrinum, Thalassictis* sp. (1 species), *Adcrocuta* *eximia* (as "*Crocuta eximia*") and *Machairodus* cf. *aphanistus*. Therefore, the guild of the locality includes 8 species.

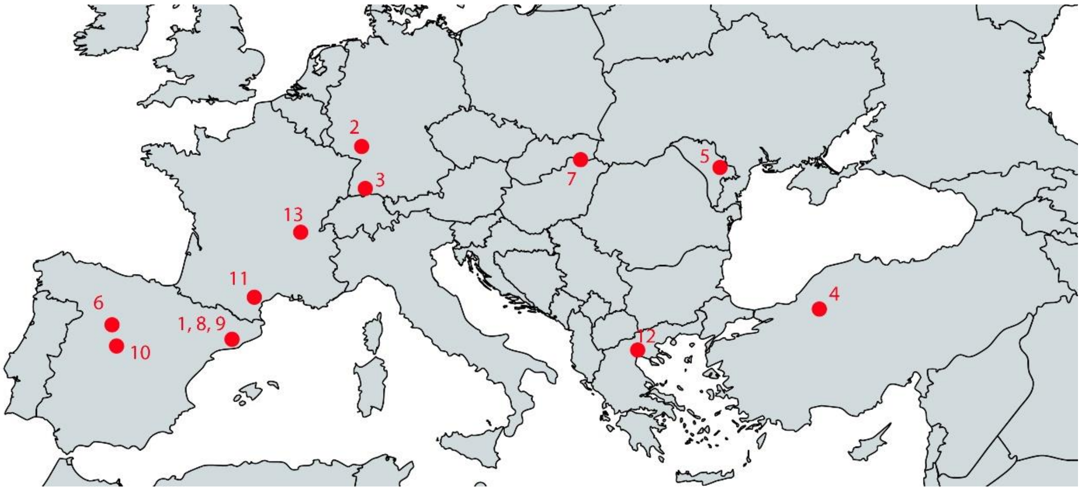

Fig. 2.4: Vallesian localities: 1 – Castell de Barberà, 2 – Eppelsheim, 3 – Howenegg, 4 – Yassiören, 5 – Kalfa, 6 – Los Valles de Fuentidueña, 7 – Rudabánya, 8 – Can Ponsic, 9 – Can Llobateres, 10 – Batallones, 11 – Montredon, 12 – Ravin de la Pluie and 13 – Soblay.

MN 11 & MN 12

Dorn-Dürkheim 1: This locality is situated near the village of Dorn-Dürkheim (Mainz, Germany) (Böhme et al., 2012). It is considered as a typical MN 11 locality (Mein, 1989; de Bruijn et al., 1992; Franzen et al., 2013). The carnivoran fauna published by Morlo (1997), Roth & Morlo (1997) and Franzen et al. (2013) includes: *Indarctos arctoides*, *Indarctos punjabensis* (as "*Indarctos atticus*"), *Ursavus depereti*, *Ursavus primaevus*, *Simocyon* sp., *Taxodon* sp., *Eomellivora wimani*, *Promeles palaeatticus*, *Baranogale* cf. *adroveri*, ?*Circamustela* sp., "*Martes*" cf. *sansaniensis*, "*Martes*" sp. (1 species), Mustelidae indet. (2 species), *Adcrocuta eximia*, *Protictitherium crassum*, *Thalassictis robusta*, *Allohyaena kadici*, *Dinocrocuta* sp. (1 species), *Pristifelis attica* (as "*Felis attica*"), *Paramachaerodus orientalis*, *Promegantereon ogygia* (as "*Paramachaerodus ogygius*") and *Machairodus* cf. *aphanistus*. Therefore, this locality includes 23 carnivoran species.

Csakvar: This locality is situated between the cities of Tatabánya and Székefehévár, west of Budapest (Hungary) (Mészáros, 1996, fig. 1). It was thought to be of MN 10 age (Mein, 1989; de Bruijn et al., 1992). However, it is now considered as an early MN 11 locality of similar age to Dorn-Dürkheim (Mészáros, 1996; Ginsburg, 1999), 8.2±0.5 Ma in Böhme et al. (2008). The carnivoran guild of the locality based on Kretzoi (1951) includes: Amphicyonidae indet. (1 species), *Agriotherium* sp. (1 species), *Simocyon hungaricus* (type locality), *Parenhydriodon csakvarensis* (type locality), *Paralutra transdanubica* (possibly conspecific with *Paralutra jaegeri*; type locality), Mustelidae indet. (1 species), *Eomellivora* sp. (as "*Eomellivora hungarica altera*"), *Protictitherium csakvarense*, *Allohyaena kadici* (type locality), Felinae indet. (as "*Felinarum* g. et sp. ind."), "*Parapseudailurus osborni*" (a generally unknown form, based on one P4 without figures or measurements; type locality), *Paramachaerodus orientalis* (as "*Paramachaerodus matthewi*") and *Machairodus* sp. (1 species). Therefore, the locality includes 13 species. The NOW database also mentions *Ursavus brevirhinus*, *Hyaenictitherium* sp. (1 species) and *Adcrocuta eximia* from the locality, but the citation of these occurrences is not mentioned.

Samos: The island of Samos has yielded fossil remains from several localities that span from the end of early Turolian until the end of the late Turolian (Qx≈8.0 Ma; MLN≈7.5 Ma, MYT≈7.3 Ma, MTL≈7.1 Ma; Q5≈6.8 Ma; Kostopoulos et al., 2009; Koufos et al., 2011). The carnivoran assemblage of all these localities based on Nagel & Koufos (2009) includes: *Ursavus* cf. *depereti*, *Indarctos punjabensis* (as "*Indarctos atticus*"), *Promeles palaeattica*, *Promephitis larteti*, *Promephitis majori* (type locality), *Parataxidea maraghana*, *Plioviverrops orbignyi*, *Protictitherium crassum*, *Ictitherium viverrinum*, *Hyaenictitherium wongii*, *Lycyaena chaeretis*, *Belbus beaumonti*, *Adcrocuta eximia*, *Pristifelis attica* (as "*Felis attica*"), *Amphimachairodus giganteus* (as "*Machairodus giganteus*"), "*Metailurus parvulus*" and *Metailurus major*. Therefore, the combined guild of these localities includes 17 species.

Pikermi: The locality of Pikermi is situated in the northeast part of Attica (Greece) (Theodorou et al., 2010, fig. 1). It is considered a typical MN 12 locality (Mein, 1989; de Bruijn et al., 1992). The age of the formation (including a number of individual sites) was calibrated to 7.37–7.11 Ma (Böhme et al., 2017). If only the classical collections are concerned (housed in Athens, Vienna, Paris and London), then the range is restricted to 7.34–7.30 Ma (Böhme et al., 2017). The carnivoran fauna based on the review of Roussiakis et al. (2019) includes: *Indarctos punjabensis* (as "*Indarctos atticus*"), *Enhydriodon latipes* (type locality), *Promeles palaeatticus* (type locality), "*Martes*" *woodwardi* (type locality), *Promephitis larteti* (type locality), *Sinictis pentelici* (type locality), *Simocyon primigenius* (type locality), *Adcrocuta eximia* (type locality), *Hyaenictis graeca* (type locality), *Lycyaena chaeretis* (type locality), *Ictitherium viverrinum* (type locality), *Hyaenictitherium wongii*, *Plioviverrops orbignyi* (type locality), *Metailurus major*, "*Metailurus parvulus*", *Amphimachairodus giganteus* (type locality), *Paramachairodus orientalis* and *Pristifelis attica* (type locality). Therefore, the carnivoran guild of Pikermi includes 18 species and for 13 of them it is their type locality.

Sahabi: Similarly to La Grive and Sinap, the As Sahabi is a large area that includes many different sites. It is situated south of the city of Ajabiya (Libya) (El-Shawaihdi et al., 2016). El-Shawaihdi et al. (2016) discussed the stratigraphy of the various levels of this region in detail. Böhme et al. (2021) calibrated the age of Sahabi at 7.3–7.2 Ma. The mammalian remains of the locality correspond to an age of latest Miocene (late MN 13), based on de Bruijn et al. (1992). The carnivoran fauna of Sahabi based on Rook & Sardella (2008) includes: *Indarctos punjabensis* (as "*Indarctos atticus*"), *Agriotherium* cf. *africanum*, Ursidae indet. (1 species), Mustelidae indet. (1 species), Phocidae indet. (1 species), *Viverra howelli*, Viverridae indet. (1 species), *Amphimachairodus* aff. *kabir*, *Dinofelis* sp., Felidae indet. (3 species), “*Hyaenictitherium*” *namaquensis*, *Chasmaporthetes* sp., *Adcrocuta eximia* (as “*Percrocuta eximia*”), Hyaenidae indet. (1 species) and doubtfully *Dinocrocuta* aff. *senyureki* (as “*Percrocuta* aff. *senyureki*”). The validity of the last species’ occurrence has been discussed in the chapter of Percrocutidae. Therefore, the fauna of the locality includes at least 17 carnivoran species.

Los Mansuetos: This locality is situated at the Teruel basin, near the city of Teruel, northwestern of Valencia (Aragon, Spain) (van Dam, 1997, figs. 2.1 & 2.2). It is considered the reference locality for MN 12 (Mein, 1989; de Bruijn et al., 1992). The age estimate based on van Dam (1997) is 6.9 Ma. The carnivoran guild of the locality based on Morales & Soria (1979) and Fraile et al. (1997) includes: “*Canis*” *cipio*, *Indarctos punjabensis* (as “*Indarctos atticus*”), *Paludolutra lluecai* (as “*Enhydriodon lluecai*”), *Baranogale adroveri* (type locality), *Plioviverrops guerini*, *Hyaenictitherium wongii* (as “*Thalassictis adroveri*”), *Lycyaena* sp. (1 species), *Adcrocuta eximia*, “*Metailurus parvulus*” and *Amphimachairodus giganteus*. Therefore, the fauna of Los Mansuetos includes 10 species.

Los Aljezares: This locality is situated at the Teruel basin, near the city of Teruel, northwestern of Valencia (Aragon, Spain) (van Dam, 1997, figs. 2.1 & 2.2). It is considered an MN 12 locality (Mein, 1989; de Bruijn et al., 1992). The age based on van Dam (1997) is similar to that of Concud and Los Mansuetos, so 6.9–6.8 Ma The carnivoran guild of the locality based on Morales & Soria (1979) includes: “*Martes*” *basilii*, *Plesiogulo* sp. (1 species), *Paludolutra lluecai* (as “*Enhydriodon lluecai*” and “*Sivaonyx lehmani*”; type locality), *Dinocrocuta gigantea* and *Amphimachairodus giganteus*. Therefore, the fauna of Los Aljezares includes 5 species.

Concud: This locality is situated at the Teruel basin, near the city of Teruel, northwestern of Valencia (Aragon, Spain) (van Dam, 1997, figs. 2.1 & 2.2). It is considered an MN 12 locality (Mein, 1989; de Bruijn et al., 1992). The age estimate based on van Dam (1997) is 6.8 Ma. The carnivoran guild of the locality based on Morales & Soria (1979) includes: “*Canis*” *cipio* (type locality), *Indarctos punjabensis* (as “*Indarctos atticus*”), *Simocyon primigenius*, “*Martes*” *basilii*, *Baranogale adroveri*, *Paludolutra lluecai* (as “*Enhydriodon lluecai*” and “*Sivaonyx lluecai*”), *Plioviverrops guerini*, *Percrocuta minor*, *Metailurus major*, *Paramachaerodus orientalis* and *Amphimachairodus giganteus*. Therefore, the fauna of Concud includes 11 species.

MN 13

El Arquillo: This locality is situated at the Teruel basin, near the city of Teruel, northwestern of Valencia (Aragon, Spain) (van Dam, 1997). It is considered the reference locality for MN 13 (Mein, 1989; de Bruijn et al., 1992). The age estimate based on van Dam (1997) is similar to or slightly younger than Las Casiones (6.1 Ma). The carnivoran guild of the locality based on Morales & Soria (1979) includes: *Paludolutra lluecai* (as “*Sivaonyx lluecai*” and “*Sivaonyx lehmani*”), *Hyaenictitherium* *wongii* (as "*Thalassictis adroveri*"), *Lycyaena* sp. (1 species), *Adcrocuta eximia*, "*Metailurus parvulus*" and *Amphimachairodus giganteus*. Therefore, the locality of El Arquillo includes 6 species.

Las Casiones: This locality is situated at the Teruel basin, near the city of Teruel, northwestern of Valencia (Aragon, Spain) (van Dam, 1997). The age estimate based on van Dam (1997) is 6.1 Ma. Based on Salesa et al. (2012b), the carnivoran guild of the locality includes: *Indarctos punjabensis* (as "*Indarctos atticus*"), *Plesiogulo monspessulanus*, *Baranogale adroveri*, "*Mustela*" sp. (1 species), Mustelidae indet. aff. *Sabadellictis*, *Plioviverrops* cf. *guerini*, *Hyaenictitherium wongii* (as "*Thalassictis hipparionum*"), *Pristifelis attica*, Felinae indet. (1 species), *Metailurus major*, *Paramachaerodus orientalis* and *Amphimachairodus giganteus*. Therefore, the fauna of Las Casiones includes 12 species.

Venta del Moro: The locality of Venta del Moro is situated a few miles west of the city of Valencia (Spain) (Opdyke et al., 1989, fig. 1). Magnetostratigraphic correlations calibrated an age of 5.8 Ma for this locality (Opdyke et al., 1989), which was then corrected into 6.23 Ma (Gibert et al., 2013). The carnivoran fauna of the locality based on Ginsburg (1999) and Montoya et al. (2006) includes: *Eucyon debonisi*, *Nyctereutes donnezani*, *Vulpes adoxus*, *Agriotherium roblesi* (type locality), "*Martes*" *ginsburgi* (type locality), *Plesiogulo monspessulanus*, "*Lutra*" *affinis*, *Promephitis alexejewi*, *Hyaenictitherium* aff. *hyaenoides* (as "*Thalassictis* aff. *hyaenoides*"), *Felis christoli*, *Fortunictis* sp., *Paramachairodus maximiliani* and *Amphimachairodus giganteus*. Therefore, this locality includes 13 carnivoran species.

Maramena: The locality of Maramena is situated between the small towns of Serres and Sidirokastro (Greece) (Schmidt-Kittler et al., 1995, fig. 1). No absolute age calibrations have been conducted. However, biostratigraphic comparisons have revealed a mix of MN 13 and MN 14 taxa (Schmidt-Kittler et al., 1995). Therefore, a terminal Miocene age was suggested for this locality. The carnivorans of Maramena were published by Schmidt-Kittler (1995): "*Martes*" *lefkonensis* (type locality), *Promeles macedonicus* (type locality), *Promephitis* sp., "*Lutra*" *affinis*, Viverridae indet. (1 species) and *Chasmaporthetes* sp. (1 species). Therefore, the locality includes 5 carnivoran species.

Monticino: The Monticino Quarry is situated near the town of Brisighella (the name of which is also commonly used for the locality) (Villa et al., 2021). This locality was always thought as one of the last Miocene localities in Europe (Mein, 1989; de Bruijn et al., 1992). Rook et al. (2015) suggested an age of approximately 5.4 Ma. The carnivoran fauna of the locality based on Villa et al. (2021) and Bartolini-Lucenti et al. (2021) includes: *Eucyon monticinensis* (type locality), *Mellivora benfieldi*, *Lycyaena* sp., *Plioviverrops faventinus* (type locality) and *Felis* cf. *christoli*. Therefore, it includes 5 carnivoran species.

Fig. 2.5: Turolian localities: 1 – Dorn-Dürkheim, 2 – Csakvar, 3 – Samos, 4 – Pikermi, 5 – Sahabi, 6 – Los Mansuetos, 7 – Los Aljezares, 8 – Concud, 9 – El Arquillo, 10 – Las Casiones, 11 – Venta del Moro, 12 – Maramena and 13 – Monticino.

Palaeogeography

The following pages will consider the palaeogeographical data for Europe and the nearby regions throughout the Miocene. These data are crucial in the understanding of the palaeoecology of Europe, the evolution of the lineages and the dispersal patters of the carnivoran groups.

Usually, the defined mammalian dispersals are defined based on herbivores: usually micromammals, artiodactyls, perissodactyls and proboscideans. However, there are some cases that these dispersals were correlated with the arrival of carnivorans, possibly following the herbivores as hunters.

Dispersals are affected by the presence of natural barriers. Concerning land mammals, this could mean high mountains, water or even desert areas (Böhme et al., 2021). On the other hand, aquatic or semi-aquatic species require the presence of water connections in order to migrate. Depending on the studied group this could mean either salt or sweet water connections.

At the beginning of the Miocene, most of southern Europe was occupied by the widely confluent Tethys and Paratethys (Fig. 2.7; taken from Rögl, 1997). This fact explains the absence of southern Europe localities during the Early Miocene. A very wide connection existed between the Tethys/Mediterranean and the Indian Ocean. No land connection was present between Anatolia and the Balkans or North Africa and the Iberian Peninsula. Therefore, the only dispersal pathway for land carnivorans was with Asia through northeastern Europe (todays Russia, Ukraine etc.).

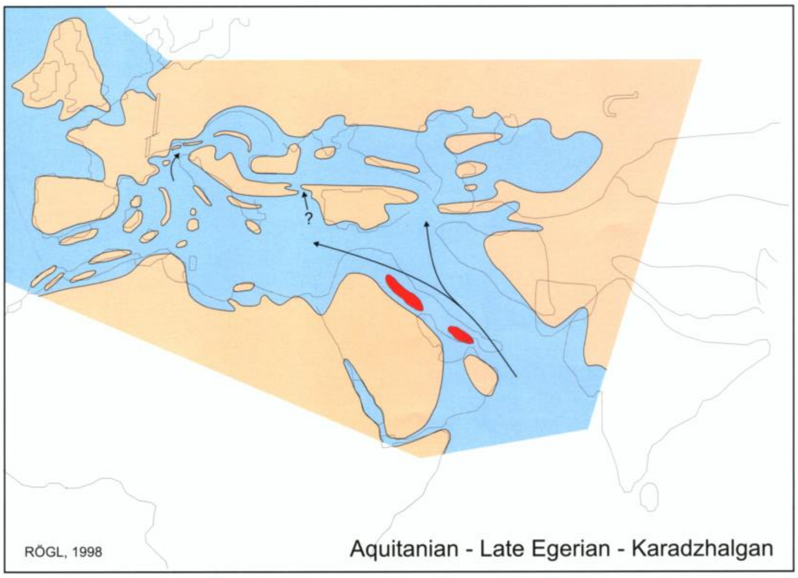

Fig. 2.7: Map of Europe, North Africa and West Asia during the Aquitanian. Source: Rögl (1997).

The transition to the Burdigalian led to distinction between Tethys and Paratethys (Fig. 2.8; taken from Rögl, 1997). Of course, this separation created a land bridge that was connecting Anatolia with the northern Balkans. Additionally, the Arabian Peninsula was connected with northeastern Africa. Therefore, during this time, land dispersals were possible between North Africa, West Asia and East Europe. On the contrary, the water connections have been restricted with Tethys, Paratethys and the Indian Ocean forming being separated.

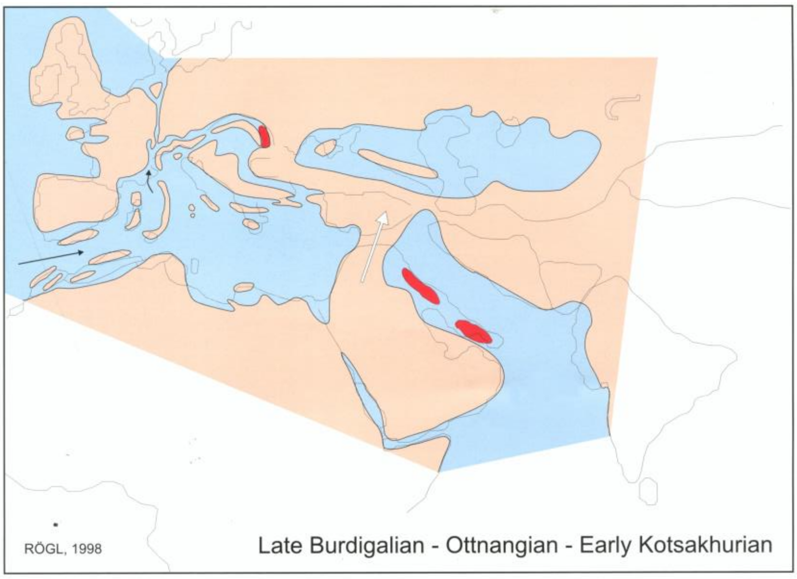

Fig. 2.8: Map of Europe, North Africa and West Asia during the Burdigalian. Source: Rögl (1997).

During the Langhian, the interconnections between the Indian Ocean, Tethys and Paratethys were re-established (Fig. 2.9; taken from Rögl, 1997). However, the Tethys-Paratethys connection is far more restricted in comparison to the Aquitanian. Their connection is mainly evident through todays Middle East. The land connections were therefore again closed. The only route in or out of Europe was once again through its north-eastern part.

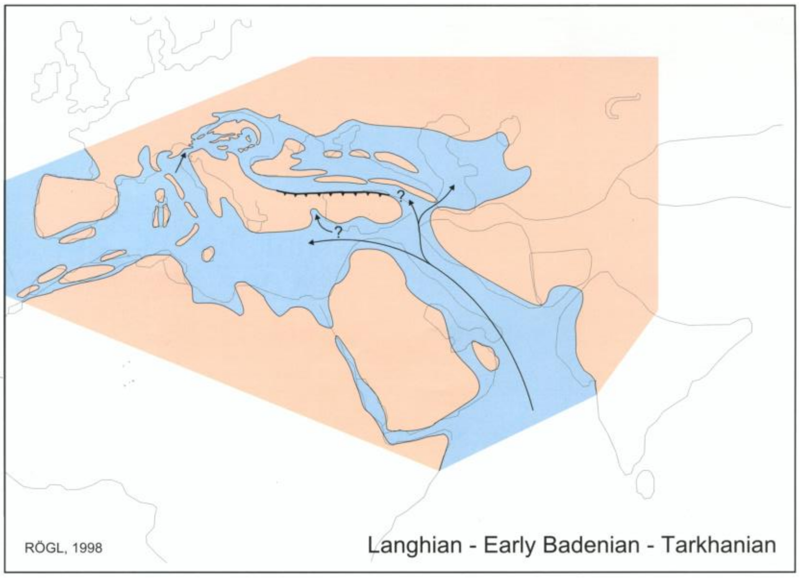

Fig. 2.9: Map of Europe, North Africa and West Asia during the Langhian. Source: Rögl (1997).

Through the Serravallian, the Arabian Peninsula was connecting North Africa with West Asia (Fig. 2.10; taken from Rögl, 1997). Similarly to the Langhian, the only connection between Tethys and Paratethys was through the East Anatolia. However, this time there is no connection between the two former Seas and the Indian Ocean. No direct land bridges are evident. However, the close proximity between Anatolia and

Middle East and northwestern Africa and southwestern Europe supports the possibility of dispersals at these regions.

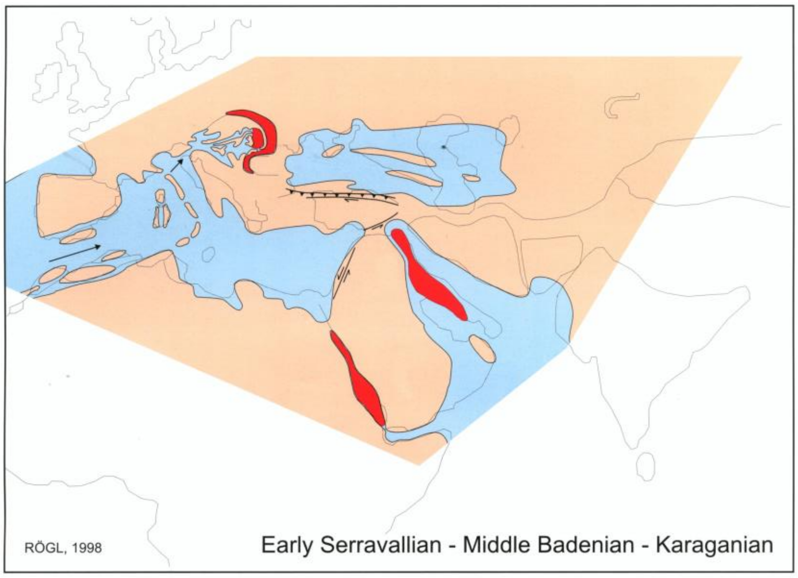

Fig. 2.10: Map of Europe, North Africa and West Asia during the Serravalian. Source: Rögl (1997).

The beginning of the Late Miocene witnessed a geographical profile that is more similar to today's Europe (Fig. 2.11; taken from Steininger & Rögl, 1984). A distinct difference is the large size of Paratethys, which was extended through the northern Balkans. However, a narrow water connection was present between Paratethys and Tethys, similar to today's Dardanelles' region. Additionally, part of southern Europe was still occupied by Tethys. However, mammal dispersal was possible through the Anatolian-Balkan connection (especially during the late MN 12; Kostopoulos, 2009), while the Arabian Peninsula was connecting Anatolia with North Africa. Additionally, the constant connection of northeastern Europe with northwestern Asia was still present. Therefore, Late Miocene was a period that enabled the dispersal of land groups throughout these three continents. On the other hand, the water connections were more restricted.

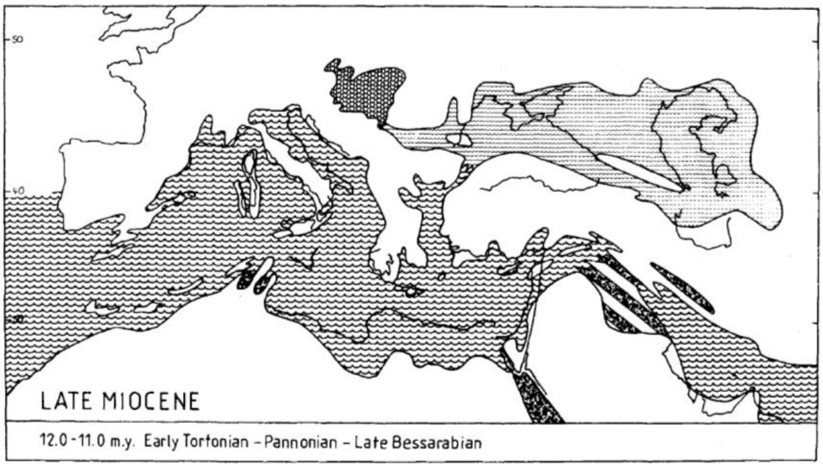

Fig. 2.11: Map of Europe, North Africa and West Asia during the Tortonian. Source: Steininger & Rögl (1984).

The most characteristic arrival at the base of this period is that of the hipparionin horses. Concerning carnivores Koufos et al. (2005) mention *Dinocrocuta*, *Adcrocuta*, *Plesiogulo* and *Chasmaporthetes* as followers of this dispersal. However, the latter refers to "*Chasmaporthetes bonisi*", whose validity has been doubted (Werdelin & Solounias, 1991).

Finally, the Messinian is a very distinct period in terms of palaeogeography (Fig. 2.12; taken from Steininger & Rögl, 1984). Nearly the whole Tethys/Mediterranean Sea was evaporated during the Messinian Salinity Crisis. This created wide connections between North Africa, Arabia, Anatolia, northeastern Asia and Europe. The Paratethys was split in three distinct regions. Therefore, the water dispersals were at the time impossible.

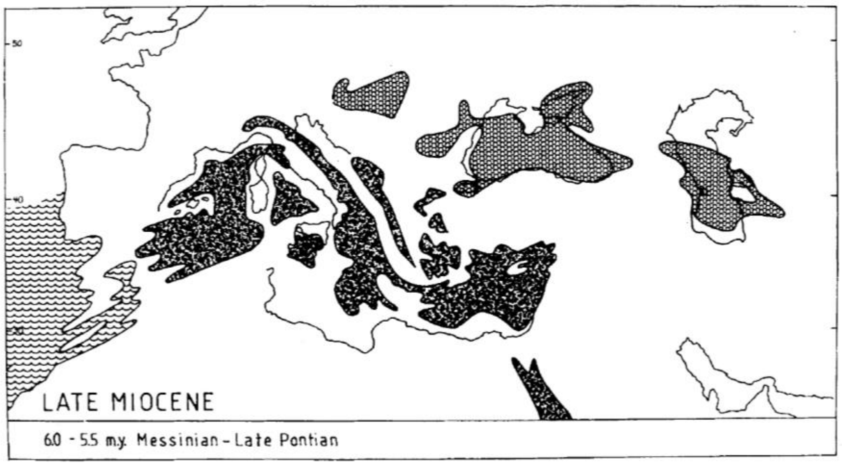

Fig. 2.12: Map of Europe, North Africa and West Asia during the Messinian. Source: Steininger & Rögl (1984).

Koufos et al. (2005) mention that this dramatic change led to the extinction of several mammalian groups, including *Adcrocuta* and *Thalassictis*. This extinction concerns several hyaenid forms (Turner et al., 2008). These forms were replaced by canids, such as *Nyctereutes* (Böhme et al., 2021). This replacement is evident in the locality of Venta del Moro, where canids (*Eucyon debonisi*, *Nyctereutes donnezani* and *Vulpes adoxus*) coexist with ictitheres (*Hyaenictitherium* aff. *hyaenoides*) (Ginsburg, 1999; Montoya et al., 2006). An important new element is the connection between African and the Iberian Peninsula that enabled dispersals several times (Gibert et al., 2013).

Palaeoclimate

The climate of Europe during the Miocene has been a matter of debate in numerous publications. In general, the climate was warmer than today, reaching its maximum Mean Annual Temperature (MAT) during the so-called Middle Miocene Climatic Optimum (MMCO). Research on the Eurasian palaeoclimate has been conducted from several points of view, using different inorganic parameters and taxonomic groups as case-studies. Some of the most commonly used proxies are Mean Annual Temperature (MAT), Mean Temperature of Warmest Quarter (MTWQ)/Warm Month Mean Temperature (WMMT), Cold Month Mean Temperature (CMMT), Mean Annual Precipitation (MAP) and Precipitation Seasonality (CoV).

Based on the website climatic-data.org, the MAT for Munich today is 8.8^{o}C, while the MAP is approximately 1000 mm (Fig. 2.13).

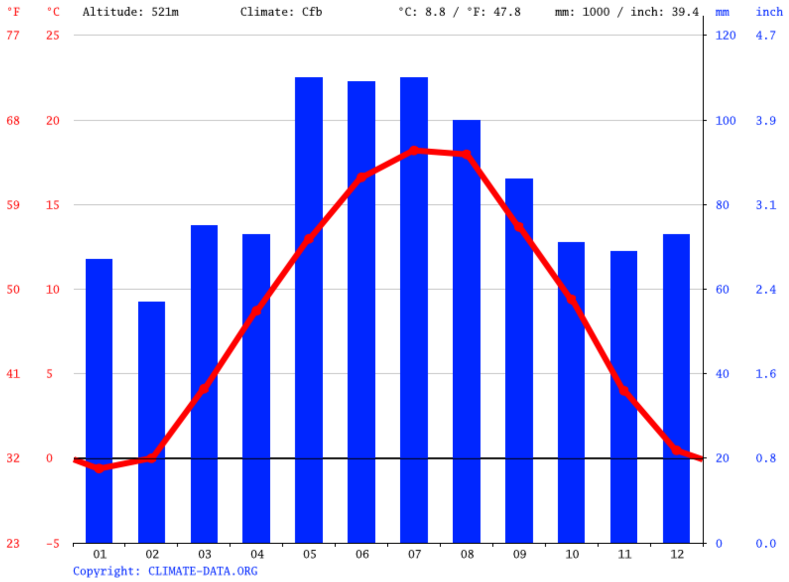

Fig. 2.13: Temperature and rainfall variation in Munich per month today. Source: climate-data.org.

Böhme (2003) studied a wide group of ectothermic vertebrates from Central Europe. The beginning of the MMCO was correlated to two migrational events at 20 Ma and 18 Ma, whereas its zenith was pinpointed during 18.0–16.5 Ma, estimating a MAT of at least 17.4^{o}C (even up to 22^{o}C). A considerable fall of MAT was revealed during 14.0–13.5 Ma, down to 14.8–15.7^{o}C. Depiction of these changes can be seen in Fig. 2.14.

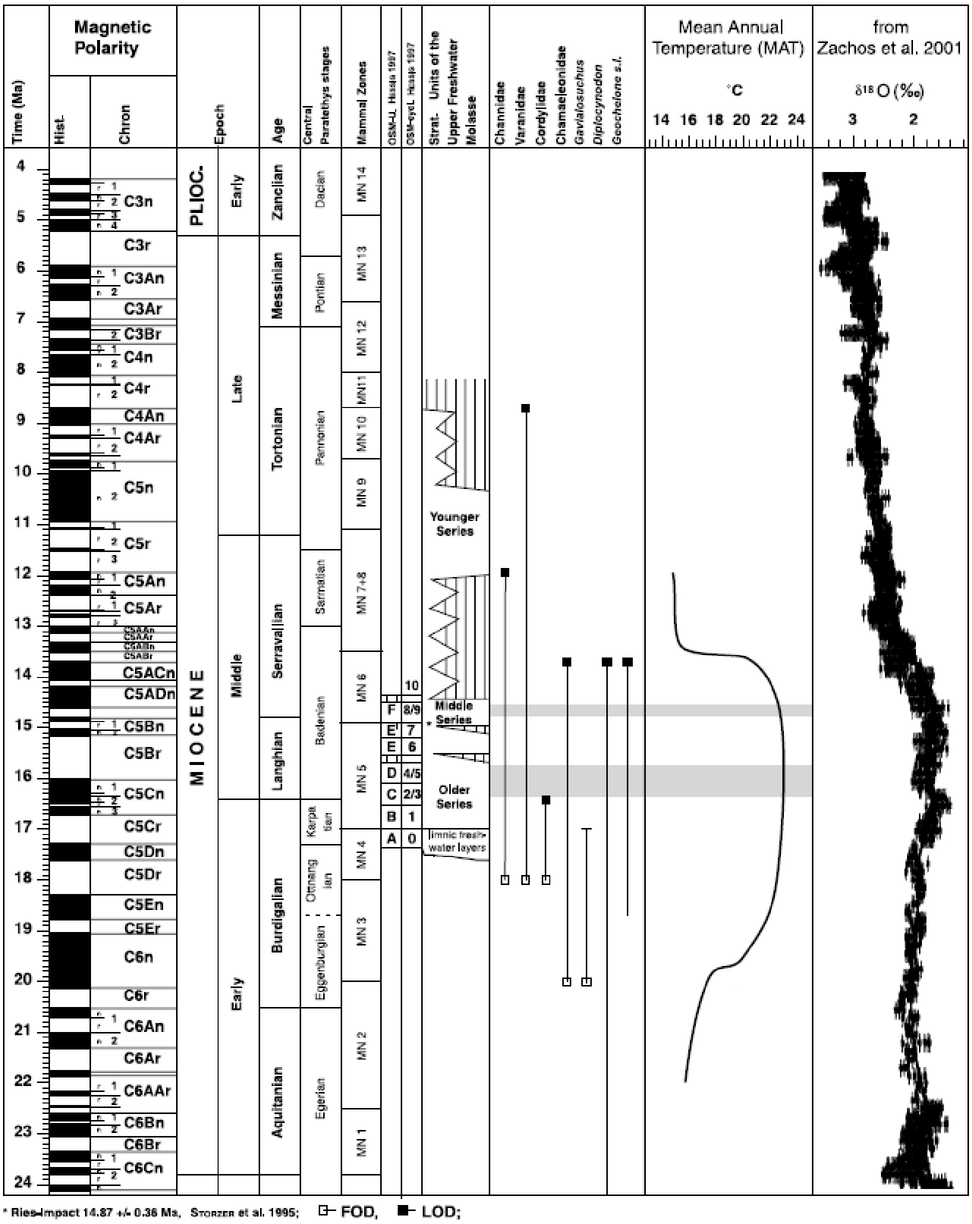

Fig. 2.14: MAT temporal change during the Early and Middle Miocene. Source: Böhme (2003).

Bruch et al. (2004) studied several localities in Europe in terms of palaeovegetation. For NW Germany the suggested a drop in MAT (from 16.85°C to 15.4°C), CMMT (10.65°C to 7.25°C) and WMT (26.75°C to 25.8°C) from the Langhian to the early Tortonian. The same was found in central Europe (Czech Republic): MAT from 17.05°C to 16.05°C, CMMT from 8.75°C to 5.7°C and WMMT from 26.4°C to 26.05°C.

Böhme et al. (2006) developed a method that is estimating MAP based on the herpetofauna of a locality. This method was used by Klembara et al. (2010) that concluded that the Miocene species of *Pseudopus* were able to live in a wide range of MAP, but the majority of the studied localities were sub-humid or humid (400–1000 mm). In particular, Klembara et al. (2010, table 2) considered Hammerschmiede as a humid locality with a MAP of approximately 1000 mm (974±256 mm for HAM 1 and 1196±263 mm for HAM 3).

Tütken et al. (2006) used isotopic analysis (C, O and Sr), in order to study the palaeoecology of the Steinheim basin (14.3–13.5 Ma). Their results suggested a MAT of approximately 19^{o}C and a water temperature of 17–22^{o}C.

Ivanov et al. (2011) studied the vegetation of North Germany, Ukraine, Serbia and Bulgaria through the Miocene. They provided a very detailed frame of MAT, WMMT, CMMT and MAP for the main regional stages (Fig. 2.15). It is not in the scope of this introduction to display all these data in detail. However, focusing on spatiotemporal proximity to Hammerschmiede, the authors suggest that during the beginning of the Late Miocene there was a slight drop in MAT and a considerable drop in MAP, resulting in a drier and colder climate. However, this didn't affect the whole Europe, as northwestern Germany remained humid (Utescher et al. 2000, 2009).

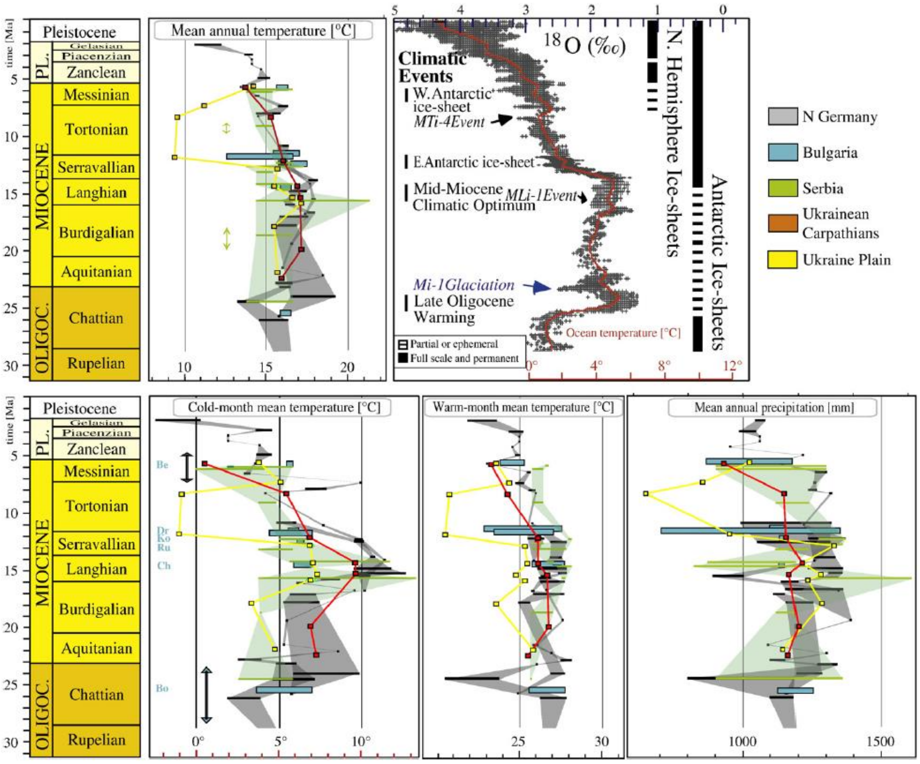

Fig. 2.15: Alternations of MAT, CMMT, WMMT and MAP in North Germany, Bulgaria, Serbia and Ukraine (Carpathians and Plains) through the Miocene. Source: Ivanov et al. (2011).

Rey et al. (2013) used $\delta^{18}O_{p}$ and $\delta^{13}C$ isotopic analysis based on several late Vallesian to late Turolian localities from Greece. Their results suggested a MAT rise from approximately 13^{o}C during the late Vallesian up to 17^{o}C during the late Turolian. Additionally, the MAP decreased from 890 mm to 471 mm.

Denk et al. (2019) studied the palaeobotanical record of the Early Miocene of Anatolia. They concluded that their data suggest a warm climate with mild temperatures of the coolest month and moderate rainfall seasonality. The best correlated biome to the studied assemblage was the Laurel Forest Biome. The presence of mountainous coniferous forests was also suggested outside the basins.

Romero et al. (2021) based their methodology on fungal remains from the Early and Middle Miocene of Thailand and Slovakia. Regarding the European material, it was concluded that during the Langhian MMCO, MAT was 10.5^{o}C (approximately 20^{o}C during the summer and 3.5^{o}C during winter) and MAP was 967 mm. The same values were estimated for the Serravallian of Slovakia. Therefore, the overall climate was estimated to be seasonal warm temperate.

Therefore, it is clear that during the transition from the Middle to Late Miocene in central Europe the temperature was much higher than today (MAT approximately 19^{o}C instead of 9^{o}C), but equally humid (MAP approximately 1000 mm). Similar values are seen today in most of Rwanda and Zambia in Africa or in Sichuan (southwest China) (climate-data.org). Additionally, during this time the climate was becoming gradually colder and drier affecting the existing faunas and floras.

Chapter 3

The locality of Hammerschmiede: History, Geology and Fauna

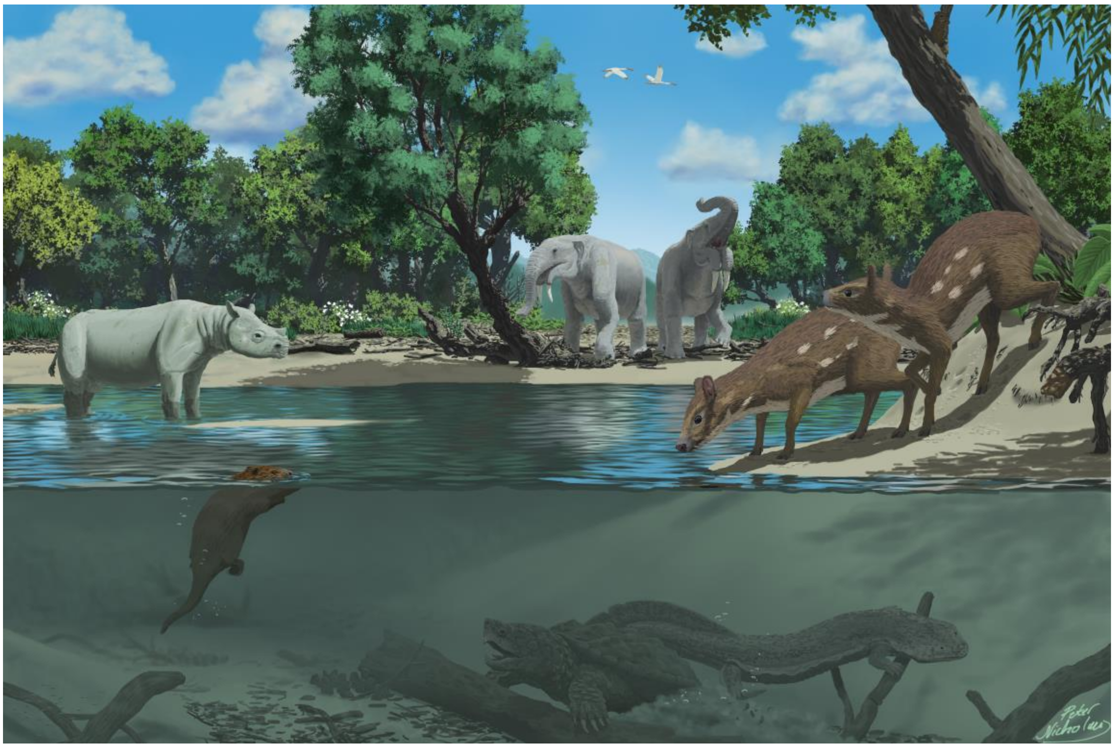

Fig. 3.1: Depiction of the Hammerschmiede ecosystem. Artist: Peter Nickolaus.

History of the Locality

The locality of Hammerschmiede is situated at the southwestern part of Bavaria, Germany southwest of the small town of Pforzen (eastern Allgäu region; 47.923° N, 10.588° E) (Fig. 3.2). The altitude of the region today is at approximately 700 m. It is located slightly north of Riedgraben, a rivulet that flows into the river Wertach. The clay pit is accessible by car from the Kemptener Straße via the Bergwertkstraße.

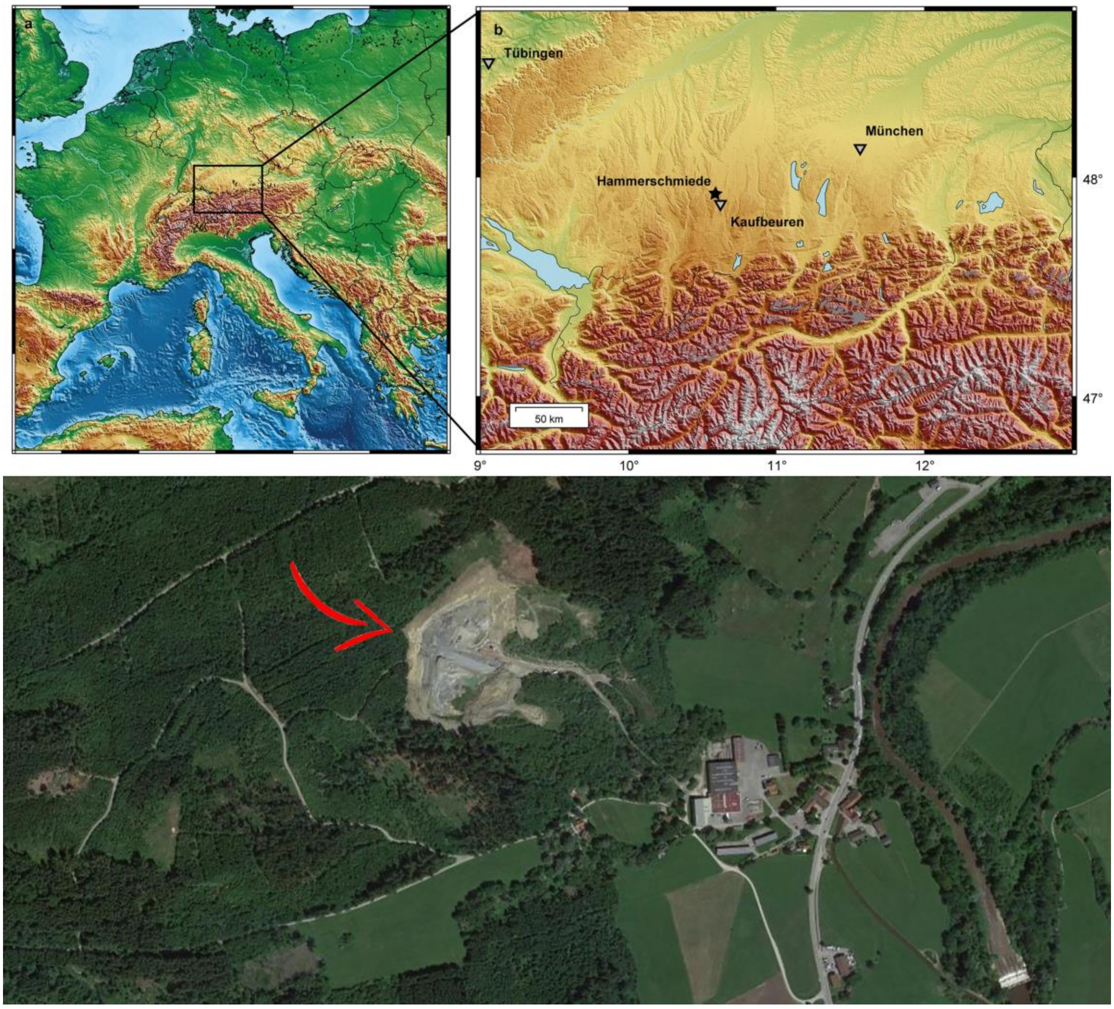

Fig. 3.2: The geographic position of Hammerschmiede. Modified from: Böhme et al. (2019).

The vertebrate fossils of the locality were discovered during the early 1970s by S. Guggenmos (Dösingen, Bayerischer Archäologiepreis) and Dr. H. Mayr (Bayerische Staatssammlung für Paläontologie und Geologie, München). The first scientific papers were published in 1975 by Dr. H. Mayr and Dr. V. Fahlbusch as Fahlbusch (1975), Fahlbusch & Mayr (1975) and Mayr & Fahlbusch (1975) concerning the micromammals they have collected. Guggenmos and M. Schmid continued to collect specimens for their private collections until the 1980s. Three publications concerning Hammerschmiede were published in the following years (Schleich, 1985; Bolliger, 1999; Hugueney, 1999). Several years later, the study of the fossil collection from Hammerschmiede hosted in the Bavarian Museum of Munich was restarted. This effort resulted in the publication of several articles concerning the micromammals and invertebrates of the locality.

New excavations on Hammerschmiede started in 2011 by the Eberhard Karls University of Tübingen led by Prof. M. Böhme and they are continued since then. The new excavations revealed an astonishingly variable ecosystem with more than 100 species of vertebrates being recorded. Several articles have been published based on this new material, mostly focusing on the mammalian and avian remains.

Summary of the Publications Concerning Hammerschmiede

- Meyer (1956) reported the presence of coal, fossil leaves and helicids in the locality. He discovered the following microfloran components in the studied layers: *Monocolpopollenites areolatus* (Palmae = Arecaceae), *Zonalapollenites igniculus* (*Tsuga diversifolia*), *Multiporopollenites maculosus* (*Juglans* sp.) and *Tacolpopollenites microhenrici* (Cupuliferae = Fagaceae). The author considered the locality to be at the end of Miocene/beginning of Pliocene.
- Mayr & Fahlbusch (1975) described the new genus and species *Microtocricetus molassicus* (Cricetidae, Rodentia) from the localities of Hammerschmiede and Marktl.
- Fahlbusch & Mayr (1975) mentioned the presence of gastropods, bivalves (*Margaritifera flabellata bavarica*), fish (*Leuciscus* sp., *Scardinius* sp., Esocidae indet.), lizards, snakes turtles (Testudinidae and Trionychidae), insectivores (*Plesiosorex* aff. *schaffneri*, *Angustidens excultus*, *Desmanella quinquecuspidata*), carnivorans (*Proputorius sansaniensis* and *Proputorius pusillus* as "*Martes pusillus*") and rodents (*Spermophilinus bredai*, *Miopetaurista albanensis quiricensis*, *Steneofiber minutus*, *Steneofiber jaegeri*, *Microdyromys miocaenicus*, *Paraglirulus* sp., *Eomuscardinus* aff. *sansaniensis*, *Myoglis larteti*, *Eliomys* n. sp., *Leptodontomys catalaunicus*, *Anomalomys gaudryi*, *Democricetodon minor brevis*, *Democricetodon gaillardi freisingensis*, *Megacricetodon* aff. *debruijni*, *Microtocricetus mollasicus*) perissodactyls (*Aceratherium* sp.), artiodactyls (*Dorcatherium* sp. and a smaller form) and lagomorphs (*Amphilagus fontannesi*).
- Jung & Mayr (1980) placed Hammerschmiede to their MN 9 group of localities based on the high frequency of *Glyptostrobus* and *Fagus* and the micromammalian components. They also commented on the low number of cricetids and glirids and the high number of eomyids in the locality.
- Seitner (1987) studied the microflora of the locality.
- Mein (1989) placed Hammerschmiede in MN 9.
- de Bruijn et al. (1992) also placed Hammerschmiede in MN 9.
- Bolliger (1999) mentioned the presence of *Anomalomys gaudryi* in Hammerschmiede, considering the locality as MN 9.
- Daams (1999) mentioned the presence of *Eliomys assimilis* and *Eliomys reductus* in the locality, considering it as MN 9.
- Fejfar (1999) mentioned the presence of *Microtocricetus mollasicus* in the locality, considering it as MN 9.
- Hugueney (1999) just mentioned the presence of *Chalicomys jaegeri* and *Trogontherium minutum* in the locality considering it as MN 9.

- Ziegler (1999) considered Hammerschmiede to be MN 9, while commenting on the presence of *Plesiosorex* aff. *schaffneri* and *Angustidens excultus* in the locality.
- Seitner (2004) uploaded a list of the microflora of the locality.
- Prieto (2007) studied the micromammals of the locality in a taxonomic, biostratigraphic and palaeoecological view.
- Prieto & Rummel (2009a) included data for *Collimys hiri* in their tables.
- Prieto & Rummel (2009b) erected the species *Collimys hiri* based on material from HAM 1 and HAM 3.
- Klembara et al. (2010) mentioned the presence in HAM 1 and HAM 3 of *Pseudopus pannonicus*, *Andrias* sp. (HAM 1), aff. *Palaeoproteus* sp., Batrachosauroidae indet. (HAM 3), Urodela indet. (HAM 3), *Mioproteus* aff. *wezei*, *Chelotriton paradoxus*, *Triturus roersi*, *Triturus* aff. *montadoni* (HAM 3), *Latonia gigantea*, *Palaeobatrachus* sp. (HAM 3), *Bufo* sp. (HAM 3), *Hyla* sp. (HAM 1), *Pelophylax* sp., *Eopelobates* sp. (HAM 3), *Lazarussuchus* sp. (HAM 3), *Trionyx* sp. (HAM 1), *Chelydropsis* sp., *Clemmydopsis* sp., Amphosbaenidae indet. (HAM 1), *Testudo* sp., *Lacerta* sp., *Chalcides* sp. (HAM 1), Scincidae indet. (HAM 3) and *Ophisaurus* sp.
- van Dam (2010) published material of *Crusafontina exculta* from HAM 1.
- Prieto et al. (2011) published material of *Galerix* cf. *exilis* from HAM 3.
- Schneider & Prieto (2011) published the presence of the bivalves *Margaritifera flabellata*, *Sphaerium rivicola* and *Pisidium amnicum* and the gastropods *Borysthenia* sp., *Bithynia* sp. 1 and *Bithynia* sp. 2.
- Prieto (2012) published specimens of *Eomyops catalaunicus* from HAM 1, HAM 2 and HAM 3.
- Prieto & van Dam (2012) described material of *Crusafontina exculta* from HAM 1 and HAM 2.
- Fuss et al. (2015) published remains of *Miotragocerus monacensis* (Bovidae, Artiodactyla) from HAM 5.
- Kirscher et al. (2016) discussed the geology of the locality in detail, calibrating the age of HAM 4 at 11.44 Ma and of HAM 5 at 11.62 Ma. They also published a summary of the fauna of the locality.
- Böhme et al. (2019) published the presence of the new ape *Danuvius guggenmosi* from HAM 5, demonstrating adaptations in the vertebral column and the limbs that were associated with partial bipedalism.
- Böhme et al. (2020) furtherly supported their arguments on the locomotor adaptations of *Danuvius*.
- Lechner & Böhme (2020) made a review of the history and findings of the locality.
- Mayr et al. (2020a) published specimens of *Anhinga pannonica* (Anhingidae, Suliformes) from HAM 4 and HAM 5.
- Mayr et al. (2020b) described a skull of a crane (Gruidae, Gruiformes) from HAM 4.
- Hartung et al. (2020) published cranial material of *Miotragocerus monacensis* from HAM 4 and HAM 5.

- Kargopoulos et al. (2021a) published the presence of *Semigenetta sansaniensis* from HAM 4 and HAM 5 and *Semigenetta grandis* in HAM 4.
- Kargopoulos et al. (2021b) erected the new species *Vishnuonyx neptuni* based on material from HAM 4.
- Kargopoulos et al. (2021c) published specimens of *Thalassictis montadai* from HAM 5 and HAM 6 and of a large bone-cracking hyena from HAM 5.
- Mayr et al. (2022) reported a new genus and species of a goose, *Allgoviachen tortonica*.
- Kargopoulos et al. (In Press) published a detailed review of the small carnivorans of the locality, reporting the presence of “*Martes*” *sansaniensis*, “*Martes*” cf. *munki*, “*Martes*” sp., *Circamustela hartmanni* (new species), *Laphyctis mustelinus*, Guloninae indet., *Eomellivora moralesi*, *Vishnuonyx neptuni*, *Paralutra jaegeri*, *Lartetictis* cf. *dubia*, *Trocharion albanense*, *Palaeomeles pachecoi*, *Proputorius sansaniensis*, *Proputorius pusillus*, *Alopecocyon goeriachensis*, Simocyoninae indet., *Potamotherium* sp., *Semigenetta sansaniensis*, *Semigenetta grandis* and *Viverrictis modica*. Additionally, they presented a preliminary palaeoecological analysis for these species.

Geology

Hammerschmiede is part of the North Alpine Foreland Basin (NAFB; also called Molasse basin). This basin was formed from the late Eocene until the end of the Miocene, following the orogeny of the Alps. The basin is composed of four large parts: the Lower Marine Molasse (LMM), the Upper Marine Molasse (UMM), the Lower Freshwater Molasse (LFM) and the Upper Freshwater Molasse (UMM) (Kuhlemann & Kempf, 2002, fig. 2). The clay pit of Hammerschmiede is part of the Upper Freshwater Molasse that spans through the Middle and Late Miocene. Regionally, the UMM is divided in four units: Limnische Untere Serie, Fluviatile Untere Serie, Geröllsandserie and Obere Serie (Doppler et al., 2005). Hammerschmiede is part of the latter.

Kirscher et al. (2016) discussed the geology of the locality in detail. The clay pit has been depicted through a 25.7 m thick section (Fig. 3.3). From a sedimentological point of view, the major part of the clay pit consists of grey, carbonatic, fine grained sediment (ranging from clay to fine sand). The base of the section is formed by a marlstone horizon (45 cm thick) that contains gastropods. The top of the pit is formed by a lignite horizon (25 cm) that contains xylit. The upper 10 cm of it are carbonatic organic clay.

Six stratigraphic layers have been described, coded as HAM 1, HAM 2, HAM 3, HAM 4, HAM 5 and HAM 6. HAM 1 corresponds to the layer were H. Mayr and S. Guggenmos were excavating. Publications in the early 2000s corresponded to excavations in the layers HAM 2 and HAM 3. The excavations of the University of Tübingen are held in the layers HAM 4 and HAM 5. Finally, the layer HAM 6 corresponds to the layer were S. Guggenmos and M. Schmid were excavating during the 1970s and 1980s.

The recent excavations have provided an astonishing amount of specimens from the layers HAM 4 and HAM 5. These two layers correspond to two rivulets, a fact also supported by the presence of freshwater mollusks and the high frequency of freshwater turtles. Kirscher et al. (2016) correlated HAM 5 with C5r.2n with an age of 11.62 Ma, whereas the age for HAM 4 was estimated at 11.44 Ma. As mentioned in Kargopoulos et al. (2021c), the layer HAM 6 has been completely outcropped today. However, based on the sedimentological profile of the whole clay pit and the available data from the old excavations, it has been suggested that the age of this layer would be approximately 11.42 Ma, being slightly younger than HAM 4. The exact position of HAM 1, HAM 2 and HAM 3 to this scheme is not very clear. Fuss et al. (2015) suggested that HAM 4 might in fact correlate with one of these three levels.

Therefore, the interval between the two main levels of Hammerschmiede is 18.000 years. This time span is long enough to make us entertain the possibility of faunal differences between them. Additionally, both levels fit to the base of the Late Miocene and the Tortonian, but they belong to the late Aragonian (MN 8) (and not to the Vallesian, MN 9) in faunal terms. Therefore, the main fossiliferous sediments of Hammerschmiede are considered to fall between those of La Grive-Saint Alban in France (Mein, 1984; Freudenthal & Mein, 1989; de Bruijn et al., 1994; Mein & Ginsburg, 2002) and those of Rudabánya in Hungary (Rabeder, 1985; Kordos, 1988; de Bruijn et al., 1994).

Finally, the fossils are usually laterally compressed, due to the use of machines in the clay pit (Böhme et al., 2019). In some cases, associated elements are found in a small area, while infrequently some articulated elements are found in anatomical position.

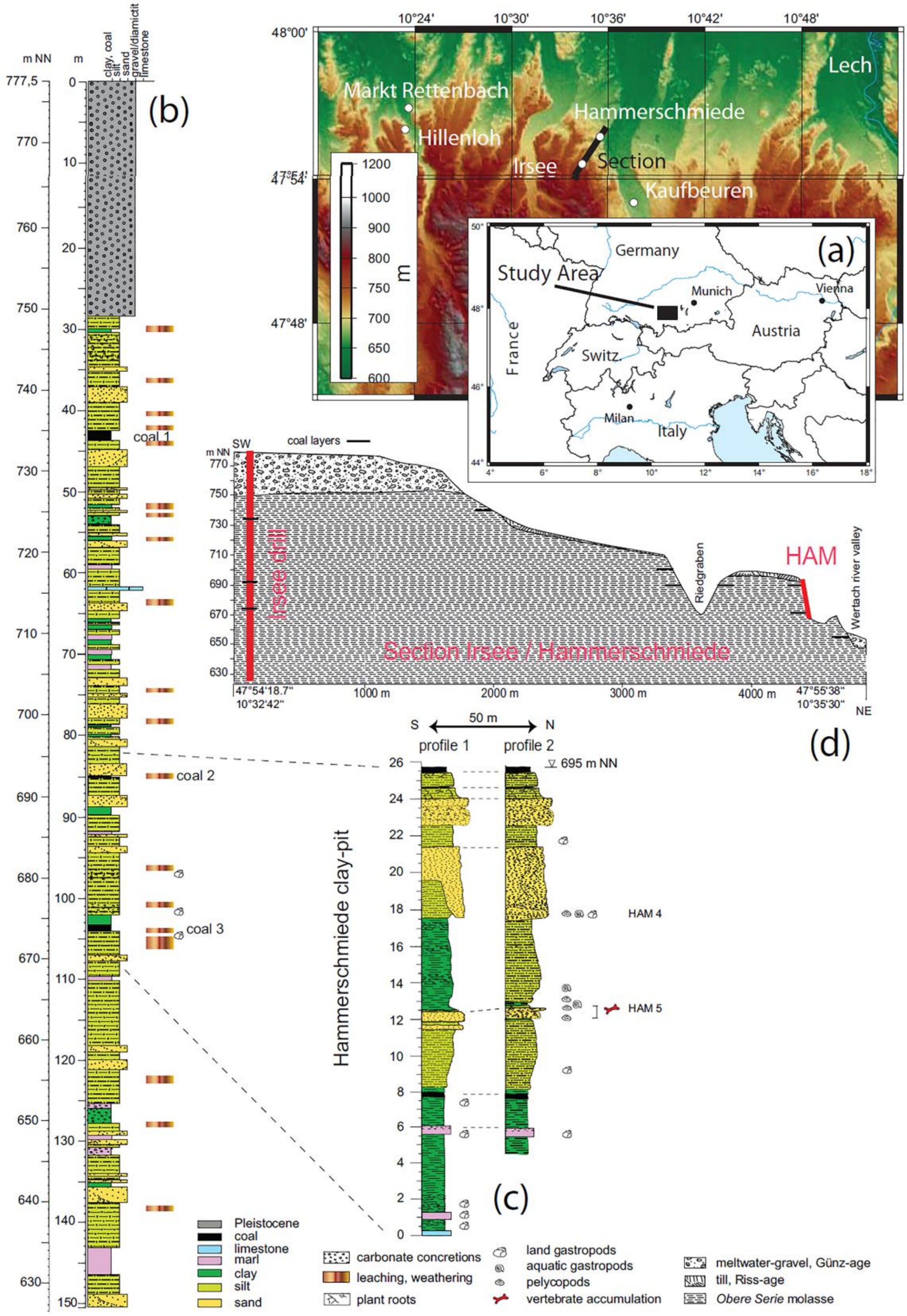

Fig. 3.3: Stratigraphical section of the Hammerschmiede clay pit. Source: Kirscher et al. (2016).

Fauna

The updated vertebrate faunal list of Hammerschmiede combined levels can be seen in Table 3.1. This list is based on the fauna provided by Kirscher et al. (2016) and Böhme et al. (2019), with some recent changes concerning the carnivorans and aves.

Table 3.1: The combined faunal list of all the Hammerschmiede layers based on Kirscher et al. (2016) and Böhme et al. (2019), including the present data for carnivorans and aves.

Class	**Order**	**Family**	**Species**
Actinopterygii	Esociformes	Esocidae	*Esox* sp.
	Siluriformes	Siluridae	*Silurus* sp. nov.
	Cypriniformes	Cyprinidae	*Tinca* sp.
			Palaeoleuciscus sp.
			Leuciscus sp.
			Barbus sp.
	Perciformes	Gobiidae	*Gobius* sp.
		Percidae	*Perca* sp.
		Sciaenidae	indet.
Amphibia	Urodela	Proteidae	*Mioproteus* sp.
		Cryptobranchidae	*Andrias scheuchzeri*
		Scapherpetontidae	indet.
		Batrachosauroidae	indet.
		Salamandridae	*Chelotriton* sp.
			Triturus sp.
	Anura	Discoglossidae	*Latonia gigantea*
		Bufonidae	*Bufo* cf. *viridis*
		Ranidae	*Pelophylax* sp.
		Pelobatidae	*Eopelobates* sp.
Reptilia	Choristodera		*Lazarussuchus* sp.
	Chelonia	Trionychidae	*Trionyx* sp.
		Chelydridae	*Chelydropsis* sp.
		Geoemydidae	*Clemmydopsis* sp.
			Mauremys sarmatica
		Testudinidae	*Testudo* sp.
			Titanochelon sp.
	Squamata	Lacertidae	*Lacerta* sp.
		Anguidae	*Pseudopus pannonicus*
			Ophisaurus sp.
		Boidae	Erycinae indet.
		Colubridae	Colubrinae sp. 1
			Colubrinae sp. 2
			Natricinae sp. 1
			Natricinae sp. 2
Aves	Suliformes	Anhingidae	*Anhinga pannonica*
	Anseriformes	Anatidae	*Allgoviachen tortonica*
	Gruiformes	Gruidae	indet.
	Accipitriformes	indet.	indet.
Mammalia	Eulipotyphla	Erinaceidae	Erinaceinae indet.

	Plesiosoricidae	*Plesiosorex schaffneri*
	Talpidae	*Gehardstorchia qunquecuspidata*
		Desmanella sp.
		Talpa sp.
		Proscapanus sp.
	Dimylidae	*Plesiodimylus johanni*
		Metacordylodon schlosseri
	Soricidae	*Crusafontina exculta*
		Paenelimnoecus crouzeli
		Dinosorex sp. nov.
		indet. 1
		indet. 2
Chiroptera	div. fam.	div. sp.
Primates	Pliopithecidae	*Pliopithecus* sp. nov.
	Hominidae	*Danuvius guggenmosi*
Carnivora	Amphicyonidae	indet.
	Ursidae	*Kretzoiarctos beatrix*
	Phocidae	indet.
	Mustelidae	“*Martes*” *sansaniensis*
		“*Martes*” *munki*
		“*Martes*” sp.
		Circamustela hartmanni
		Laphictis mustelinus
		Guloninae indet.
		Eomellivora moralesi
		Vishnuonyx neptuni
		Lartetictis cf. *dubia*
		Paralutra jaegeri
		Trocharion albanense
	Mephitidae	*Palaeomeles pachecoi*
		Proputorius sansaniensis
		Proputorius pusillus
	Ailuridae	*Alopecocyon goeriachensis*
		Simocyoninae indet.
	indet.	*Potamotherium* sp.
	Felidae	*Pseudaelurus quadridentatus*
		Metailurini indet.
	Barbourofelidae	indet.
	Viverridae	*Semigenetta sansaniensis*
		Semigenetta grandis
		Viverrictis modica
	Hyaenidae	*Thalassictis montadai*
		indet.
Proboscidea	Gomphotheriidae	*Tetralophodon longirostris*
	Deinotheriidae	*Deinotherium* sp.
Perissodactyla	Rhinocerotidae	*Hoploaceratherium belvederense*
	Schizotheriidae	*Ancylotherim* sp.
	Equidae	*Sinohippus* sp.
Artiodactyla	Suidae	*Listriodon splendens*
		Parachleuastochoerus steinheimensis

		Tragulidae	*Dorcatherium naui*
		Moschidae	indet.
		Cervidae	*Euprox furcatus*
		Bovidae	*Miotragocerus monacensis*
			Boselaphinae indet.
	Lagomorpha	Ochotonidae	*Prolagus oeningensis*
			Eurolagus fontannesi
	Rodentia	Sciuridae	*Spermophilus bredai*
			Albanensia grimmi
			Blackia miocaenica
			Petauristinae indet.
		Castoridae	*Euroxenomys minutus*
			Chalicomys jaegeri
		Gliridae	*Microdyromys complicates*
			Muscardinus hispanicus
			Glirulus conjunctus
			Eliomys sp.
			Myoglis meini
		Eomyidae	*Eomyops catalaunicus*
			Keramidomys sp.
		Cricetidae	*Democricetodon* sp. nov.
			Collimys hiri
			Megacricetodon minutus
			Microtocricetus molassicus
			Eumyarion latior
		Anomalomyidae	*Anomalomys gaudryi*

This very long faunal list includes an impressive sum of 115 species. 9 of them are fish, 10 amphibians, 15 reptiles, 4 birds and 77 mammals: 35 micromammals (Eulipotyphla, Chiroptera, Lagomorpha and Rodentia) and 42 macromammals (Primates, Carnivora, Proboscidea, Perissodactyla and Artiodactyla) (Fig. 3.4).

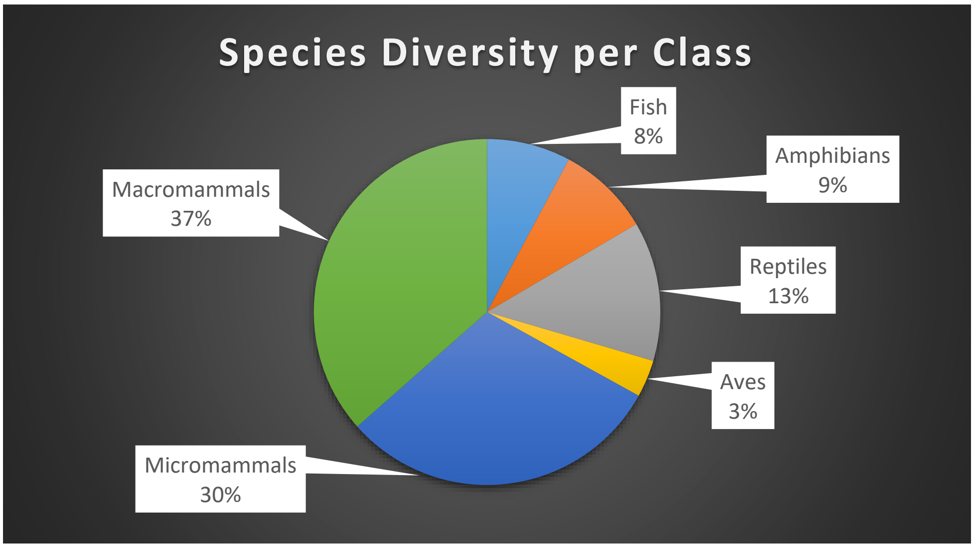

Fig. 3.4: Species diversity per Class in the Hammerschmiede locality.

Summing up, the research efforts of the past 50 years have proven that Hammerschmiede is an extremely valuable locality for the study of the Miocene of Europe. The main points supporting this are the following:

- The age of the main levels perfectly fits to the base of the Late Miocene, reflecting the faunal changes that happened during that period.
- The presence of several different levels can be very informative in uncovering the faunal alternations during their intervals.
- Several new species have been reported from the locality, with *D. guggenmosi* being the one that gets the most attention, because of its phylogenetic position and locomotor behavior.
- The extremely high number of species (even for carnivoran species, which are very rare and not variable in other localities) provides a fruitful field of discussion about their ability to coexist in the same environment.
- The location of Hammerschmiede at the middle of Europe, above the Alps, and the presence of the river make it a keystone locality for the study of dispersals/migrations in Europe during the beginning of Late Miocene.
- The abundance of fossils, independently to their biodiversity, offer a detailed view for the ecosystem.
- A detailed analysis of the ecological relationships between the different species of Hammerschmiede can enrich our understanding for the role of hominids during the Miocene, helping us to clarify the forces that directed their evolution.

Chapter 4

Material and Methods

Material

The material studied in this Thesis has been discovered in the layers HAM 1, HAM 4, HAM 5 and HAM 6 of the locality of Hammerschmiede. The material from HAM 1 corresponds to the material published by Mayr & Fahlbusch (1975) and it is hosted in the collections of SNSB-BSPG. The material from HAM 4 and HAM 5 comes from the excavations organized by the Eberhard Karls University of Tübingen under the supervision of Prof. M. Böhme. Finally, the material from HAM 6 comes from private collections. The material from HAM 4, HAM 5 and HAM 6 are currently at GPIT. A detailed list of the material accompanied by the anatomical and taxonomical identification is provided in Table 4.1. The coprolites are mentioned in the corresponding section.

Table 4.1: The carnivoran material from Hammerschmiede.

Code	**Layer**	**Element**	**Taxonomy**
SNSB-BSPG-1973-XIX-34	HAM 1	left P4	“*Martes*” sp.
SNSB-BSPG-1973-XIX-23	HAM 1	right P4	*Circamustela hartmanni*
SNSB-BSPG-1973-XIX-24	HAM 1	right p4	*Proputorius sansaniensis*
SNSB-BSPG-1973-XIX-25	HAM 1	right m1	*Proputorius sansaniensis*
SNSB-BSPG-1973-XIX-30	HAM 1	right p3	*Proputorius pusillus*
SNSB-BSPG-1973-XIX-31	HAM 1	right p3	*Proputorius pusillus*
SNSB-BSPG-1973-XIX-32	HAM 1	right m1	*Proputorius pusillus*
SNSB-BSPG-1973-XIX-33	HAM 1	right m1	*Proputorius pusillus*
SNSB-BSPG-1973-XIX-26	HAM 1	right m2	*Semigenetta sansaniensis*
SNSB-BSPG-1973-XIX-22	HAM 1	right I3	Carnivora indet.
SNSB-BSPG-1973-XIX-28	HAM 1	left I1	Carnivora indet.
SNSB-BSPG-1973-XIX-29	HAM 1	left I1	Carnivora indet.
SNSB-BSPG-1973-XIX-27	HAM 1	left I2	Carnivora indet.
GPIT/MA/10959	HAM 4	skull	“*Martes*” *sansaniensis*
SNSB-BSPG-2020-XCIV-4065	HAM 4	right P4	“*Martes*” *sansaniensis*
GPIT/MA/16963	HAM 4	right P4	“*Martes*” *sansaniensis*
GPIT/MA/16924	HAM 4	right hemimandible	“*Martes*” *munki*
GPIT/MA/17238	HAM 4	right hemimandible	*Circamustela hartmanni*
GPIT/MA/17033	HAM 4	left hemimandible	*Circamustela hartmanni*
SNSB-BSPG-2020-XCIV-3395	HAM 4	right M1	*Laphyctis mustelinus*
SNSB-BSPG-2020-XCIV-6821	HAM 4	right M1	*Paralutra jaegeri*
SNSB-BSPG-2020-XCIV-5703	HAM 4	left M1	*Paralutra jaegeri*
SNSB-BSPG-2020-XCIV-5704	HAM 4	left M1	*Paralutra jaegeri*
GPIT/MA/17790	HAM 4	left hemimandible	*Lartetictis* cf. *dubia*
GPIT/MA/17065	HAM 4	left hemimandible	*Lartetictis* cf. *dubia*
SNSB-BSPG-2020-XCIV-2683	HAM 4	left m1	*Lartetictis* cf. *dubia*
SNSB-BSPG-2020-XCIV-6826	HAM 4	left m1	*Lartetictis* cf. *dubia*
SNSB-BSPG-2020-XCIV-1022	HAM 4	left P3	*Vishnuonyx neptuni*
GPIT/MA/17347	HAM 4	right P4	*Vishnuonyx neptuni*
SNSB-BSPG-2020-XCIV-5702	HAM 4	right M1	*Vishnuonyx neptuni*
SNSB-BSPG-2020-XCIV-1552	HAM 4	left M1	*Vishnuonyx neptuni*

SNSB-BSPG-2020-XCIV-0301	HAM 4	right hemimandible	*Vishnuonyx neptuni*
GPIT/MA/16733	HAM 4	left hemimandible	*Vishnuonyx neptuni*
SNSB-BSPG-2020-XCIV-1301	HAM 4	right p4	*Vishnuonyx neptuni*
SNSB-BSPG-2020-XCIV-5700	HAM 4	right p4	*Vishnuonyx neptuni*
SNSB-BSPG-2020-XCIV-4029	HAM 4	right m1	*Vishnuonyx neptuni*
SNSB-BSPG-2020-XCIV-5701	HAM 4	left m1	*Vishnuonyx neptuni*
SNSB-BSPG-2020-XCIV-5708	HAM 4	right m1	*Vishnuonyx neptuni* (?)
GPIT/MA/16564	HAM 4	distal humerus	Lutrinae indet.
GPIT/MA/17149	HAM 4	distal humerus	Lutrinae indet.
GPIT/MA/16579	HAM 4	skull	*Trocharion albanense*
GPIT/MA/12553	HAM 4	right M1	*Trocharion albanense*
SNSB-BSPG-2020-XCIV-2690	HAM 4	left M1	*Trocharion albanense*
SNSB-BSPG-2020-XCIV-5705	HAM 4	right m2	Simocyoninae indet.
SNSB-BSPG-2020-XCIV-3551	HAM 4	P3	*Potamotherium* sp.
GPIT/MA/16463	HAM 4	left MtII	Musteloidea indet.
SNSB-BSPG-2020-XCIV-0899	HAM 4	left MtIII	Musteloidea indet.
GPIT/MA/16183	HAM 4	distal Mp	Musteloidea indet.
GPIT/MA/10970	HAM 4	pisiform	Musteloidea indet.
SNSB-BSPG-2020-XCIV-1155	HAM 4	calcaneum	Musteloidea indet.
SNSB-BSPG-2020-XCIV-5724	HAM 4	calcaneum	Musteloidea indet.
SNSB-BSPG-2020-XCIV-1612	HAM 4	calcaneum	Musteloidea indet.
SNSB-BSPG-2020-XCIV-2688	HAM 4	calcaneum	Musteloidea indet.
GPIT/MA/17373	HAM 4	calcaneum	Musteloidea indet.
GPIT/MA/12528	HAM 4	Os cuneiform III	Musteloidea indet.
GPIT/MA/17500	HAM 4	Right MtV	Musteloidea indet.
SNSB-BSPG-2020-XCIV-4270	HAM 4	right P4	*Kretzoiarctos beatrix*
SNSB-BSPG-2020-XCIV-2676	HAM 4	right P4	*Kretzoiarctos beatrix*
SNSB-BSPG-2020-XCIV-0162	HAM 4	right M1	*Kretzoiarctos beatrix*
SNSB-BSPG-2020-XCIV-4014	HAM 4	left m2	*Kretzoiarctos beatrix*
GPIT/MA/16996	HAM 4	premolar	Phocidae indet.
GPIT/MA/17520	HAM 4	left hemimandible	Caniformia indet.
GPIT/MA/17876	HAM 4	left hemimandible	Caniformia indet.
SNSB-BSPG-2020-XCIV-2678	HAM 4	milk enamel	Caniformia indet.
SNSB-BSPG-2020-XCIV-5734	HAM 4	proximal ulna	Caniformia indet.
GPIT/MA/17947	HAM 4	proximal ulna	Caniformia indet.
GPIT/MA/17442	HAM 4	Phalanx	Caniformia indet.
SNSB-BSPG-2020-XCIV-4220	HAM 4	right m1	*Semigenetta grandis*
GPIT/MA/1245	HAM 4	right m1	*Semigenetta grandis*
GPIT/MA/17698	HAM 4	right P4	*Semigenetta sansaniensis*
GPIT/MA/12451	HAM 4	right P4	*Semigenetta sansaniensis*
SNSB-BSPG-2020-XCIV-2682	HAM 4	right P4	*Semigenetta sansaniensis*
SNSB-BSPG-2020-XCIV-0364	HAM 4	right P4	*Semigenetta sansaniensis*
SNSB-BSPG-2020-XCIV-6825	HAM 4	left P4	*Semigenetta sansaniensis*
GPIT/MA/18081	HAM 4	right hemimandible	*Semigenetta sansaniensis*
SNSB-BSPG-2020-XCIV-4024	HAM 4	right hemimandible	*Semigenetta sansaniensis*

GPIT/MA/16973	HAM 4	right hemimandible	*Semigenetta sansaniensis*
GPIT/MA/17351	HAM 4	right p4	*Semigenetta sansaniensis*
SNSB-BSPG-2020-XCIV-6824	HAM 4	right p4	*Semigenetta sansaniensis*
GPIT/MA/No Nu	HAM 4	left p4	*Semigenetta sansaniensis*
SNSB-BSPG-2020-XCIV-3614	HAM 4	right m1	*Semigenetta sansaniensis*
SNSB-BSPG-2020-XCIV-5706	HAM 4	right m1	*Semigenetta sansaniensis*
GPIT/MA/18115	HAM 4	right m1	*Semigenetta sansaniensis*
GPIT/MA/10967	HAM 4	right m1	*Semigenetta sansaniensis*
GPIT/MA/18110	HAM 4	left ulna	*Semigenetta sansaniensis*
GPIT/MA/16617	HAM 4	proximal ulna	*Semigenetta sansaniensis*
GPIT/MA/17774	HAM 4	distal radius	*Semigenetta sansaniensis*
GPIT/MA/17878	HAM 4	astragalus	*Semigenetta sansaniensis*
SNSB-BSPG-2020-XCIV-1119	HAM 4	MtIV	*Semigenetta sansaniensis*
SNSB-BSPG-2020-XCIV-3995	HAM 4	right P4	*Viverrictis modica*
GPIT/MA/16659	HAM 4	right P4	*Viverrictis modica*
SNSB-BSPG-2020-XCIV-5715	HAM 4	P2 (?)	*Thalassictis montadai* (?)
SNSB-BSPG-2020-XCIV-3550	HAM 4	right D3	Feliformia indet.
SNSB-BSPG-2020-XCIV-2004	HAM 4	distal humerus	Feliformia indet.
GPIT/MA/16142	HAM 4	left McII	Feliformia indet.
GPIT/MA/16712	HAM 4	right McIII	Feliformia indet.
SNSB-BSPG-2020-XCIV-5729	HAM 4	Os cuneiform III	Feliformia indet.
SNSB-BSPG-2020-XCIV-2126	HAM 4	right MtIV	Feliformia indet.
GPIT/MA/16697	HAM 4	I/i	Carnivora indet.
GPIT/MA/17738	HAM 4	right C	Carnivora indet.
GPIT/MA/12576	HAM 4	right C	Carnivora indet.
GPIT/MA/16936	HAM 4	right C	Carnivora indet.
GPIT/MA/17069	HAM 4	right C	Carnivora indet.
GPIT/MA/17994	HAM 4	right C	Carnivora indet.
GPIT/MA/17688	HAM 4	right C	Carnivora indet.
GPIT/MA/16410	HAM 4	right C	Carnivora indet.
SNSB-BSPG-2020-XCIV-5709	HAM 4	right C	Carnivora indet.
SNSB-BSPG-2020-XCIV-3552	HAM 4	right C	Carnivora indet.
SNSB-BSPG-2020-XCIV-5711	HAM 4	left C	Carnivora indet.
GPIT/MA/17526	HAM 4	left C	Carnivora indet.
GPIT/MA/16927	HAM 4	left C	Carnivora indet.
GPIT/MA/16949	HAM 4	left C	Carnivora indet.
GPIT/MA/17116	HAM 4	left C	Carnivora indet.
GPIT/MA/17096	HAM 4	left C	Carnivora indet.
GPIT/MA/18073	HAM 4	left C	Carnivora indet.
SNSB-BSPG-2020-XCIV-5713	HAM 4	C	Carnivora indet.
GPIT/MA/17570	HAM 4	p1	Carnivora indet.
SNSB-BSPG-2020-XCIV-4134	HAM 4	premolar	Carnivora indet.
SNSB-BSPG-2020-XCIV-4166	HAM 4	premolar	Carnivora indet.
GPIT/MA/17219	HAM 4	premolar	Carnivora indet.
SNSB-BSPG-2020-XCIV-5707	HAM 4	premolar	Carnivora indet.

SNSB-BSPG-2020-XCIV-6823	HAM 4	premolar	Carnivora indet.
SNSB-BSPG-2020-XCIV-6822	HAM 4	premolar	Carnivora indet.
GPIT/MA/16403	HAM 4	premolar	Carnivora indet.
GPIT/MA/16658	HAM 4	premolar	Carnivora indet.
GPIT/MA/16923	HAM 4	right hemimandible	Carnivora indet.
GPIT/MA/16556	HAM 4	right c	Carnivora indet.
GPIT/MA/16992	HAM 4	right c	Carnivora indet.
GPIT/MA/16131	HAM 4	right c	Carnivora indet.
GPIT/MA/16821	HAM 4	right c	Carnivora indet.
SNSB-BSPG-2020-XCIV-5716	HAM 4	left c	Carnivora indet.
SNSB-BSPG-2020-XCIV-5714	HAM 4	left m1	Carnivora indet.
GPIT/MA/16954	HAM 4	proximal humerus	Carnivora indet.
GPIT/MA/18090	HAM 4	proximal ulna	Carnivora indet.
GPIT/MA/16606	HAM 4	distal ulna	Carnivora indet.
GPIT/MA/17602	HAM 4	proximal radius	Carnivora indet.
GPIT/MA/17866	HAM 4	distal radius	Carnivora indet.
GPIT/MA/17104	HAM 4	distal radius	Carnivora indet.
GPIT/MA/17695	HAM 4	Os trapezoideum	Carnivora indet.
GPIT/MA/16714	HAM 4	Os trapezoideum	Carnivora indet.
GPIT/MA/16508	HAM 4	McI	Carnivora indet.
GPIT/MA/16713	HAM 4	right McIV	Carnivora indet.
SNSB-BSPG-2020-XCIV-5745	HAM 4	Patella	Carnivora indet.
GPIT/MA/17920	HAM 4	Patella	Carnivora indet.
GPIT/MA/18075	HAM 4	Patella	Carnivora indet.
GPIT/MA/17524	HAM 4	Tibia	Carnivora indet.
GPIT/MA/16738	HAM 4	Tibia	Carnivora indet.
GPIT/MA/16479	HAM 4	Tibia	Carnivora indet.
GPIT/MA/12539	HAM 4	Calcaneum	Carnivora indet.
SNSB-BSPG-2020-XCIV-2167	HAM 4	Calcaneum	Carnivora indet.
GPIT/MA/16175	HAM 4	Navicular	Carnivora indet.
GPIT/MA/17328	HAM 4	Cuboid	Carnivora indet.
GPIT/MA/16872	HAM 4	Cuboid	Carnivora indet.
GPIT/MA/12704	HAM 4	Mp	Carnivora indet.
GPIT/MA/12507	HAM 4	distal Mp	Carnivora indet.
SNSB-BSPG-2020-XCIV-5721	HAM 4	Phalanx	Carnivora indet.
SNSB-BSPG-2020-XCIV-5722	HAM 4	Phalanx	Carnivora indet.
SNSB-BSPG-2020-XCIV-5738	HAM 4	Phalanx	Carnivora indet.
SNSB-BSPG-2020-XCIV-5740	HAM 4	Phalanx	Carnivora indet.
SNSB-BSPG-2020-XCIV-5741	HAM 4	Phalanx	Carnivora indet.
SNSB-BSPG-2020-XCIV-5744	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/17442	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/10969	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/17928	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/17809	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/17978	HAM 4	Phalanx	Carnivora indet.

GPIT/MA/10972	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/17528	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/17289	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/18079	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/18034	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/10975	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/17612	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/17319	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/17667	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/12531	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/18024	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/16993	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/10973	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/16603	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/17674	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/17885	HAM 4	Phalanx	Carnivora indet.
GPIT/MA/17248	HAM 4	3rd Phalanx	Carnivora indet.
GPIT/MA/16349	HAM 5	left P4	“*Martes*” *sansaniensis*
GPIT/MA/09882	HAM 5	right M1	“*Martes*” *sansaniensis*
GPIT/MA/12308	HAM 5	left M1	“*Martes*” *sansaniensis*
GPIT/MA/18606	HAM 5	right M1	“*Martes*” *munki*
GPIT/MA/10666	HAM 5	right M1	“*Martes*” *munki*
GPIT/MA/10636	HAM 5	left m1	“*Martes*” *munki*
GPIT/MA/10388	HAM 5	right P4	*Circamustela hartmanni*
GPIT/MA/10297	HAM 5	left hemimandible	Guloninae indet.
GPIT/MA/10665	HAM 5	right c	Guloninae indet. (?)
GPIT/MA/10958	HAM 5	left femur	Guloninae indet.
GPIT/MA/09877	HAM 5	left I3	*Eomellivora moralesi*
GPIT/MA/12347	HAM 5	left p3	*Eomellivora moralesi*
GPIT/MA/09875	HAM 5	right hemimandible	*Eomellivora moralesi*
GPIT/MA/10302	HAM 5	right m1	*Eomellivora moralesi*
GPIT/MA/09632	HAM 5	left m2	*Eomellivora moralesi*
GPIT/MA/10393	HAM 5	left P4	*Paralutra jaegeri*
GPIT/MA/12322	HAM 5	left M1	*Paralutra jaegeri*
GPIT/MA/18607	HAM 5	right M1	*Trocharion albanense*
GPIT/MA/31712	HAM 5	right M1	*Trocharion albanense*
GPIT/MA/13462	HAM 5	right M1	*Trocharion albanense*
GPIT/MA/18601	HAM 5	right M1	*Trocharion albanense*
GPIT/MA/12650	HAM 5	right P4	*Palaeomeles pachecoi*
GPIT/MA/09884	HAM 5	right M1	*Palaeomeles pachecoi*
GPIT/MA/09926	HAM 5	right M1	*Palaeomeles pachecoi*
GPIT/MA/13711	HAM 5	right hemimandible	*Palaeomeles pachecoi*
SNSB-BSPG-2020-XCV-0032	HAM 5	left hemimandible	*Palaeomeles pachecoi*
GPIT/MA/13749	HAM 5	left m1	*Palaeomeles pachecoi*
GPIT/MA/18620	HAM 5	left m1	*Proputorius sansaniensis*

SNSB-BSPG-2020-XCV-382	HAM 5	right M1	*Alopecocyon goeriachensis*
SNSB-BSPG-2020-XCV-0021	HAM 5	right hemimandible	cf. *Alopecocyon goeriachensis*
GPIT/MA/10300	HAM 5	left hemimandible	cf. *Alopecocyon goeriachensis*
GPIT/MA/10505	HAM 5	left M1	*Potamotherium* sp.
GPIT/MA/13741	HAM 5	pisiform	Musteloidea indet.
GPIT/MA/12663	HAM 5	right McIV	Musteloidea indet.
GPIT/MA/12706	HAM 5	astragalus	Musteloidea indet.
GPIT/MA/16352	HAM 5	calcaneum	Musteloidea indet.
GPIT/MA/12598	HAM 5	Os cuneiform III	Musteloidea indet.
GPIT/MA/13743	HAM 5	Os cuneiform III	Musteloidea indet.
GPIT/MA/16329	HAM 5	Os cuneiform III	Musteloidea indet.
SNSB-BSPG-2020-XCV-0294	HAM 5	right MtII	Musteloidea indet.
GPIT/MA/09878	HAM 5	left MtII	Musteloidea indet.
GPIT/MA/09631	HAM 5	right C	*Kretzoiarctos beatrix*
GPIT/MA/09893	HAM 5	right C	*Kretzoiarctos beatrix*
GPIT/MA/10306	HAM 5	right P4	*Kretzoiarctos beatrix*
GPIT/MA/09628	HAM 5	right M1	*Kretzoiarctos beatrix*
GPIT/MA/13464	HAM 5	right M1	*Kretzoiarctos beatrix*
GPIT/MA/09894	HAM 5	left c	*Kretzoiarctos beatrix*
GPIT/MA/10304	HAM 5	right m1	*Kretzoiarctos beatrix*
GPIT/MA/10305	HAM 5	right m2	*Kretzoiarctos beatrix*
GPIT/MA/13717	HAM 5	right m2	*Kretzoiarctos beatrix*
GPIT/MA/18604	HAM 5	p1	Phocidae indet.
GPIT/MA/18608	HAM 5	p1	Phocidae indet.
GPIT/MA/09629	HAM 5	d3 (?)	Phocidae indet.
GPIT/MA/12132	HAM 5	left McIII	Amphicyonidae indet.
GPIT/MA/12178	HAM 5	left hemimandible	Caniformia indet.
GPIT/MA/13458	HAM 5	milk enamel	Caniformia indet.
GPIT/MA/13454	HAM 5	right P4	Caniformia indet.
GPIT/MA/10301	HAM 5	d4	Caniformia indet.
GPIT/MA/09921	HAM 5	right m1	Caniformia indet.
GPIT/MA/09927	HAM 5	left m2	Caniformia indet.
GPIT/MA/12760	HAM 5	distal humerus	Caniformia indet.
GPIT/MA/12336	HAM 5	left McV	Caniformia indet.
GPIT/MA/12671	HAM 5	Os cuneiform I	Caniformia indet.
GPIT/MA/12684	HAM 5	Os cuneiform I	Caniformia indet.
GPIT/MA/13733	HAM 5	left McIV	Caniformia indet.
GPIT/MA/13452	HAM 5	right M1	*Semigenetta sansaniensis*
GPIT/MA/12130	HAM 5	left p4	*Semigenetta sansaniensis*
GPIT/MA/13729	HAM 5	right m1	*Semigenetta sansaniensis*
GPIT/MA/18602	HAM 5	left m1	*Semigenetta sansaniensis*
GPIT/MA/09925	HAM 5	left ulna	*Semigenetta sansaniensis*
GPIT/MA/12732	HAM 5	proximal right ulna	*Semigenetta sansaniensis*
GPIT/MA/12649	HAM 5	left P4	*Viverrictis modica*
GPIT/MA/09633	HAM 5	left P4	*Thalassictis montadai*

GPIT/MA/13720	HAM 5	left P4	*Thalassictis montadai*
GPIT/MA/13726	HAM 5	right p3	*Thalassictis montadai*
GPIT/MA/12164	HAM 5	left p3	*Thalassictis montadai*
GPIT/MA/09634	HAM 5	left m1	*Thalassictis montadai*
GPIT/MA/10506	HAM 5	right m2	*Thalassictis montadai*
GPIT/MA/12147	HAM 5	right I3	Hyaenidae indet.
GPIT/MA/09635	HAM 5	right distal humerus	Barbourofelidae indet.
GPIT/MA/18115	HAM 5	right C	*Pseudaelurus quadridentatus*
GPIT/MA/13999	HAM 5	right p4	*Pseudaelurus quadridentatus*
GPIT/MA/13719	HAM 5	right C	Metailurini indet.
GPIT/MA/12340	HAM 5	right D3	Feliformia indet.
GPIT/MA/13730	HAM 5	left humerus	Feliformia indet.
SNSB-BSPG-2020-XCV-0028	HAM 5	pisiform	Feliformia indet.
GPIT/MA/12179	HAM 5	left McIII	Feliformia indet.
GPIT/MA/10385	HAM 5	right McIV	Feliformia indet.
SNSB-BSPG-2020-XCV-0228	HAM 5	left McIV	Feliformia indet.
GPIT/MA/16348	HAM 5	right McV	Feliformia indet.
SNSB-BSPG-2020-XCV-355	HAM 5	left McV	Feliformia indet.
GPIT/MA/13721	HAM 5	left McV	Feliformia indet.
GPIT/MA/12306	HAM 5	femur	Feliformia indet.
GPIT/MA/12646	HAM 5	Os cuneiform III	Feliformia indet.
GPIT/MA/13722	HAM 5	left MtIV	Feliformia indet.
GPIT/MA/10392	HAM 5	distal Mp	Feliformia indet.
GPIT/MA/12661	HAM 5	I/i	Carnivora indet.
GPIT/MA/16306	HAM 5	I/i	Carnivora indet.
GPIT/MA/12583	HAM 5	I/i	Carnivora indet.
GPIT/MA/13747	HAM 5	I/i	Carnivora indet.
GPIT/MA/09973	HAM 5	I/i	Carnivora indet.
GPIT/MA/13465	HAM 5	I/i	Carnivora indet.
GPIT/MA/13748	HAM 5	I/i	Carnivora indet.
GPIT/MA/12600	HAM 5	I/i	Carnivora indet.
GPIT/MA/12200	HAM 5	right C	Carnivora indet.
GPIT/MA/13713	HAM 5	right C	Carnivora indet.
GPIT/MA/12647	HAM 5	right C	Carnivora indet.
GPIT/MA/09886	HAM 5	right C	Carnivora indet.
GPIT/MA/12199	HAM 5	right C	Carnivora indet.
GPIT/MA/09888	HAM 5	left C	Carnivora indet.
GPIT/MA/12299	HAM 5	left C	Carnivora indet.
GPIT/MA/13451	HAM 5	left C	Carnivora indet.
GPIT/MA/13715	HAM 5	C/c	Carnivora indet.
GPIT/MA/10722	HAM 5	right hemimandible	Carnivora indet.
GPIT/MA/13722	HAM 5	right hemimandible	Carnivora indet.
GPIT/MA/12162	HAM 5	right hemimandible	Carnivora indet.
GPIT/MA/12298	HAM 5	left hemimandible	Carnivora indet.
GPIT/MA/13450	HAM 5	right c	Carnivora indet.

GPIT/MA/10382	HAM 5	right c	Carnivora indet.
GPIT/MA/10394	HAM 5	right c	Carnivora indet.
GPIT/MA/10872	HAM 5	right & left c	Carnivora indet.
GPIT/MA/16293	HAM 5	p1 (?)	Carnivora indet.
GPIT/MA/13751	HAM 5	p1 (?)	Carnivora indet.
GPIT/MA/10303	HAM 5	p4 (?)	Carnivora indet.
GPIT/MA/09885	HAM 5	premolar	Carnivora indet.
GPIT/MA/09883	HAM 5	premolar	Carnivora indet.
GPIT/MA/09881	HAM 5	premolar	Carnivora indet.
GPIT/MA/10504	HAM 5	premolar	Carnivora indet.
GPIT/MA/16298	HAM 5	premolar	Carnivora indet.
GPIT/MA/12648	HAM 5	premolar	Carnivora indet.
GPIT/MA/10794	HAM 5	premolar	Carnivora indet.
GPIT/MA/12696	HAM 5	premolar	Carnivora indet.
GPIT/MA/13460	HAM 5	premolar	Carnivora indet.
GPIT/MA/09928	HAM 5	3 premolars	Carnivora indet.
GPIT/MA/13716	HAM 5	right m1	Carnivora indet.
GPIT/MA/13750	HAM 5	left m1	Carnivora indet.
GPIT/MA/18603	HAM 5	right m2	Carnivora indet.
GPIT/MA/13466	HAM 5	right m2	Carnivora indet.
GPIT/MA/09890	HAM 5	left m2	Carnivora indet.
GPIT/MA/12645	HAM 5	right proximal ulna	Carnivora indet.
GPIT/MA/13754	HAM 5	right proximal ulna	Carnivora indet.
GPIT/MA/13742	HAM 5	proximal radius	Carnivora indet.
GPIT/MA/09974	HAM 5	left McV	Carnivora indet.
GPIT/MA/12240	HAM 5	patella	Carnivora indet.
GPIT/MA/12689	HAM 5	patella	Carnivora indet.
GPIT/MA/13737	HAM 5	patella	Carnivora indet.
GPIT/MA/10724	HAM 5	patella	Carnivora indet.
GPIT/MA/10723	HAM 5	patella	Carnivora indet.
GPIT/MA/13736	HAM 5	patella	Carnivora indet.
SNSB-BSPG-2020-XCV-0193	HAM 5	tibia	Carnivora indet.
GPIT/MA/13744	HAM 5	tibia	Carnivora indet.
GPIT/MA/12662	HAM 5	distal fibula	Carnivora indet.
GPIT/MA/12359	HAM 5	astragalus	Carnivora indet.
GPIT/MA/12138	HAM 5	astragalus	Carnivora indet.
GPIT/MA/13723	HAM 5	distal Mp	Carnivora indet.
GPIT/MA/10389	HAM 5	distal Mp	Carnivora indet.
GPIT/MA/12720	HAM 5	distal Mp	Carnivora indet.
GPIT/MA/13456	HAM 5	distal Mp	Carnivora indet.
GPIT/MA/13735	HAM 5	distal Mp	Carnivora indet.
GPIT/MA/10378	HAM 5	Phalanx	Carnivora indet.
GPIT/MA/10503	HAM 5	Phalanx	Carnivora indet.
GPIT/MA/10387	HAM 5	Phalanx	Carnivora indet.
GPIT/MA/10386	HAM 5	Phalanx	Carnivora indet.

GPIT/MA/12188	HAM 5	Phalanx	Carnivora indet.
GPIT/MA/12705	HAM 5	Phalanx	Carnivora indet.
GPIT/MA/12227	HAM 5	Phalanx	Carnivora indet.
GPIT/MA/13740	HAM 5	Phalanx	Carnivora indet.
GPIT/MA/12281	HAM 5	Phalanx	Carnivora indet.
GPIT/MA/16291	HAM 5	Phalanx	Carnivora indet.
GPIT/MA/13724	HAM 5	Phalanx	Carnivora indet.
GPIT/MA/10390	HAM 5	Phalanx	Carnivora indet.
GPIT/MA/13455	HAM 5	Phalanx	Carnivora indet.
GPIT/MA/16370	HAM 5	Phalanx	Carnivora indet.
GPIT/MA/13463	HAM 5	Phalanx	Carnivora indet.
GPIT/MA/12157	HAM 5	Phalanx	Carnivora indet.
GPIT/MA/13738	HAM 5	Phalanx	Carnivora indet.
GPIT/MA/112273	HAM 5	Phalanx	Carnivora indet.
GPIT/MA/16358	HAM 5	3rd Phalanx	Carnivora indet.
GPIT/MA/13457	HAM 5	3rd Phalanx	Carnivora indet.
GPIT/MA/13739	HAM 5	3rd Phalanx	Carnivora indet.
GPIT/MA/10391	HAM 5	3rd Phalanx	Carnivora indet.
GPIT/MA/13718	HAM 5	3rd Phalanx	Carnivora indet.
GPIT/MA/10802	HAM 6	right p2 & p3	*Thalassictis montadai*
GPIT/MA/18116	HAM 6	D4	Amphicyonidae indet.

The total sum of the studied specimens is 365 for all three layers (HAM 1: 13; HAM 4: 169; HAM 5: 181; HAM 6: 2). However, as demonstrated in Table 4.1, a very large percentage of the material was identified as "Carnivora indet.". 122 specimens (33%) were identified at genus- or species- level. This has happened because of two main reasons:

1. Most of the material was at least partially damaged. Especially the postcranial material was nearly always broken in the epiphyses and deformed in the diaphyses, due to taphonomic or excavation/preparation effects. This made the identification in a lower taxonomic level impossible.
2. The discovered dental specimens uncovered an extraordinary variability of carnivorans (especially of small size) in the locality. Even though this made the study of this material more interesting, it resulted in an inevitable inability to attribute postcranial material to specific forms. For example, there are four small- to medium-sized gulonines in the locality. Therefore, even when a postcranial element was attributed to this group, it wasn't possible to distinguish between these species. A similar problem was faced concerning the isolated incisors and canines. Finally, this situation was furtherly problematic, since several forms are known only from dental material and their postcranial morphology is not known.

In general, 59% of the material included teeth or jaws and 41% included postcranial elements. In HAM 4, the postcranial elements were slightly more frequent (44%) in comparison to HAM 5 (41%), while the specimens from HAM 1 and HAM 6 corresponded only to dental material.

Methods

The taxonomic part of the present PhD Thesis was conducted based on metrical and morphological comparisons, between the Hammerschmiede material and previously published carnivorans. Material of fossil and extant carnivorans was studied in several collections for taxonomic and ecologic comparisons. The methodology of Dental Microwear Texture Analysis (DMTA) is discussed in the manuscript concerning *Kretzoiarctos beatrix*. The use of the μCT and relevant software in order to visualize specific structures is also discussed in the relevant papers.

Dental Nomenclature

The upper teeth are symbolized with capital letters and their structures are named as **cusps** and **crests**, with the suffixes -cone, -conule, -style, -crista etc. On the contrary, the lower teeth are symbolized with lower case letters and their structures are named as **cuspids** and **cristids**, with the suffixes -conid, -conulid, -stylid, -cristid etc.

The dental nomenclature for the upper dentition is demonstrated in Fig. 4.1. The premolars (except of P4) have a **main cusp**, which is possibly accompanied by mesial or distal **accessory cusps**. The nomenclature of the upper carnassial (P4) follows the nomenclature of the upper molars. This paradox creates problems of ambiguous homology between relevant structures, but this aspect is beyond the scope of this study. This tooth is characterized by a **carnassial blade**, which is formed mesially by the **paracone** and distally by the **metastyle**. Mesially to the paracone, there is a cusp of varying size, which is called **parastyle**. The plesiomorphic P4 of carnivorans has an L-shaped structure. The lingual part is called the **protocone region**, as it hosts the **protocone**. The area between the protocone and the base of the paracone can be narrow (and it may be called “protocone neck”), or it can be wide (and it may be called “protocone valley”). In some rare cases (e.g. in mephitids and ursids), an additional cusp is present distally to the protocone. This has usually been called a **hypocone**. The upper molars always have two large cusps in their buccal side. The mesial one is called the **paracone** (and is usually the largest one) and the distal one is called the **metacone**. Usually, a smaller cusp is present lingually to the **paracone**. This is called protocone and it is usually the highest part of a crest that runs distally parallel to the sagittal axis of the tooth. Additional cusps can be found in some forms. These cusps are usually named based on the largest neighboring cusp. For example, a protoconule is a small cusp that is near the protocone. The crests on the upper molars are named based on their neighboring cusps by inserting the prefixes -pro (mesial to) or -post (distal to) and the suffix -crista. For example, the postmetacrista is the crest that stems from the metacone and runs distally from it.

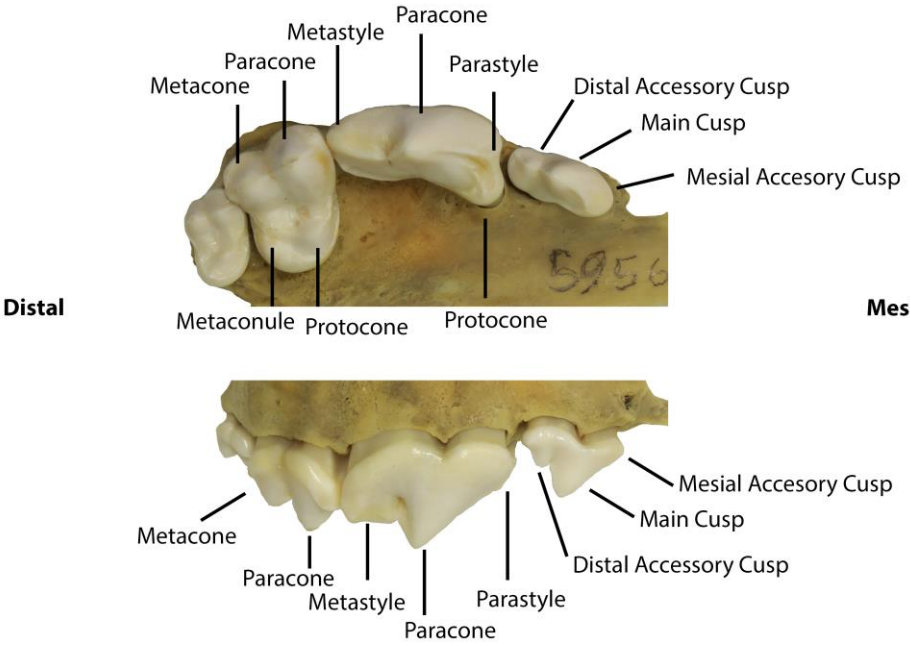

Fig. 4.1: Dental nomenclature of the upper cheek teeth in *Canis lupus* (ZMUP-5956).

The dental nomenclature for the lower dentition is demonstrated in Fig. 4.2. Similarly to the upper teeth, the premolars have a **main cuspid**, which may be accompanied by some mesial or distal **accessory cuspids**. This also concerns the p4 (in contrast to the different approach on P4). The lower carnassial (m1) is the most complex tooth of the lower dentition of carnivorans. Similarly to the upper carnassial, it possesses a carnassial blade that is formed distally by the **protoconid** (usually the largest cuspid) and mesially by the **paraconid** (usually the second largest cuspid). At the distolingual side of the protoconid there is a smaller cuspid, which is named **metaconid**. The size of this cuspid is frequently used as a diagnostic character and there are several groups that have lost the metaconid (e.g. the derived felids and weasels). These three cusps consist of the **m1 trigonid**. The remaining distal part of the tooth is named **m1 talonid**. The talonid possesses a central part that doesn’t host any cuspids and it is named **talonid valley**. The perimeter of the m1 talonid may host a variable number of cuspids. Usually, the largest one in the buccal part is called **hypoconid** and the largest one in the lingual side is called an **entoconid**. A third cuspid can be situated between these two (in the distal part of the tooth) and it is called a **hypoconulid**.

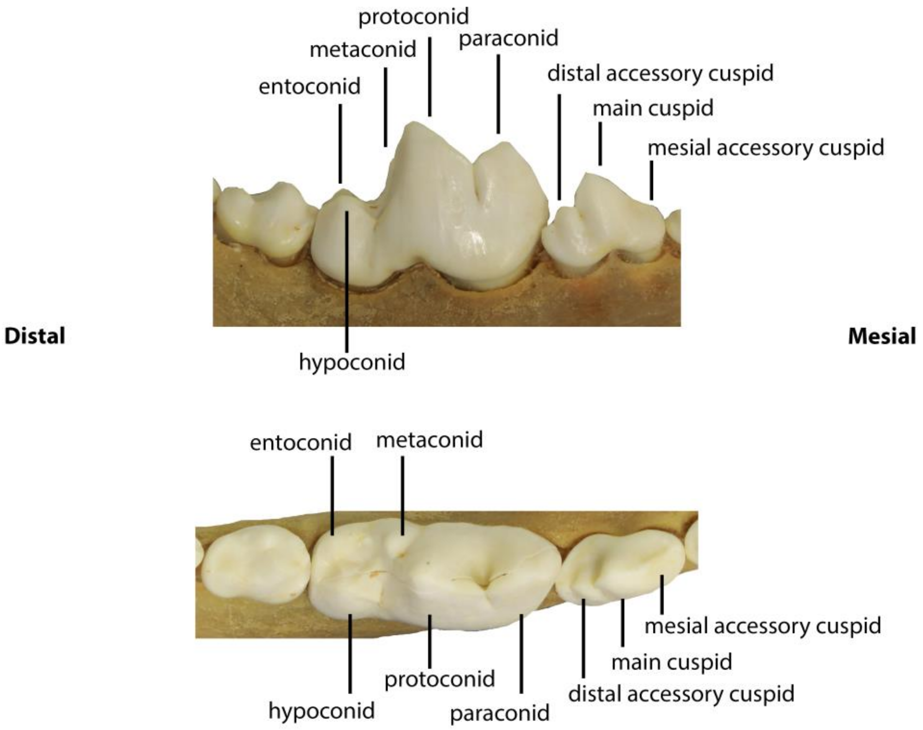

Fig. 4.2: Dental nomenclature of the lower cheek teeth in *Canis lupus* (ZMUP-5956).

Abbreviations

Measurements' Abbreviations: **APDd**: anteroposterior diameter of the distal epiphysis; **APDm**: anteroposterior diameter of the midshaft; **APDpr**: anteroposterior diameter of the proximal epiphysis; **H**: dorsoventral height; **L**: mesiodistal length; **TDd**: transverse diameter of the distal epiphysis; **TDm**: transverse diameter of the midshaft; **TDpr**: transverse diameter of the proximal epiphysis; **W**: buccolingual width.

Institutional Abbreviations: **AMPG**: Athens Museum of Geology and Palaeontology, Greece; **EPTP**: Exhibition of Palaeontological Treasures of Pikermi, Pikermi, Greece; **GMNH**: Goulandris Museum of Natural History, Athens, Greece; **GPIMH**: Geologisch-Paläontologischen Instituts und Museums Hamburg, Germany; **GPIT**: Paleontological Collection of the University of Tübingen, Germany; **HNHM**: Hungarian Natural History Museum, Budapest, Hungary; **ICP (IPS)**: Institut Català de Palaeontologia Miquel Crusafont, Barcelona, Spain; **LGPUT**: Laboratory of Geology and Palaeontology, University of Thessaloniki; Greece; **MGL**: Musée cantonal de Géologie de Lausanne, Switzerland; **MHNG**: Muséum d'Histoire Naturelle de Genève, Switzerland; **MHNL**: Muséum d'Histoire Naturelle de Lyon, Lyon, France; **MHNM:** Muséum d'Histoire Naturelle de Marseille, France; **MNHN**: Musée National d'Histoire Naturelle, Paris, France; **NMA**: Naturmuseum der Stadt Augsburg, Augsburg, Germany; **NHMA**: Natural History Museum of the Aegean, Samos, Greece; **NHMBA:** Naturhistorisches Museum Basel, Switzerland; **NHMBE:** Naturhistorisches Museum Bern, Switzerland; **NHMC-UOC**: Natural History Museum of Crete, University of Crete, Heraklion, Greece; **NHMUK**: Natural History Museum, London, United Kingdom; **NHMW**: Naturhistorisches Museum Wien, Vienna, Austria; **NMNHS**: National Museum of Natural History, Sofia, Bulgaria; **SMNS**: Staatliches Museum fur

Naturkunde, Stuttgart, Germany; **SNSB-BSPG**: Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **UCBL-FSL**: Faculté des Sciences de la Terre, Université Claude Bernard, Lyon, France; **ZMH**: Zoologisches Museum Hamburg, Germany; **ZMUA**: Zoological Museum, University of Athens; Greece; **ZMUP**: Zoological Museum, University of Patras; Greece; **ZSUT**: Zoologische Schausammlung der Universität Tübingen, German.

Guild Analysis

The guild analysis was made based on three palaeoecological parameters: body mass, locomotor habits and dietary habits. The differentiation of the categories of each parameter is given below:

Body Mass (BM)

1. Species weighting less than 1 kg.
2. Species weighting between 1 and 3 kg.
3. Species weighting between 3 and 10 kg.
4. Species weighting between 10 and 30 kg.
5. Species weighting between 30 and 100 kg.
6. Species weighting over 100 kg.

Locomotor Lifestyle (LL)

1. Generalized Terrestrial (GT)
2. Semi-aquatic (SA)
3. Semi-fossorial (SF)
4. Scansorial (Sc)
5. Arboreal (Ar)
6. Cursorial (Cu)

Dietary Habits (DH)

1. Hypercarnivorous (HC)
2. Carnivorous (C)
3. Durophagous (D)
4. Piscivorous/Mollusk-eater (PM)
5. Hypocarnivorous (hC)
6. Insectivorous (I)
7. Herbivorous (He)

Many more categories for each one of these parameters could have been added. Additionally, more parameters could have been regarded (e.g. method of hunting, ability to hunt larger prey, sociality). However, based on the absence of complete specimens or even complete skeletons in Hammerschmiede, it is considered more realistic to retain the approach mentioned above (based mostly on Morlo et al., 2010, Kargopoulos, 2019 and references therein) and a more detailed discussion will be held in a non-quantitative frame.

These species were clustered using Paired Group (UPGMA) classic clustering, in order to depict the palaeoecological groups that were formed. Species that are closely clustered are expected to be competitive to each other in coexistence. Afterwards, XY plots of the body mass (x-axis) and dietary habits (y-axis) including the locomotor habits (different symbols) were created for Hammerschmiede, HAM 4 and HAM 5, in order to depict the niche partitioning between the carnivorans in each plot.

The Species Diversity of the Hammerschmiede guild was estimated using the Individual Rarefaction analysis in comparison to the data for Eppelsheim and Dorn-Dürkheim (provided by Morlo et al., 2021), Rudabánya (Werdelin, 2005; Kargopoulos et al., In Press), Wintershof-West (Dehm, 1950), Steinheim (Helbing, 1936; Heizmann, 1973; Morlo et al., 2020), La Grive-Saint Alban (Viret, 1951) and Sansan, (Ginsburg, 1961; Peigné, 2012). The localities of Can Ponsic and Can Llobateres were not added to this analysis, because for these localities the exact number of specimens per species remains unclear. The analysis was performed using Species Richness and Shannon Index. The only deviation from the use of rarefaction by Morlo et al. (2021) is that, based on the detailed comments by Tipper (1979), rarefaction methodology is based on some assumptions that are impossible to be applied to palaeocommunities (similar ecosystems, similar sampling methods, homogenous distribution of the species etc.). Therefore, the predictability (extrapolation) of rarefaction for palaeoenvironments is doubted, and, thus, herein avoided. However, the non-extrapolated rarefaction graphs are presented, in order to demonstrate the high number of species in the relatively restricted number of specimens in Hammerschmiede. The methodology was applied in three levels: (1) including all the aforementioned localities, (2) including all the aforementioned localities (excluding Wintershof-West, because of the very high number of specimens) and (3) including only Hammerschmiede, Rudabánya and Steinheim (since the material from Eppelsheim and La Grive-Saint-Alban is considered to be a mix from several layers).

Chapter 5

Study of the carnivorans of Hammerschmiede

Journal Articles

This chapter contains five journal articles that have been published or submitted to academic journals through the past months. These articles deal with the majority of the carnivoran forms from Hammerschmiede by: taxonomically identifying the new material, introducing two new species and discussing the palaeoecology and evolution of some lineages in the fossil record of Europe. They consist of the published outcome of the current work on the Hammerschmiede carnivorans.

The publications are herein listed based on the date of first submission.

Publication 1

Kargopoulos N., P. Kampouridis, T. Lechner & M. Böhme. 2021a. A review of *Semigenetta* (Viverridae, Carnivora) from the Miocene of Eurasia based on material from the hominid locality of Hammerschmiede (Germany). Geobios 69:25–36. DOI: 10.1016/j.geobios.2021.07.001.

Personal Contribution: The author conducted most of the literature review, described the material, took the measurements, partly compared the material, discussed the diet and body mass of the three members of the genus and partially conducted the taxonomic review.

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Publication 2

Kargopoulos N., A. Valenciano, P. Kampouridis, T. Lechner & M. Böhme. 2021b. New early Late Miocene species of *Vishnuonyx* (Carnivora, Lutrinae) from the hominid locality of Hammerschmiede, Bavaria, Germany. Journal of Vertebrate Paleontology 41(3). DOI: 10.1080/02724634.2021.1948858.

Personal Contribution: The author conducted most of the literature review, described the material, took the measurements, partly compared the material, and discussed the diet, the body mass and partly the palaeogeography and evolution of the genus.

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Publication 3

Kargopoulos N., P. Kampouridis, T. Lechner & M. Böhme. 2021c. Hyaenidae (Carnivora) from the Late Miocene hominid locality of Hammerschmiede (Bavaria, Germany). Historical Biology. DOI: 10.1080/08912963.2021.2010193.

Personal Contribution: The author conducted most of the literature review, described the material, took the measurements, partly compared the material, and discussed the evolution of the two relevant groups in the fossil record of Europe.

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Publication 4

Kargopoulos N., A. Valenciano, J. Abella, P. Kampouridis, T. Lechner & M. Böhme. In Press. The exceptionally high diversity of small carnivorans from the Late Miocene hominid locality of Hammerschmiede (Bavaria, Germany). PLoS ONE.

Personal Contribution: The author conducted most of the literature review, described the material, took the measurements, partly compared the material, and discussed the biostratigraphy and palaeoecology of the discussed forms.

Publication 4 is an open access article distributed under the terms of Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Publication 5

Kargopoulos N., J. Abella, A. Daasch, T. Kaiser, P. Kampouridis, T. Lechner & M. Böhme. In Preparation. The primitive giant panda *Kretzoiarctos beatrix* (Ursidae, Carnivora) from the hominid locality of Hammerschmiede.

Personal Contribution: The author conducted most of the literature review, described the material, took the measurements, partly compared the material, and partly conducted the ecomorphological part of the study.

Publication 5 is in Preparation, so no specific permits are required.

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Original article

A review of *Semigenetta* (Viverridae, Carnivora) from the Miocene of Eurasia based on material from the hominid locality of Hammerschmiede (Germany)[☆]

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Hammerschmiede

ABSTRACT

The present article offers a detailed review of the taxonomy, distribution and palaeoecology of the genus *Semigenetta*. The study is based on new craniodental and postcranial remains of the genus from the early late Miocene (Tortonian) locality of Hammerschmiede (Bavaria, Germany). Most of the new specimens are attributed to the medium-sized species *Semigenetta sansaniensis*, whereas one lower carnassial is assigned to the large-sized *Semigenetta grandis*, making Hammerschmiede 4 the first known locality with two species of the genus. The variability of the material of *S. sansaniensis* from Europe allows us to revise the taxonomic weight of some previously used characters, and to identify the smaller-sized late Miocene form *Semigenetta ripolli* as a junior synonym of the former. Such an evolutionary transition of *S. sansaniensis* towards smaller forms is explained by niche partitioning with larger carnivorans of similar ecology, such as the herein reported *S. grandis*. Additionally, the species *Semigenetta huaiheensis* is here considered as a junior synonym of *Semigenetta elegans*.

1. Introduction

The family Viverridae includes relatively primitive feliforms, usually adapted to a niche similar to that of the extant martens as small-sized, agile omnivores. Today, they inhabit most of Africa and Southeastern Asia, while they have been introduced in a part of Western Europe (Hutchins et al., 2003). The taxonomic status of the family has changed dramatically from the traditional view of Simpson (1945), with the families Herpestidae, Eupleridae, Nandiniidae and Prionodontidae now considered distinct, while the remaining extant members of Viverridae are divided in the subfamilies Genettinae, Viverrinae, Paradoxurinae, and Hemigalinae (Hassanin et al., 2021). The most diverse extant genus is *Genetta* with 17 species in Africa (Gaubert et al., 2005).

The family is represented by three genera during the Miocene of Europe: *Semigenetta*, *Viverrictis*, and *Jourdanictis*. Only one of them (*Semigenetta*) is present also in Asia. One additional genus of small feliforms is *Leptoplesictis*, which includes eight species from Europe, Asia, and Africa. It has been referred to in the literature as a viverrid (Major, 1903; Schmidt-Kittler, 1987; Roth, 1988; Nagel et al., 2009) or as a herpestid (de Beaumont, 1972; Peigné, 2012; Gagnaison et al., 2017; Grohé et al., 2020). Based on its resemblance with the genus *Herpestes* (Gaillard, 1899; Viret, 1951; Nagel et al., 2009), this genus is herein considered as a herpestid.

Viverrictis is a rather rare, small-sized genus including two species: *Viverrictis vetusta* is known from Vieux-Collonges (MN5; Mein, 1958) and Sansan (MN6; Peigné, 2012), whereas *Viverrictis modica* has been documented only in La Grive-Saint-Alban (MN7/8; Viret, 1951; de Beaumont, 1972). These two forms have been considered as conspecific by some authors (e.g., Rook and Martínez-Navarro, 2004).

The second genus, *Jourdanictis*, is represented by a single species, *Jourdanictis grivensis*, which has been reported only from La Grive-Saint-Alban by Viret (1951), represented by three fragmentary hemimandibles and a partial maxilla. The maxilla was later attributed to *Plioviverrops gaudryi* by de Beaumont and Mein (1972). Therefore, only the lower dentition of this species is known.

Semigenetta is the most common and most diverse genus of the Miocene viverrids of Europe. It is considered similar to the extant *Genetta*, with the exception of the reduced m2 and the absent M2; it has been suggested that it possibly occupied a similar ecological niche (Nagel, 2009). The genus was erected by Helbing

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(1927), based on material of *Semigenetta* "*repelini*" from Captieux (France), which represents a junior synonym of *Semigenetta sansaniensis* (Lartet, 1851) (Heizmann, 1973). The reviews of Heizmann (1973), de Bonis (1994), Nagel (2003) and Peigné (2012), include seven species in the genus:

- *S. sansaniensis* (Lartet, 1851) (type locality: Sansan) [= *Semigenetta steinheimensis* (Fraas, 1870) (type locality: Steinheim), *Semigenetta mutata* (Filhol, 1883) (type locality: La Grive-Saint-Alban), and *Semigenetta repelini* Helbing, 1927 (type locality: Captieux)];
- *Semigenetta cadeoti* Roman and Viret, 1934 (type locality: La Romieu);
- *Semigenetta elegans* Dehm, 1950 (type locality: Wintershof-West);
- *Semigenetta laugnacensis* (de Bonis, 1973) (type locality: Laugnac);
- *Semigenetta ripolli* Petter, 1976 (type locality: Can Llobateres);
- *Semigenetta grandis* Crusafont Pairó and Golpe Posse, 1981 (type locality: Castell de Barberá);
- *Semigenetta huaiheensis* Qiu and Gu, 1986 (type locality Xiacaowan).

A detailed temporal distribution of all the species of the genus can be seen in Fig. 1 and Table S1 (Appendix A).

The present study aims to document new material of *S. sansaniensis* and *S. grandis* from the locality of Hammerschmiede, along with a review of the taxonomy and distribution of the genus. The taxonomic status of *S. ripolli* and *S. huaiheensis* is re-evaluated and certain palaeoecological and evolutionary interpretations for the genus are presented. This offers an up-to-date overview of the taxonomy, intra- and inter-specific variability, ecology and evolution of *Semigenetta*, hopefully creating a useful tool for further studies concerning these viverrids.

2. Geological and palaeontological setting

The Hammerschmiede locality is an active clay pit situated in southern Germany (Bavaria), near the small town of Pforzen. The outcropping sediments represent fluvio-alluvial floodplain deposits. At least six different fossiliferous levels have been identified in the clay pit, with the majority of the fossils being found at the fluvial levels HAM 4 and HAM 5. These levels have been dated magnetostratigraphically to 11.44 and 11.62 Ma, respectively (Kirscher et al., 2016). Therefore, the age of the locality is just at the base of the Tortonian, i.e., the late Miocene. A preliminary faunal list for the locality was published by Kirscher et al. (2016) and then updated by Böhme et al. (2019). The first studies for Hammerschmiede were published in 1975, focusing on some small mammals from the material collected by H. Mayr (Fahlbusch and Mayr, 1975; Mayr and Fahlbusch, 1975). Schneider and Prieto (2011) studied the molluscs of the locality. Fuss et al. (2015) reported the presence of the bovid *Miotragocerus monacensis*, a subject recently discussed also in Hartung et al. (2020). The discovery of a new hominid, *Danuvius guggenmosi*, with an advanced positional behaviour (Böhme et al. 2019) led to the discussion of the involvement of bipedalism in its locomotion (Böhme et al., 2020; Williams et al., 2020). Beside the mammalian remains, Mayr et al. (2020a), Mayr et al. (2020b) described two avian taxa (*Anhinga pannonica* and Gruinae indet.). The present study is the first publication solely concerning the carnivorans from Hammerschmiede.

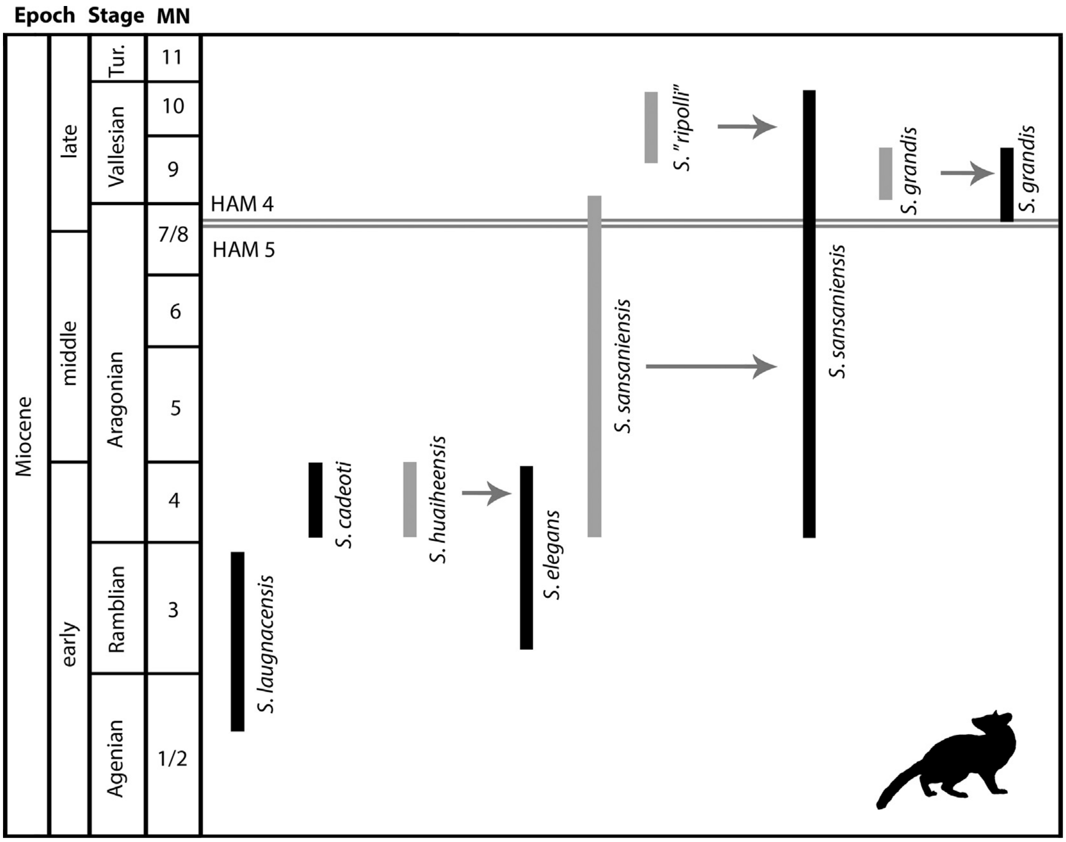

Fig. 1. Biochronological distribution of the species of *Semigenetta*. Grey lines indicate species ranges based on data previous to the present study; black vertical lines indicate species ranges resulting from the present study; grey horizontal lines indicate the chronological position of HAM 4 and HAM 5 localities.

3. Material and methods

The specimens studied herein come from the layers HAM 4 (11.44 Ma) and HAM 5 (11.62 Ma) of the fossil locality of Hammerschmiede (Bavaria, Germany). They have been unearthed during the excavations held by the University of Tübingen between 2011 and 2020. The material is stored at the Palaeontological Collection of the University of Tübingen, Germany (GPIT) and at the Bavarian State Collection of Palaeontology and Geology in Munich, Germany (SNSB-BSPG). The specimens coded as SNSB-BSPG 2020 XCIV were excavated from HAM 4 locality in 2020; their codes in the tables are mentioned as BSPG 2020 XCIV for practical reasons. All measurements were taken with a digital calliper and rounded to the first decimal point. Statistical analyses were made using PAST v.3.1 (Hammer et al., 2001).

Institutional abbreviations: **GPIT**, Palaeontological collection of the University of Tübingen, Germany; **ICP** (**IPS**), Institut Català de Palaeontologia Miquel Crusafont, Barcelona, Spain; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **MHNM**, Muséum d'Histoire Naturelle de Marseille, France; **SNSB-BSPG**, Bavarian State Collection of Palaeontology and Geology in Munich, Germany; **UCBL-FSL**, Faculté des Sciences de la Terre, Université Claude Bernard, Lyon, France; **ZSUT**, Zoologische Schausammlung der Universität Tübingen, Germany.

4. Systematic palaeontology

Class Mammalia Linnaeus, 1758
Order Carnivora Bowdich, 1821
Suborder Feliformia Kretzoi, 1945
Family Viverridae Gray, 1821
Subfamily Genettinae Rochebrune, 1883
Genus ***Semigenetta*** Helbing, 1927

Type species: *Semigenetta sansaniensis* (Lartet, 1851).

Included species: *S. sansaniensis*, *S. laugnacensis* (de Bonis, 1973), *S. elegans* Dehm, 1950, *S. cadeoti* Roman and Viret, 1934, and *S. grandis* Crusafont Pairó and Golpe Posse, 1981.

Chronological range: late Agenian (MN2b) to late Vallesian (MN10).

Emended diagnosis: Genus of the Genettinae with M2 absent; m1 talonid much reduced; m1 hypoconid present; m1 entoconid and hypoconulid absent, replaced by a lingual talonid ridge; m2 reduced.

Semigenetta sansaniensis (Lartet, 1851)
Figs. 2, 3, 4(A–C), 5
v.1851. *Viverra sansaniensis* – Lartet, p. 18.
v.1870. *Viverra steinheimensis* – Fraas, p. 9.
v.1883. *Plesictis mutatus* – Filhol, p. 64.
vp.1903. *Progenetta gaillardi* – Major, p. 535.
v.1927. *Semigenetta repelini* – Helbing, p. 306.
v.1976. *Semigenetta ripolli* – Petter, p. 146.
v.1994. *Semigenetta steinheimensis* – de Bonis, p. 86.
v.2009. *Semigenetta* sp. –Nagel, p. 608.
vp.2021. *Semigenetta steinheimensis* – de Bonis et al., p. 319.

Lectotype: MNHN Sa 808, left hemimandible with p3–m1.

Type locality: Sansan, France (middle/late Aragonian, middle Miocene, MN6).

Occurence: Spain: Buñol (Adrover, 1968), Can Llobateres (Petter, 1976), Masia de la Roma 604 (Montoya et al., 2001), Hostalets de Pierola Inferior (Villalta Comella and Crusafont Pairó, 1943), and Manchones (von Koenigswald and Crusafont Pairo, 1961). France: Sansan (Lartet, 1851; Gervais, 1859; Filhol, 1890; Ginsburg, 1961), Pelmer (Gagnaison et al., 2009), Captieux (Helbing, 1927), Pontlevoy (Ginsburg, 1990), Noyant-sous-le-Lude (Ginsburg, 2001), Contres (Augé et al., 2002), Vieux Collonges (Mein, 1958), Castelnau d'Arbieu (Bulot et al., 1992), and La Grive-Saint-Alban (Depéret, 1892). Switzerland: Rümikon (Helbing, 1928) and Anwil (Engesser, 1972). Germany: Steinheim (Fraas, 1870), Hammerschmiede (this study), Edelbeuren-Maurerkopf (Sach, 1999), Bohlinger Schlucht 6 (Giersch, 2004), and Großlappen (Heizmann, 1973). Austria: Grund (Nagel, 2003) and Atzelsdorf (Nagel, 2009; this study). Serbia: Mala Miliva (Petronijevic, 1967) and Sibnica (Petronijevic, 1967).

Chronological range: early Aragonian (MN4) to late Vallesian (MN10).

Material: HAM 4: Four P4 (GPIT/MA/12451 right; GPIT/MA/17698 right; SNSB-BSPG 2020 XCIV-0364 right; SNSB-BSPG 2020 XCIV-2682 right), two hemimandibles (GPIT/MA/16973 right with p1–m1; GPIT/MA/18081 right with m1), two m1 (GPIT/MA/10967 right; GPIT/MA/18115 right), one ulna (GPIT/MA/16617 left), one radius (GPIT/MA/17774 left), and one MtIV (SNSB-BSPG 2020 XCIV-1119 right). Minimum number of individuals: six. HAM 5: One m1 (GPIT/MA/13729 right) and one ulna (GPIT/MA/09925 left). Minimum number of individuals: one.

Measurements: see Tables 1–3.

Emended diagnosis: Species of *Semigenetta* of moderate size (m1L = 8.5–11.5 mm); m1 talonid lingual ridge without distinct cuspids; slender mandibular ramus; moderately trenchant premolars and m1 trigonid.

Description: The material includes four complete, right upper carnassials with no traces of wear. Each tooth preserves three roots: one broad root under the metastyle blade, one smaller under the parastyle, and one of intermediate size under the protocone. A smooth cingulum exists in the perimeter of the tooth, being more robust at its buccal side. The protocone is relatively thin, high and mesially situated. Its mesial border is located slightly mesially in regard to the parastyle. A very small parastyle is present. The paracone is the highest cusp of the tooth, being pyramidal-shaped, sectorial and separated from the metastyle by a deep notch.

The preserved parts of the two mandibular rami enable a short description of the mandibular corpus. It is relatively thin, with a faint decrease in height rostrally. Two large mental foramina are observed: one ventral to the mesial root of p3 and one ventral to the mesial root of p2. The masseteric fossa is deep and expanded until the plane of the distal border of m2. There is a very faint subangular enhancement of the mandibular body. All the teeth are separated by distinct diastemata, with the exception of m1 and p4, which are marginally overlapping.

The first premolar is minute, one-rooted, mesially bent with a distinct distal faint cingulum. The second premolar is significantly smaller than p3 and p4, two rooted and with only a faint mesial cingulum. These two premolars are asymmetrical, in contrast to the more symmetrical p3 and p4. The third premolar is very high and sectorial with a cingulum through its perimeter and a blunt distal accessory cuspid. The fourth premolar is similar to p3 but larger. Due to a distodorsal damage in the single available specimen (GPIT/MA/16973), the distal accessory cuspid is not visible. The lower carnassial bears two roots: one under the paraconid and one under the talonid. The roots in GPIT/MA/13729 are diverging slightly more than in the other specimens, resembling the form of the milk teeth. However, the size of the tooth and the similarities in morphology to the other studied specimens indicate that it is a permanent tooth and that this divergence must be interpreted as intraspecific variability or as a deformation during fossilization. A smooth cingulum is present at the base of the tooth, being more robust at its buccal part. The trigonid covers ca. 80% of the carnassial's length. The protoconid is the highest cuspid, separated from the (also high) paraconid by a deep notch. The metaconid is present, detached from the protoconid, relatively low

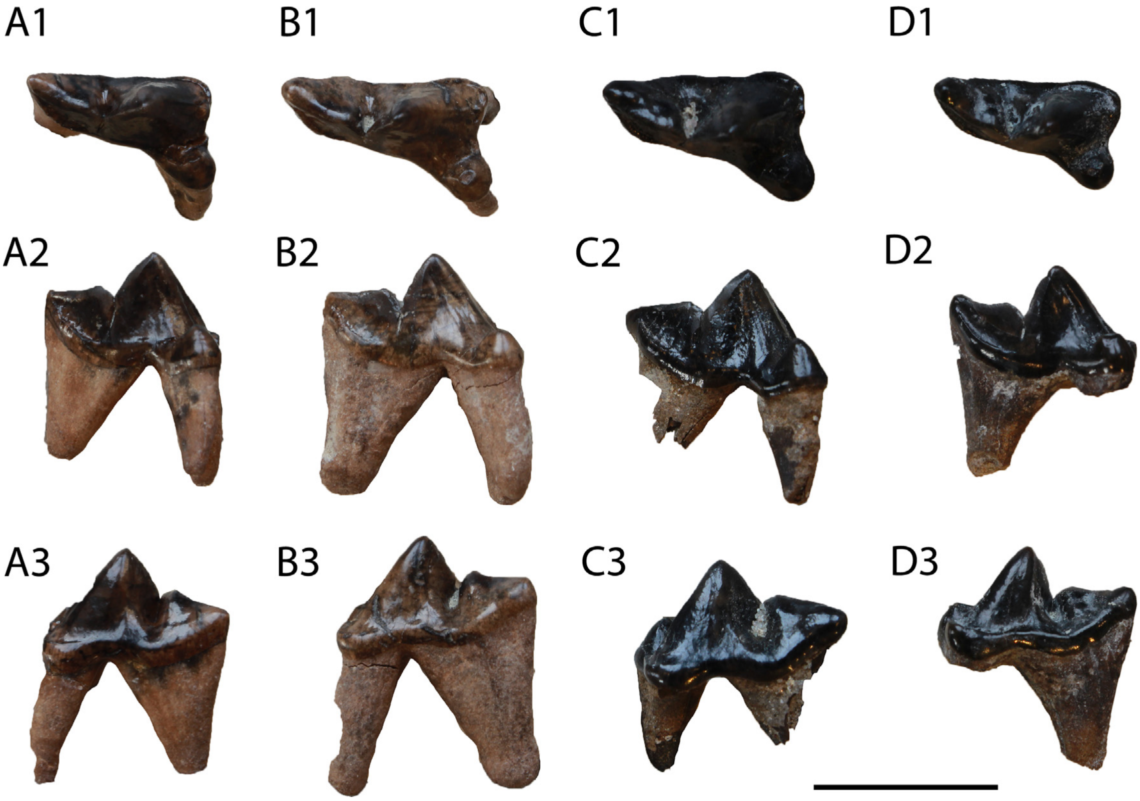

Fig. 2. The four right upper carnassials of *Semigenetta sansaniensis* from Hammerschmiede in occlusal (1), lingual (2), and buccal (3) views. **A**. GPIT/MA/12451. **B**. GPIT/MA/17698. **C**. SNSB-BSPSG 2020 XCIV-0364. **D**. SNSB-BSPSG 2020 XCIV-2682. Scale bar: 10 mm.

and moderately pointy. The talonid is slender, shallow and U-shaped. It hosts only a small hypoconid, while there are no traces of other cuspids in the surrounding ridge. The only specimen that departs from this description is GPIT/MA/18115 (Fig. 4(C)), which is characterized by a more developed metaconid and two small cuspids in the lingual side of the paracone. These features are considered as abnormalities and lacking taxonomical significance, because of their irregularity (especially the presence of the lingual cuspids) and because of the similar morphology of the talonid (which is the diagnostic feature of the group) to that of the other specimens.

The specimen GPIT/MA/17774 is a radius, broken at the middle of the diaphysis, retaining only its distal part, which is partially damaged cranially. The shaft is relatively slender and craniocau-

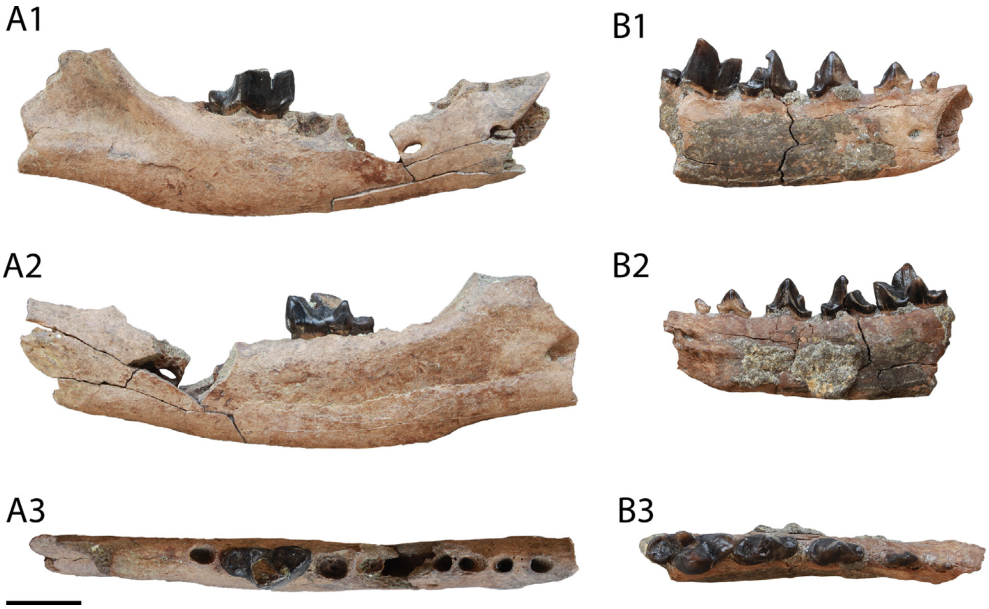

Fig. 3. The two right hemimandibles of *Semigenetta sansaniensis* from Hammerschmiede in buccal (1), lingual (2), and occlusal (3) views. **A**. GPIT/MA/18081, hemimandible with m1. **B**. GPIT/MA/16973, hemimandible with p1–m1. Scale bar: 10 mm.

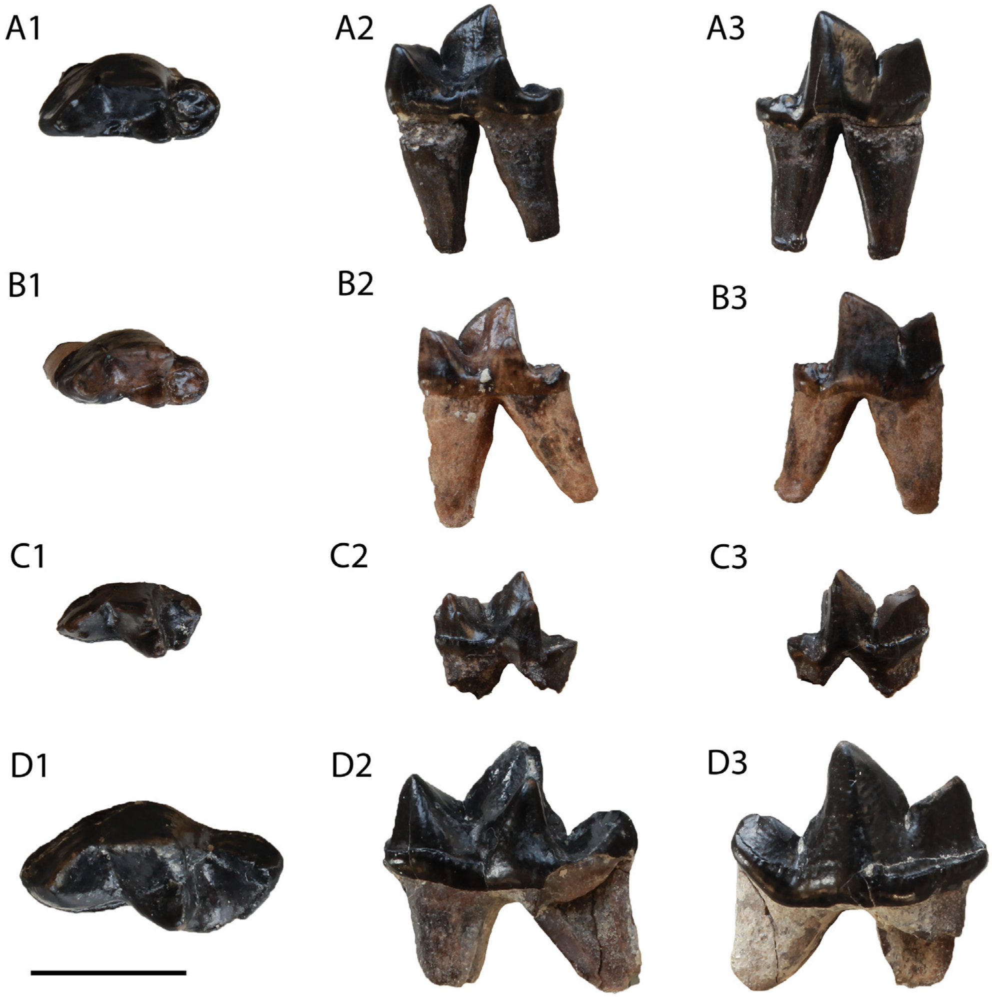

Fig. 4. Lower carnassials of *Semigenetta sansaniensis* (A–C) and *Semigenetta grandis* (D) from Hammerschmiede in occlusal (1), lingual (2), and buccal (3) views. **A**. GPIT/MA/10967. **B**. GPIT/MA/13729. **C**. GPIT/MA/18115. **D**. GPIT/MA/12452. Scale bar: 10 mm.

dally compressed. The styloid process is pointy and the lateral side of the distal articular process is well-bordered. The articular surface for the ulna is circular. The dorsal tubercle is well-marked and the ulnar notch is faint.

GPIT/MA/09925 is a relatively complete ulna with a partially damaged distal epiphysis, while GPIT/MA/16617 retains only the proximal part of the diaphysis and the proximal epiphysis. The former specimen is slightly deformed due to an excavation artefact. The articular surface in the radial notch of the olecranon is extended in the medial part of the coronoid process. The fossa in the head of the proximal epiphysis is well-marked. The shaft is relatively compressed laterally and moderately slender. The distal epiphysis is damaged. However, it is clear that it has a relatively long styloid process with a robust base.

The fourth metatarsal (SNSB-BSPG 2020 XCIV-1119) is almost complete, having only a slight damage in the plantar part of the proximal base. The proximal part is characterized by a simple trochlea followed distomedially by a step-like tubercle. The tubercle in the medioplantar part of the distal portion of the proximal base is absent. The shaft is long and slender, with a faint ridge in its lateroplantar side. The head is relatively globular and its sagittal ridge slightly extended proximally in the shaft.

Remarks: Comparison of the new material: The lower carnassials described here exhibit the characteristic short talonid with only one cuspid, typical of *Semigenetta*. It is evident from the metrical comparison (Tables 1, 2) that there are three size groups in the studied viverrids: the small-sized *Viverrictis*, *Jourdanictis* and *S. cadeoti*, the large-sized *S. grandis*, and the medium-sized remaining species of *Semigenetta*.

Most of the studied material falls into the range of variation for the medium-sized *Semigenetta*. During the interval of middle/late Miocene, the only medium-sized species of *Semigenetta* present in Europe are *S. sansaniensis* and *S. ripolli* (Fig. 1; Table S1, Appendix A). These two species differ in the presence of a shallower talonid with fainter surrounding ridge and the smaller size of *S. ripolli* (Petter, 1976). The material from Hammerschmiede includes some specimens closer to the mean values of *S. sansaniensis* (e.g., GPIT/MA/18081), some closer to the dimensions of *S.* “*ripolli*” (e.g., GPIT/MA/18115), but also some in the range between them (GPIT/MA/16973 and GPIT/MA/10967).

Concerning the postcranial material, the morphology of the radius and the ulnae fit very well with the descriptions and figures of Helbing (1927), Heizmann (1973) and Peigné (2012). A metrical comparison with the material from Sansan (Table 3) also points out the similarities between these specimens.

The pointy styloid process and the well-bordered lateral side of the distal articular process of the radius differentiate this specimen from the radii of the musteloids. The diaphysis is slender, different from the robust diaphyses of the felids. Therefore, it is here considered to belong to a viverrid and the only possible species of that size in Hammerschmiede is *S. sansaniensis*.

Fig. 5. The postcranial material of *Semigenetta sansaniensis* from Hammerschmiede. **A**. GPIT/MA/09925, left ulna in medial (1) and cranial (2) views. **B**. GPIT/MA/16617, left ulna in medial (1) and cranial (2) views. **C**. GPIT/MA/17774, left radius in cranial (1) and caudal (2) views. **D**. SNSB-BSPG 2020 XCIV-1119, right MtIV in plantar (1) and dorsal (2) views. Scale bar: 20 mm.

The most characteristic part of the ulnar morphology is the articular surface in the radial notch of the olecranon. In mustelids, it is generally small and in felids it is extended medially. In viverrids, it is moderately developed medially and the surface is extended in the medial part of the coronoid process of the olecranon.

The identification of the MtIV is made tentatively, because no MtIV of *Semigenetta sansaniensis* have been found so far. However, the small size and the absence of the tubercle in the medioplantar part of the distal portion of the proximal base differentiate it from the morphology of felids, so it is here considered to belong to *Semigenetta*.

Remarkss on other material: The material from Atzelsdorf published by Nagel (2009) does not exhibit any metrical or morphological differences with the known specimens of *S. sansaniensis* and it seems doubtful that it may belong to a different species. Therefore, it is suggested here that it shall be included in the range of *S. sansaniensis*. As also mentioned by Peigné (2012), it has to be noted that the presence of *S. sansaniensis* in Rudabánya (early Vallesian of Hungary), cited by Nagel (2003) without providing any further information or any source, is doubtful based on the material published by Werdelin (2004). Robles (2014) mentioned the presence of unpublished specimens of *Semigenetta* cf. *sansaniensis* from Abocador de Can Mata (ACM/C4-C2 and ACM/C6-A) and Torrent de Febulines, but until this material is published, it is not possible to add these occurrences in the range of the species. Viret (1951) suggested that the specimen from Siwaliks published by Pilgrim (1932: pl. V, fig. 5) as Viverridae indet. may belong to *Semigenetta*. However, we agree with Qiu and Gu (1986) that this specimen has a significantly larger talonid and it is different from *Semigenetta*. Finally, a detailed analysis on the status of *S. ripolli* is made below, in the Discussion Section.

Table 1
Measurements of P4 of the specimens from Hammerschmiede, compared to that of *Semigenetta* species. Data from Mein (1958), Heizmann (1973), de Bonis (1994), Nagel (2003, 2009), and Peigné (2012).

Code/Species	P4L	P4W
GPIT/MA/12451	9.4	6.2
GPIT/MA/17698	10.3	6.5
BSPG 2020 XCIV-0364	11.2	7.3
BSPG 2020 XCIV-2682	10.3	6.0
V. vetusta	6.2 [5.9–6.6] (n = 6)	3.8 [3.3–4.0] (n = 6)
S. elegans	8.7	4.8
S. sansaniensis	10.5 [9.7–11.5] (n = 9)	6.1 [5.5–6.8] (n = 9)
S. laugnacensis	8.0	4.4

Semigenetta laugnacensis (de Bonis, 1973)
v.1929. *Stenoplesictis* sp. – Viret.
v.1973. *Plesictis laugnacensis* – de Bonis, p. 114.

Holotype: UCBL-FSL Lg M9: a left hemimandible with p3–m1.

Type locality: Laugnac, France (late Agenian, middle early Miocene, MN2b).

Occurrence: France: Noyant-sous-le-Lude (Ginsburg, 2001) and La Guimardière (Gagnaison and Gillet, 2005).

Chronological range: late Agenian (MN2b) to Ramblian (MN3).

Measurements: See Tables 1, 2.

Emended diagnosis: Species of *Semigenetta* of very small size (m1L = 7.1–7.5 mm); slender mandibular ramus; moderately trenchant premolars and m1 trigonid.

Semigenetta cadeoti Roman and Viret, 1934
v.1930. *Herpestes*? *aurelianensis* – Roman and Viret, p. 594.
v.1989. *Herpestes cadeoti* – Roth, p. 186.
v.1996. ?*Leptoplesictis cadeoti* – Werdelin, p. 276.

Holotype: UCBL-FSL 320087: a right hemimandible with p3–m1.

Type locality: La Romieu, France (early Aragonian, late early Miocene, MN4).

Occurrence: France: Pellecahus (Antoine et al., 2000).

Chronological Range: early Aragonian (MN4).

Measurements: See Table 2.

Emended diagnosis: Species of *Semigenetta* of exceptionally small size (m1L ≈ 6 mm); slender mandibular ramus; moderately trenchant premolars and m1 trigonid.

Remarks: The taxonomic position of *S. cadeoti* has been doubted by Roth (1989) and Werdelin (1996), which considered this form to be a herpestid. The holotype is somewhat fragmentary, creating identification problems. However, the description and the figure of Roman and Viret (1934: pl. II, fig. 10) as well as the photograph of the specimen uploaded in the E-RECOLNAT website (recolnat.org) clearly fit to the diagnosis of *Semigenetta*, while Roman and Viret (1934) also make a convincing comparison with the herpestids. Until further material supports this change, we prefer to consider *S. cadeoti* as a species of *Semigenetta*.

Semigenetta elegans Dehm, 1950
v.1937. *Semigenetta* n. sp.? – Dehm, p. 361.
v.1986. *Semigenetta huaiheensis* – Qiu and Gu, p. 20.
v.2021. *Semigenetta gracilis* – de Bonis et al., p. 323.

Holotype: BSPG 1937 II 13311, a right hemimandible with p2–m2.

Type locality: Wintershof-West, Germany (Ramblian, middle early Miocene, MN3).

Occurrence: France: Estrepouy (Ginsburg, 2011), Hommes/Les Beilleaux (reworked) (Ginsburg, 1990), Savigné-sur-Lathan (reworked) (Ginsburg et al., 1981), Noyant-sous-le-Lude (reworked) (Ginsburg, 2001), and Artenay (Ginsburg, 1990). Germany: Erketshofen 2 (Roth, 1989). Czech Republic: Ahníkov 1 (Fejfar et al., 2003). Turkey: Sabuncubeli (Mayda, 2010). China: Xiacaowan (Qiu and Gu, 1986).

Table 2
Measurements of the lower teeth of the specimens from Hammerschmiede, compared to that of other viverrid species from genera *Jourdanictis*, *Viverrictis* and *Semigenetta*. Data from Roman and Viret (1934), Dehm (1950), Viret (1951), Petter (1976), Qiu and Gu (1986), de Bonis (1994), Montoya et al. (2001), Werdelin (2004), Nagel (2009), and Peigné (2012).

Code/Species	p1L	p1W	p2L	p2W	p3L	p3W	p4L	p4W	m1L	m1W
GPIT/MA/18081	–	–	–	–	–	–	–	–	10.6	5.2
GPIT/MA/16973	2.3	1.5	4.9	1.8	6.4	2.8	7.3	3.3	9.7	4.7
GPIT/MA/13729	–	–	–	–	–	–	–	–	11.1	5.3
GPIT/MA/10967	–	–	–	–	–	–	–	–	9.5	4.7
GPIT/MA/18115	–	–	–	–	–	–	–	–	9.0	4.5
GPIT/MA/12452	–	–	–	–	–	–	–	–	15.6	7.7
J. grivensis	–	–	–	–	–	–	–	–	6.1 [5.8–6.3] (n = 2)	3.4
V. modica	–	–	4.3	1.6	4.2	1.6	5.4 [5.0–5.9] (n = 6)	2.1 [2.0–2.2] (n = 6)	6.1 [5.6–6.5] (n = 29)	3.0 [2.7–3.3] (n = 29)
V. vetusta	–	–	–	–	–	–	–	–	6.3	3.0 [2.8–3.1] (n = 2)
S. grandis	–	–	8.2 [8.0–8.3] (n = 2)	3.2 [3.1–3.3] (n = 2)	9.9	4.1	10.0 [8.5–11.4] (n = 2)	4.6 [4.5–4.8] (n = 3)	13.8 [12.7–14.5] (n = 4)	6.3 [5.7–6.9] (n = 4)
S. sansaniensis	2.6 [2.2–2.8] (n = 5)	1.5 [1.3–1.7] (n = 5)	5.7 [4.7–6.4] (n = 13)	2.3 [2.0–2.6] (n = 13)	7.4 [6.4–8.4] (n = 18)	2.9 [1.8–3.5] (n = 17)	8.0 [7.0–9.0] (n = 18)	3.5 [2.9–4.1] (n = 17)	9.9 [9.0–11.4] (n = 22)	4.5 [4.1–5.4] (n = 22)
S. "*ripolli*"	–	–	–	–	6.3	2.6	7.4	3.0	8.6 [8.5–8.7] (n = 2)	3.8 [3.5–4.1] (n = 2)
S. elegans	–	–	–	–	6.0 [5.7–6.4] (n = 9)	–	6.7 [6.1–7.3] (n = 10)	–	8.1 [7.7–8.8] (n = 10)	–
S. "*huaiheensis*"	–	–	5.0	1.9	6.1	2.4	7.0	2.9	8.7	4.0
S. cadeoti	–	–	–	–	–	–	–	–	6.0	–
S. laugnacensis	–	–	–	–	5.0 [4.8–5.1] (n = 2)	1.9 [1.8–1.9] (n = 2)	6.0 [5.8–6.2] (n = 5)	2.3 [2.0–2.5] (n = 5)	7.4 [7.1–7.5] (n = 5)	3.4 [3.2–3.6] (n = 5)

Chronological range: Ramblian (MN3) to early Aragonian (MN4).

Measurements: See Tables 1, 2.

Emended diagnosis: Species of *Semigenetta* of small size (m1L = 7.5–9.0 mm); m1 lingual talonid ridge usually with distinct cuspids; slender mandibular ramus; moderately trenchant premolars and m1 trigonid.

Remarks: A short comment is added here regarding the status of *S. huaiheensis*. This form has been known only by a hemimandible with p2–m1 (V 8068) and an isolated p4 (V 8069) from Xiacaowan in China by Qiu and Gu (1986). This is the only known presence of the genus outside Europe, together with that from Sabuncubeli (Turkey) by Mayda (2010). The provided diagnosis of the species by Qiu and Gu (1986) points out three characteristics of the mandible: the flat (instead of a cusped) ridge in the m1 talonid, the more rostral position of the mandibular foramen, and the more convex lower border of the mandible below m2. These traits aim to differentiate this form from the contemporary *S. elegans*. Concerning the talonid ridge, Heizmann (1973) states that there is an important variability of the development of these "pearly" formations in the material from Steinheim, an argument also noted by Viret (1951) based on the material from La Grive-Saint-Alban. The presence of a subangular enhancement of the mandibular corpus seems also to be intraspecifically variable in *S. sansaniensis*, since it is present in GPIT/MA/18081 from Hammerschmiede (Fig. 3(C)), but absent in Sa 961 from Sansan (Peigné, 2012: figs. 160–162). This point has also been noted by Golpe-Posse (1981c). The more rostral position of the mandibular foramen alone is not enough for the establishment of a new species. The great geographical difference between China and Europe is a considerable indication for the differentiation of this material, especially regarding a small carnivore. However, geographic distance

Table 3
Measurements of the postcranial material from Hammerschmiede, compared to that of *Semigenetta sansaniensis* from Sansan (France).

Element	Code	H	APDpr	TDpr	APDm	TDm	APDd	TDd
Ulna	GPIT/MA/09925	99.8	11.9	7.9	7.7	5.0	–	–
	GPIT/MA/16617	–	11.1	–	7.8	4.9	–	–
Radius	GPIT/MA/17774	–	–	–	4.3	6.1	–	13.2
	Sa 106831	–	10.4	6.8	–	–	9.7	13.9
	Sa 820[1]	–	–	–	–	–	9.9	14.5
MtIV	SNSB-1119	46.7	6.7	3.3	3.5	4.0	5.6	6.4

[1] Data from Peigné (2012).

is not a criterion in the distinction of morphospecies. Additionally, some extant small carnivorans have extremely wide geographical ranges, such as *Genetta genetta* (Larivière and Calzada, 2001). Therefore, in the absence of more data that support its differentiation, we prefer to consider this material as similar to *S. elegans*.

Semigenetta grandis Crusafont Pairó and Golpe Posse, 1981
Fig. 4(D)

Holotype: IPS 94790, left hemimandible with p2–m1 and the alveolus of m2.

Type locality: Castell de Barberá, Spain (early Vallesian, late Miocene, MN9).

Occurrence: Hungary: Rudabánya (Werdelin, 2004). Germany: Hammerschmiede (this study).

Chronological range: late Aragonian (MN7/8) to early Vallesian (MN9).

Material: HAM 4: One m1 (GPIT/MA/12452 right).

Measurements: See Table 2.

Emended diagnosis: Species of *Semigenetta* of large size (m1L = 12.5–15.5 mm); m1 talonid lingual ridge without distinct cuspids; robust mandibular ramus; considerably trenchant premolars and m1 trigonid.

Description: The specimen GPIT/MA/12452 is very similar to the m1 of *S. sansaniensis*, but it is clearly larger. The cingulum is more robust, especially mesiobuccally; the metaconid is slightly larger and pointier; the protocristid is much more developed, while the surrounding ridge of the talonid is more sheer than in *S. sansaniensis*.

Remarks: Only one specimen from Hammerschmiede (GPIT/MA/12452) fits within the range of the large-sized *S. grandis* (Table 1). Additionally, it exhibits some traits towards hypercarnivory (pointier metaconid, more sheer talonid ridge and more robust cingulum), which are considered typical of this species (Crusafont Pairó and Golpe Posse, 1981; Golpe Posse 1981a, 1981b, 1981c).

5. Discussion

5.1. Taxonomy

Table 2 and Figs. 6, 7 depict an overview of the metric variability of the known measurements of the genera *Semigenetta*, *Viverrictis* and *Jourdanictis* along with that of the specimens from Hammerschmiede. It is clear in Fig. 7 that the values of *S. sansaniensis* form a relatively homogenous distribution, while the two specimens of *S.* "*ripolli*" form an almost continuous expansion of the scatter-plot of *S. sansaniensis*. In general, it can be observed that the relatively older localities (early Aragonian; black symbols in Fig. 7) are characterized by slightly smaller individuals than the younger ones (late Aragonian; white symbols in Fig. 7). Additionally, while the values from some localities form relatively continuous clouds (e.g., that of La Grive-Saint-Alban, Steinheim and Sansan), the distributions from some other localities exhibit a gap in their center. This can be seen clearly in the metric data from Vieux-Collonges and Hammerschmiede: it is clear in Fig. 7 that the five specimens from Hammerschmiede cover almost the entire size-distribution of *S. sansaniensis* and present a gap between the two ends of their distribution. This pattern can be explained by a sampling bias (i.e., the gap would be filled with the discovery of more specimens) or by the existence of a sexual (size) dimorphism, which has also been recorded in the extant genets (Larivière and Calzada, 2001).

A size difference between the samples of *S. sansaniensis* and *S.* "*ripolli*" can indeed be seen in the dimensions of m1 in Table 2 and Figs. 6, 7. However, as noted above, their measurements are almost continuous and the dimensions of GPIT/MA/18115 from Hammerschmiede and the smallest specimen from Vieux-Collonges are very close to the specimen from Masia de la Roma 604 (Fig. 7). Therefore, two scenarios seem possible: either the material from Hammerschmiede (and perhaps from other localities) includes both species, or the two species are conspecific. The following facts tend to point towards the second possibility.

The species *S.* "*ripolli*" is known only from three specimens, so it is impossible to estimate its true size range, which may in fact be substantial, giving the range observed in *S. sansaniensis*. Therefore, a bias in the size estimate of this form as a whole (which is the main argument about its individuality) remains highly possible. This bias seems even more possible while considering the note of Crusafont Pairó and Golpe Posse (1981) that the assemblage of Can Llobateres also includes material of *S. sansaniensis* (mentioned by the authors as *S. mutata*). Similarly, Crusafont Pairó and Kurtén (1976) include *S. mutata* (=*S. sansaniensis*) in the faunal list of Can Llobateres. The attribution of this unpublished material to *S. sansaniensis* and its exclusion from Petter's (1976) hypodigm suggest that its dimensions were larger than those of *S.* "*ripolli*". Therefore, the small specimens from Can Llobateres are not isolated metrically in the locality, but they seem to represent the lowest values of the range of *S. sansaniensis*.

The difference in the height of the talonid cuspids and the depth of the talonid valley (both considered as diagnostic by Petter, 1976) can be explained through individual variation. Petter (1976), in the original description of the species, noticed these differences between *S.* "*ripolli*" and some mandibles of *S. sansaniensis* from Sansan (Sa 804 and Sa 811). However, she stated that these differences are not visible when comparing with other specimens from Sansan (e.g., Sa 808). It must also be added that Petter (1976) stated that the hypoconid of the known m1 from Can Llobateres was worn (also visible in Petter, 1976: pl. I, fig. 40).

There is a stratigraphic gap between the type localities of the two species, as Sansan is dated to middle/late Aragonian (MN6; Peigné, 2012), while Can Llobateres (specifically Can Llobateres 1, according to Robles, 2014) is an early/middle Vallesian (MN9) locality (Agustí et al., 1996). This gap could be interpreted as an indicator of differences in evolutionary stages between the two forms. However, there is no gap between the total temporal ranges of the two species, if their complete distribution is considered, since *S. sansaniensis* is also found in late Aragonian (MN7/8) localities such as La Grive-Saint-Alban (Mein and Ginsburg, 2002), Steinheim (Fraas, 1870) and Anwil (Engesser, 1972) (Kälin and Kempf, 2009; Fig. 1; Table S1, Appendix A). Additionally, the specimens from Atzelsdorf (early Vallesian, MN9) published by Nagel (2009) can also be attributed to *S. sansaniensis*. Therefore, the two forms are overlapping stratigraphically.

Consequently, it is here concluded that there is no significant difference between *S. sansaniensis* and *S. ripolli* and we propose that they should be considered as conspecific, the latter being a junior synonym of the former based on priority rule. However, considering the present data (Fig. 6), it is evident that a trend towards smaller size occurs during the late Aragonian to late Vallesian interval (i.e., from Steinheim to Masia de la Roma 604). Given the small sample size of the *ripolli* form, it is suggested that this difference cannot be used for specific differentiation, but it may have palaeoecological/evolutionary value, as discussed in the following section.

It can be seen in Fig. 1 that the resulting temporal range of *S. sansaniensis* covers the whole period between early Aragonian and late Vallesian, thus a span of ca. 8 myr. This is a surprisingly long period of existence for a single species, especially for a small carnivore. The reason behind this paradox stems from the preservation of the species in the fossil record. Despite its wide temporal range and its recorded presence in 25 localities (Table S1, Appendix A), no skull or complete skeleton of *S. sansaniensis* (or of any other species of the genus) have been found up to date. In the most recent review of the taxonomy of *Genetta*, no dental characters

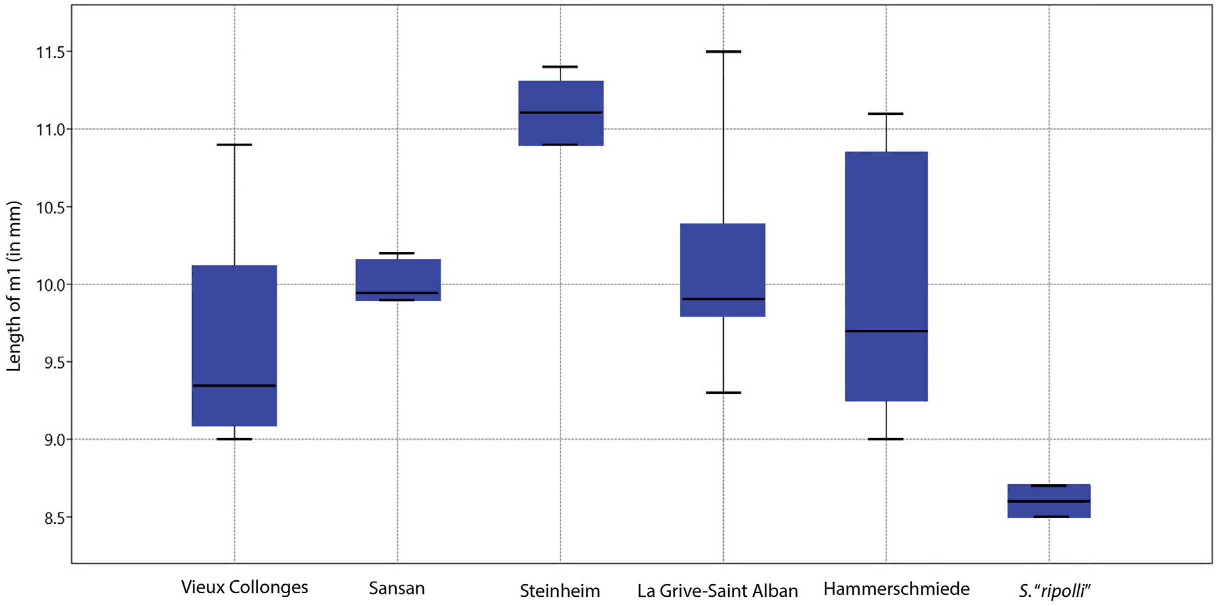

Fig. 6. Boxplots of the m1L based on material of *S.* "*ripolli*" from Can Llobateres and Masía de la Roma 604 (n = 2) and *S. sansaniensis* from Vieux Collonges (n = 8), Sansan (n = 4), Steinheim (n = 5), La Grive-Saint Alban (n = 12), and Hammerschmiede (n = 5). Data from Mein (1958), Heizmann (1973), Petter (1976), Montoya et al. (2001), and Peigné (2012).

were used in the diagnoses of the species (Gaubert et al., 2005), most probably because they were proven to be relatively homogenous interspecifically (Gaubert et al., 2002). Therefore, it is reasonable to hypothesize that this extensive temporal range could be more securely segregated in the future with the discovery of cranial specimens. However, so far the morphological homogeneity of the present material defines the presence of only one form during this period. Therefore, we argue that in the present case a strict use of the morphospecies approach must be followed, regardless of its possible conflict with other species concepts (Zachos, 2016).

Very recently, de Bonis et al. (2021) published one hemimandible (MM-106) from the K coal zone of Mae Moh (Thailand; 13.4–13.2 Ma), which they attribute to *Semigenetta* cf. *steinheimensis*. The presence of the genus in Thailand had already been recorded by Mein and Ginsburg (1997) with *Semigenetta* sp. from Li Mae Long (early MN4). Based on the figures and the descriptions of de Bonis et al. (2021), the morphology of the lower carnassial fits very well with the diagnostic morphology of *Semigenetta*. Therefore, the attribution to this genus is here considered as valid. However, the aforementioned overview of the intraspecific metrical variability of the MN4–MN10 European forms showed that the specimens from Steinheim, despite being scattered in the higher values of the *S. sansaniensis* (sensu lato) spectrum and being metrically relatively homogenous, do not exhibit any distinguishable metrical or morphological traits, so they are here considered as a

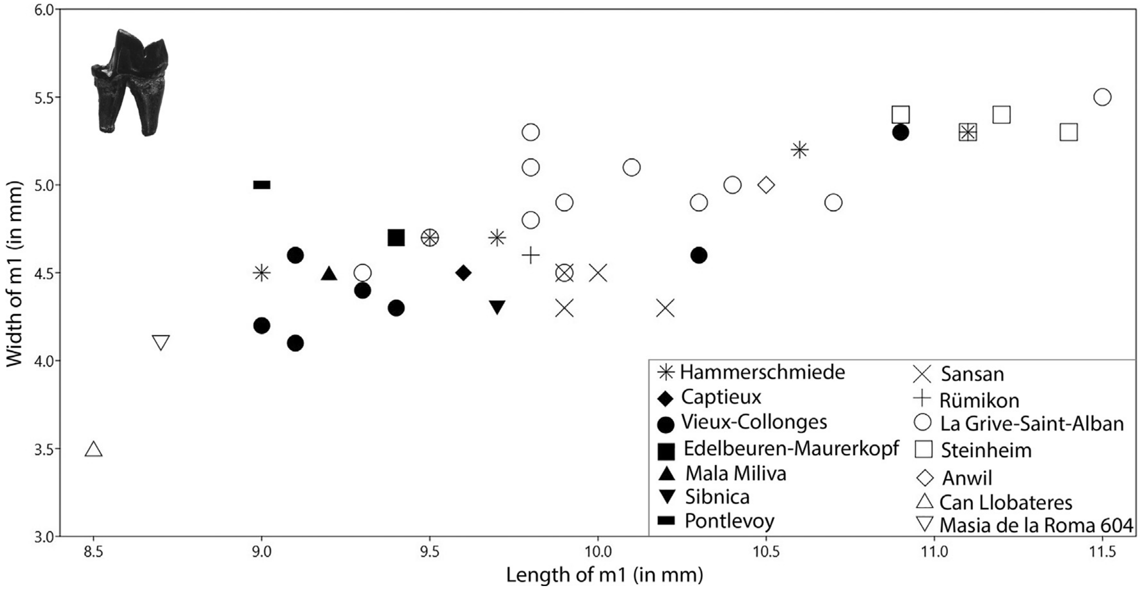

Fig. 7. Scatterplot of m1L and m1W of the material of *S.* "*ripolli*" and *S. sansaniensis*. Filled symbols: Burdigalian and Langhian localities; non-filled symbols: Serravalian and Tortonian localities. Data from Helbing (1928), Mein (1958), Petronijevic (1967), Heizmann (1973), Petter (1976), de Bonis (1994), Sach (1999), Montoya et al. (2001), and Peigné (2012).

form of *S. sansaniensis*. Though, we argue that the newly published specimen from Thailand differs from the morphology of *S. sansaniensis*. Despite the presence of a typical *Semigenetta* m1, the premolars present important differences from all the already published specimens of the genus: the main cuspids are considerably blunter and shorter, the accessory cuspids are blunter and more ventrally situated, while the mesial and distal accessory cuspids of p4 are significantly enlarged (de Bonis et al., 2021: fig. 3). Based on these differences (that distinguish this material from any other specimen of *Semigenetta* as far as we are concerned) and the considerable geographical distance from Central Europe, we consider that this form probably represents a new species, different from *S. sansaniensis* sensu lato. Hopefully, new material will shed some light on the status of this enigmatic viverrid.

5.2. Palaeoecology and evolution

Based on the present data, *Semigenetta sansaniensis* is the most common carnivoran in the locality of Hammerschmiede. Most of the material comes from HAM 4 (MNI = 6), while only two specimens come from HAM 5 (MNI = 1), so a difference in the abundance of the genus in the two levels is noted. However, this difference may be biased by the dissimilar collection of material from the two levels, as HAM 4 has provided almost twice as many specimens that HAM 5 has (up to now, 3274 and 1819 large mammal specimens, respectively). Future findings from both levels are needed to verify whether this difference is real or not.

Based on the equation of Van Valkenburgh (1990) for m1 length, the estimated body masses for *S. sansaniensis* (larger form), *S. sansaniensis* (smaller form) and *S. grandis* are approximately 4.5 kg, 1.5 kg and 11 kg, respectively. All three groups share a relatively homogenous morphology in the lower carnassial: the trigonid covers ca. 75% of the total tooth's length, the protoconid is separated from the paraconid by a carnassiform notch, the metaconid is developed and pointed, and the talonid valley is restricted without enlarged blunted cusps. The upper carnassial is also relatively trenchant, with a slender protocone neck and strong and pointed paracone. Additionally, the molar grinding area is reduced, with the absence of M2 and the reduction of m2 (Nagel, 2009). This type of cheek-tooth morphology is associated in extant carnivorans to an omnivorous diet that includes a high percentage of meat (Popowics, 2003; Friscia et al., 2006; Kargopoulos, 2019). The adaptations of *S. grandis* towards hypercarnivory have been discussed in detail in Crusafont Pairó and Golpe Posse (1981) and Golpe-Posse (1981a, 1981b, 1981c).

The postcranial skeleton of *S. sansaniensis* is relatively similar to that of the extant *Genetta* (Helbing, 1927; Heizmann, 1973; Peigné, 2012), indicating similar locomotor abilities. Some of them include the proximally positioned entepicondylar foramen of the humerus, the deep olecranon fossa of the humerus, the cranially oriented olecranon, the presence of two tubers separated by a fossa in the cranial part of the olecranon, the deep trochanter fossa of the femur, the prominent lesser trochanter of the femur, and the slender metapodials (Helbing, 1927; Heizmann, 1973; Peigné, 2012). Therefore, it is considered as a slender and agile animal, capable of a semi-arboreal lifestyle, similar to the extant genets (Larivière and Calzada, 2001). However, a future ecomorphological comparison with several different ecotypes of small carnivorans will provide a more detailed view on the locomotor abilities of this species. Unfortunately, no postcranial of *S. grandis* have been published so far.

Based on their dietary and locomotor adaptations, some extant species that cover a dietary niche similar to the smallest forms of *S. sansaniensis*, the largest forms of *S. sansaniensis* and *S. grandis* could be *Viverricula indica* (Christiansen and Wroe, 2007), the larger individuals of *Genetta genetta* (Larivière and Calzada, 2001), and *Canis mesomelas* (Walton and Joly, 2003), respectively. The ecological correlation of *S. grandis* with a canid, rather than a genet, is deemed relevant, due to the considerable size difference between this species and the extant genets and the hypercarnivorous traits of its dentition (Golpe Posse 1981a, 1981b, 1981c). Two other extant genera of the family, *Civettictis* and *Viverra*, reach similar sizes, but their dental adaptations point towards a more omnivorous/opportunistic diet. The small rodents, insectivores and reptiles listed in Böhme et al. (2019) could be possible prey groups for *S. sansaniensis*. *Semigenetta grandis* was probably capable to hunt larger prey, like small beavers, lagomorphs or even small ruminants. However, the presence of a considerable percentage of plant material in the diet of both species is highly possible.

The coexistence of *S. grandis* and *S. sansaniensis*, documented for the first time from HAM 4, can be paralleled to the coexistence of *C. mesomelas* and *G. genetta* in East and South Africa (Larivière and Calzada, 2001; Walton and Joly, 2003). Both extant species occur in a wide variety of environments, but they tend to prefer woodland areas depending on the presence of other larger predators (Larivière and Calzada, 2001; Walton and Joly, 2003).

A size reduction of *S. sansaniensis* during the late Aragonian to Vallesian interval can be explained from an ecological-evolutionary point of view. The coexistence with *S. grandis* (evident in Hammerschmiede), the rise of ictitheres (Werdelin and Solounias, 1991) and the mustelid radiation during that time (Koepfli et al., 2008) could have acted as competitive forces in terms of ecological trends. It is reasonable to suggest that larger omnivores/opportunists such as *S. grandis* and *Ictitherium* would have been more successful into preying on small-medium vertebrates (rodents, hares, insectivores, birds, etc.) than *S. sansaniensis*, due to their size difference. The size reduction of *S. sansaniensis* can be associated with a turn into more opportunistic diet, focusing on smaller prey (small reptiles and rodents, invertebrates, etc.). This niche was filled only by some members of *Martes* and *Protictitherium* during this time interval. Additionally, a more opportunistic niche always offers less competition, due to the plethora of possible food sources (Armbruster and Baldwin, 1998; Carbone et al., 2011). Therefore, the competition would be much lower, enabling an ecological transition towards this direction. The coverage of these niches by mustelids and ictitheres is considered as a force that could have possibly led to the extinction of the genus during the late Miocene.

After 9 Ma the genus *Semigenetta* disappears from the fossil record. We relate this event to the early Turolian radiation of ictitheres (Semenov, 1989) that covered most of the available niches of small- (e.g., *Plioviverrops*), medium- (e.g., *Ictitherium*) or large-sized opportunists (e.g., *Hyaenictitherium*). The absence of viverrids from Turolian and early Ruscinian ecosystems in Europe was interrupted by a short-term return of large viverrids (genus *Hesperoviverra*) during the late Ruscinian, after the extinction of ictitheres and just before the immigration of 'true' canids (Fejfar and Sabol, 2004).

6. Conclusions

The viverrid material from Hammerschmiede is attributed to two species of *Semigenetta*: the medium-sized *S. sansaniensis* and the large-sized *S. grandis*. The coexistence of the two species is reported here for the first time and indicates that they had different ecological niches, as omnivores with diets based on meat, strongly correlated to their size difference. The species *S.* "*ripolli*" is suggested to be a junior synonym of *S. sansaniensis*, while *S.* "*huaiheensis*" is considered as a junior synonym of *S. elegans*. We argue for a possible evolutionary trend towards smaller size in the *S. sansaniensis* lineage, between the late Aragonian and late

Vallesian, stimulated by competition with the relatively hypercarnivorous *S. grandis* and more omnivore/opportunistic carnivorans such as mustelids and ictitheres.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geobios.2021.07.001.

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ARTICLE

NEW EARLY LATE MIOCENE SPECIES OF *VISHNUONYX* (CARNIVORA, LUTRINAE) FROM THE HOMINID LOCALITY OF HAMMERSCHMIEDE, BAVARIA, GERMANY

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ABSTRACT—This study presents a new species of a large-sized lutrine from the upper Miocene hominid locality of Hammerschmiede, *Vishnuonyx neptuni* sp. nov., reporting the first occurrence of the genus in Europe and its most northern and western record. The new species differs from the already known members of the genus in size (intermediate between the African *Vishnuonyx*? *angololensis* and the Asiatic *Vishnuonyx chinjiensis*) and morphology, in particular in the larger P4 hypocone, the primitive morphology of M1 (paraconule present, enlarged protoconule and metaconule, labial expansion at the paracone area), the shorter and more robust lower premolars and the wider m1 trigonid. We hypothesized that the dispersal event that led to the expansion of the genus in Europe seems to be correlated with the water connection between Paratethys and the Mesopotamian Basin during the Konkian, between 13.4 and 12.65 Ma. In terms of paleoecology, it is here suggested that this form was feeding mainly on fish and less on bivalves or plant material, resembling the extant giant otter, *Pteronura brasiliensis*.

http://zoobank.org/urn:lsid:zoobank.org:pub:CE331964-FBF5-4680-A6BA-FACDABE8BD58

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INTRODUCTION

Hammerschmiede

The locality of Hammerschmiede has been studied for nearly half a century (Fahlbusch and Mayr, 1975; Mayr and Fahlbusch, 1975). At least six distinct fossiliferous levels have been identified, but the majority of fossils has been unearthed from the fluvial channels HAM 4 and HAM 5, dated to 11.44 and 11.62 Ma, respectively (Kirscher et al., 2016). Several studies have been published concerning the fauna (both vertebrate and invertebrate) of the locality (Fahlbusch and Mayr, 1975; Mayr and Fahlbusch, 1975; Schneider and Prieto, 2011; Fuss et al., 2015; Böhme et al., 2019, Mayr et al., 2020a, 2020b; Hartung et al., 2020; Kargopoulos et al., in press). They reveal an extremely high faunal diversity, comprising more than 130 terrestrial and aquatic vertebrate species, several being new to science. The hominid *Danuvius guggenmosi* Böhme et al., 2019, from Hammerschmiede, has been suggested to involve a degree of bipedalism in its locomotion (Böhme et al., 2019, 2020). So far, the only study solely concerning the carnivorans from Hammerschmiede is that of Kargopoulos et al. (in press), reporting the presence of the viverrids *Semigenetta sansaniensis* (Lartet, 1851) and *Semigenetta grandis* Crusafont-Pairó and Golpe Posse, 1981. Here we present the first remains of a bunodont otter from the locality.

Bunodont Otters

The subfamily Lutrinae includes the extant otters sensu lato and their fossil relatives. The phylogeny and systematics of the subfamily above the genus level are far from resolved (e.g., Willemsen, 1992; Bryant et al., 1993; Morales and Pickford, 2005a; Fulton and Strobeck, 2006; Pickford, 2007; Koepfli et al., 2008; Agnarsson et al., 2010; Wang et al., 2018; Hassanin et al., 2021). The clustering scheme becomes even more obscure with the consideration of Potamotheriinae (Pickford, 2007; Rybczynski et al., 2009; Paterson et al., 2020) and the group of *Lartetictis* Ginsburg and Morales, 1996, *Mionictis* Matthew, 1924 and *Siamogale* Ginsburg, Ingavat and Tassy, 1983 (Ginsburg, 1999; Wang et al., 2018; Valenciano et al., 2020).

Bunodont otters are a paraphyletic group of large- to very large-sized otters from North America, Eurasia, and Africa. It includes the genera *Djourabus* Peigné, de Bonis, Likius, Mackaye, Vignaud and Brunet, 2008; *Enhydriodon* Falconer, 1868; *Enhydritherium* Berta and Morgan, 1985; *Paludolutra* Hürzeler and Engesser, 1976; *Sivaonyx* Pilgrim, 1931; *Torolutra* Petter, Pickford and Howell, 1991; and *Vishnuonyx* Pilgrim, 1932 (Morales and Pickford, 2005a; Pickford, 2007; Grohé et al., 2020). Additionally, the genera *Enhydra* Fleming, 1822, *Aonyx* Lesson, 1827, and *Enhydrictis* Forsyth Major, 1901, have been considered to be close to these forms (Morales and Pickford, 2005a; Pickford, 2007; Valenciano and Govender, 2020). However, recent studies

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have removed *Enhydrictis* from the Lutrinae, considering it as a member of the Ictonychinae (Galictini sensu Rook et al., 2018, or Lyncodontini sensu Jiangzuo et al., 2019). The bunodont otters are characterized by a robust dentition, with strong cingula and tall and dull cusps. The developed lingual cusps in P4 (hypocone and protocone) are positioned considerably lingually to the carnassial blade, establishing a large valley between them. Additionally, they have a large distal accessory cuspid in the p4 and a deep mandibular corpus (Pickford, 2007 and references therein). Among them, the genera *Vishnuonyx* and *Torolutra* possess the lesser bunodont appearance on their cusps. Moreover, an array of different lifestyles has been suggested for these forms, ranging from terrestrial to semi-aquatic (Lewis, 2008; Peigné et al., 2008; Geraads et al., 2011; Werdelin and Lewis, 2017; Valenciano and Govender, 2020). The robustness of the mandibles and the enhancement of crushing cheek teeth in *Djourabus*, *Enhydriodon*, *Enhydritherium* and *Sivaonyx*, have been associated with a diet based on mollusks and crustaceans (Pickford, 2007; Lewis, 2008), whereas Geraads et al. (2011) suggested that the large *Enhydriodon dikikae* Geraads, Alemseged, Bobe and Reed, 2011, was possibly able to consume even armored prey such as turtles, juvenile crocodiles, or ostrich eggs.

The genus *Vishnuonyx* (Fig. 1) was introduced by Pilgrim (1932) with *Vishnuonyx chinjiensis* Pilgrim, 1932 as the type species, based on material from the upper part of the Chinji stage in the Lower Siwaliks. Pilgrim (1932) described a maxilla with P4 and the root of the M1, and a hemimandible with a complete p4 and fragmentary m1 and m2. The exact age of the fossiliferous layer is unknown, but it was estimated to be of late middle Miocene or early late Miocene age (Nanda and Sehgal, 2005). This species has also been found in the Locality 2/11 in Ngorora D in Kenya (Morales and Pickford, 2005b; late middle Miocene; firstly reported in the faunal list of Ngorora Formation by Hill et al., 1985 as *Vishnuonyx* sp. nov.), in Ramnagar in India (Nanda and Sehgal, 1993, 2005; Sehgal, 2013; only as a member of the faunal list without describing any specimens; late middle Miocene) and in the loc. Y53 and loc. Y828 of the Potwar Plateau in Pakistan (Grohé et al., 2020; late middle Miocene). Therefore, the temporal range of *V. chinjiensis* is restricted to the late middle Miocene, with a possible expansion towards the early late Miocene, if the specimens of Pilgrim (1932) proved to be slightly younger. Additionally, Werdelin (2003) described a second species, *Vishnuonyx angololensis* Werdelin, 2003, based on an upper carnassial from Lower Nawata in Lothagam (late late Miocene). This species was later attributed to the genus *Torolutra* (Haile-Selassie, 2008; Werdelin and Lewis, 2017), but its generic status still remains doubtful (Grohé et al., 2020). Recently, Grohé et al. (2020) described the third identified species of the genus, *Vishnuonyx maemohensis* Grohé, de Bonis, Chaimanee, Chavasseau, Rugbumrung, Yamee, Suraprasit, Gibert, Surault, Blondel and Jaeger, 2020, from the middle–late middle Miocene of Mae Moh in Thailand. Furthermore, Haile-Selassie (2008) published a mandibular corpus with a lower carnassial from the Haradaso Member of the Middle Awash (early Pliocene) in Ethiopia as *Vishnuonyx* sp., which represents the last known occurrence of the genus in the fossil record. No postcranial material of *Vishnuonyx* has ever been found and a plesiomorphic semi-aquatic lifestyle seems highly possible, due to the dental adaptations correlated to piscivory, as discussed below.

Therefore, no solid results regarding the taxonomy, evolution, biostratigraphy and paleoecology of bunodont otters (including the genus *Vishnuonyx*) have been reached to date. Additionally, details on the dispersal event of *Vishnuonyx* from South Asia towards the other regions of the Old World still are unclear. Consequently, every report that provides new knowledge on the fossil record of the group is decisive in order to solidify existing hypotheses on the aforementioned problems.

The present study deals with new craniodental material of a new species of *Vishnuonyx* from the upper Miocene locality of Hammerschmiede. The unexpected occurrence of the genus in Europe is investigated in terms of stratigraphy and paleogeography. Finally, an ecomorphological approach is employed in order to trace the diet specialization of the new species.

MATERIAL AND METHODS

The specimens studied herein come from the fluvial channel HAM 4 (11.44 Ma) of the fossil locality of Hammerschmiede (Bavaria, Germany) and they were unearthed during the excavations held by the Eberhard Karls University of Tübingen between 2011 and 2020. The material is stored in the Paleontological Collection of the University of Tübingen, Germany (GPIT) and is inventoried with numbers of both GPIT (for excavations from 2011 to 2019) and SNSB-BSPG (Bavarian State Collection of Paleontology and Geology in Munich, Germany; for excavations of 2020). The specimens coded as SNSB-BSPG 2020 XCIV were excavated from HAM 4 locality in 2020. Their codes in the tables are mentioned as BSPG 2020 XCIV for practical reasons.

Dental nomenclature follows Ginsburg (1999) and Smith and Dodson (2003). All measurements were taken with a digital caliper and rounded to the first decimal point. In cases of multiple specimens per skeletal element, the descriptions and comparison concern the material as a whole. The specimens were scanned in a Nikon XT H 320 μCT scanner using the 225 reflection target and the ‘Helical CT Scan’ function. The isolated teeth were scanned separately from the mandibles. The isolated teeth were scanned at 200 kV and 80 μA with a voxel size of 0.01847402 mm and 5864 projections, using a copper filter of 1 mm thickness. The mandibles were scanned at 185 kV and 86 μA with a voxel size of 0.01603859 mm and 6321 projections, using a copper filter of 1 mm thickness.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Suborder CANIFORMIA Kretzoi, 1943
Family MUSTELIDAE Fischer, 1817
Subfamily LUTRINAE Bonaparte, 1838
Genus *VISHNUONYX* Pilgrim, 1932

Diagnosis—Lutrinae of medium size; P4 triangular, labial mesiodistal length greater than lingual, and also much exceeding transverse diameter, parastyle weak, high pointed paracone, metastyle lower but elongated, protocone and hypocone much lower than paracone, protocone situated rather far forward; internal cingulum slight; M1 rather small, lingual platform reduced mesiodistally; mandible with deep ramus; p4 elongate with a distal widening and a broad cingulum, mesially tall, a high and strong distal accessory cuspid, more fused mesially with the main cuspid than in *Sivaonyx*; m1 with talonid shorter than trigonid, surrounded by a crenulated rim; m2 oval, rather longer than in *Sivaonyx*. [Modified after Werdelin and Peigné (2010) and Grohé et al. (2020).]

Type Species—*Vishnuonyx chinjiensis* Pilgrim, 1932.

Other Included Species—*V.*? *angololensis* Werdelin, 2003, *V. maemohensis*, *V. neptuni* sp. nov.

VISHNUONYX NEPTUNI sp. nov.
(Figures 2 & 3, Tables 1 & 2)

Holotype— a right hemimandible, SNSB-BSPG 2020 XCIV-0301, with p1 alveolus and complete p2–m1 from HAM 4.

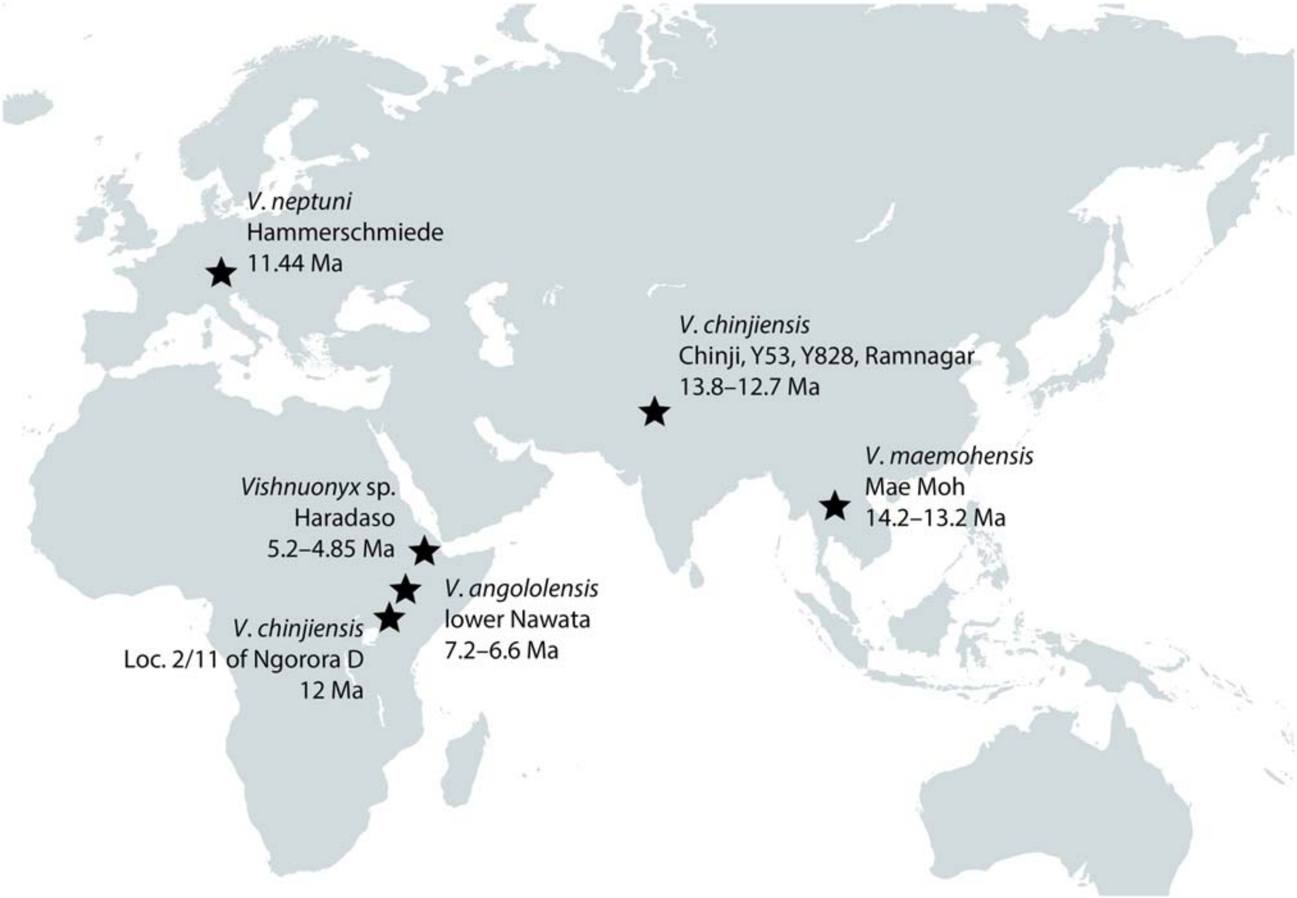

FIGURE 1. Temporospatial distribution of the known species of the genus *Vishnuonyx*.

Hypodigm— SNSB-BSPG 2020 XCIV-1022, left P3; GPIT/MA/17347, right P4; SNSB-BSPG 2020 XCIV-1552, left M1; GPIT/MA/16733, left hemimandible with p3–m1; SNSB-BSPG 2020 XCIV-1301, right p4.

Etymology—The name *neptuni* is derived from Neptune, the Roman god of water.

Type Locality—HAM 4, Hammerschmiede, Bavaria, Germany (11.44 Ma) (Fig. 1).

Diagnosis—Species of *Vishnuonyx*, intermediate in size between the larger *Vishnuonyx*? *angololensis* and the smaller *Vishnuonyx chinjiensis* and *Vishnuonyx maemohensis*; p2 bent labially; P4 hypocone large, similar in size with the protocone; M1 paraconule present and small; M1 protoconule and metaconule present and large; M1 expansion labially to the paracone enhanced; lower premolars relatively short; m1 trigonid slightly wider than m1 talonid.

Differential Diagnosis—Differs from Lutrini in the enlarged P4 hypocone, the mesiodistally narrower M1, the larger distal accessory cuspid of p4, the shorter m1 talonid, the higher m1 trigonid cuspids and a higher m1 protoconid. Differs from Aonychini in the larger P4 hypocone, the narrower M1, the more enlarged p4 distal accessory cuspid, the narrow m1 talonid and the higher m1 trigonid cuspids. Differs from the group of *Siamogale*, *Mionictis*, and *Lartetictis* in the more developed protocone area of P4, the narrower M1, the labial position of the distal accessory cuspid in p4 and the higher m1 trigonid cusps. Differs from the Potamotheriinae in the absence of a carnassial notch in P4, the presence of a hypocone, the presence of M1 paraconule and metaconule, the absence of mesial accessory cuspids in p3 and p4 and the blunter m1 trigonid. Differs from the derived bunodont otters (tribe Enhydrini sensu Pickford, 2007; *Enhydra* and *Enhydritherium*), as well as from *Enhydriodon* and *Paludolutra* in the absence of wide occlusal surfaces and bunodont cusps. Differs from *Sivaonyx* by the (usually) smaller size, the less developed protocone region of P4, the less developed m1 talonid, the smaller m1 metaconid and the smaller m2. Differs from *Torolutra* in the larger P4 hypocone, the absence of P4 protoconule, the less developed p4 distal accessory cuspid and the more robust m1 trigonid.

Differs from *V. chinjiensis* in the larger size, the shorter premolars, the more robust P4 with a more developed hypocone and stronger cingulum and parastyle, the higher m1 metaconid and the relatively slenderer talonid. Differs from *V. maemohensis* in the larger size, the shorter premolars, the more robust P4 with a stronger cingulum and parastyle, the presence of M1 paraconule, the larger M1 protoconule and metaconule, the less reduced M1 lingual platform, the less convex outline of the lower teeth, the sharper p3 and the presence of a mental foramen below p2. Differs from *V.*? *angololensis* in the smaller size, the presence of P4 parastyle, the larger P4 hypocone, the more distally situated P4 protocone and the more robust P4 cingulum.

Description—The P3 (SNSB-BSPG 2020 XCIV-1022; Fig. 2A) is asymmetrical with the distal side being larger than the mesial one. A mesial, a distal and a lingual crista diverge from the main cusp. It has three roots. The lingual ridge ends up in an expansion of the lingual wall of the tooth that also hosts an additional root. The cingulum is relatively robust and the enamel wrinkled.

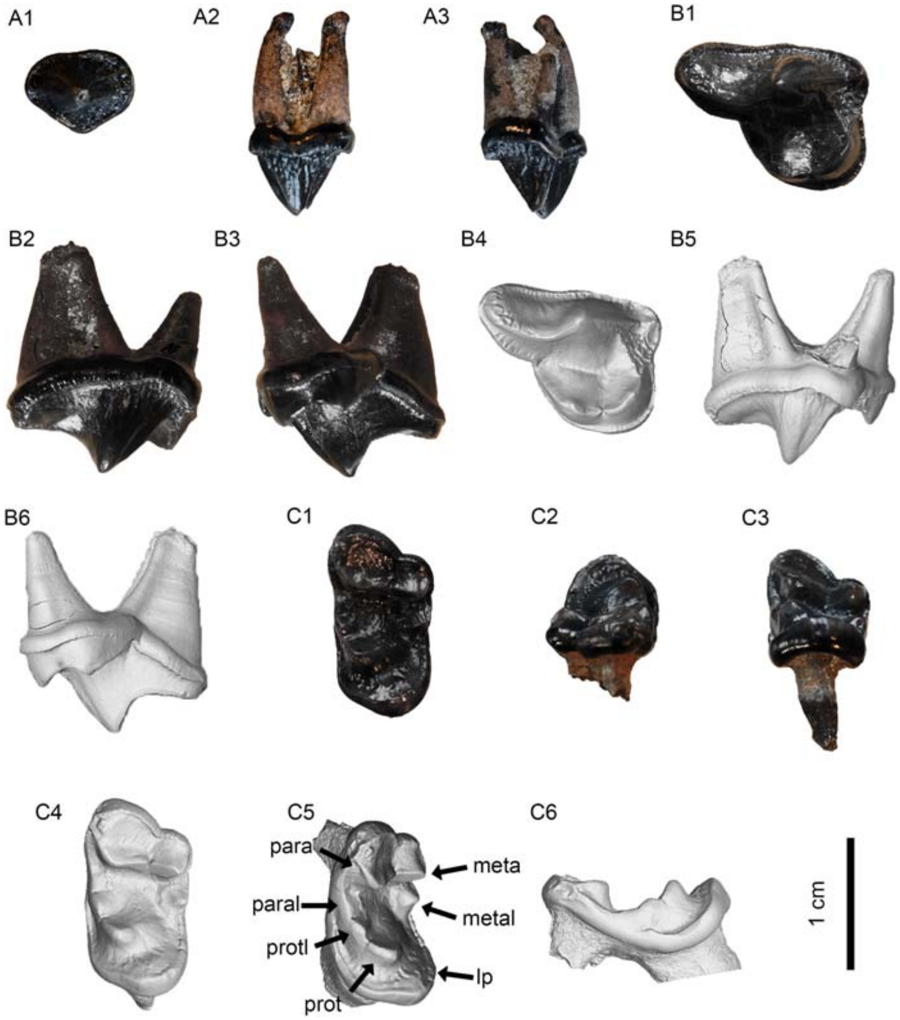

FIGURE 2. The upper dentition of *Vishnuonyx neptuni* sp. nov. **A**, SNSB-BSPG 2020 XCIV-1022, left P3 in occlusal (A1), labial (A2) and lingual (A3) views; **B**, GPIT/MA/17347, right P4 (original specimen and screenshots of its 3D model) in occlusal (B1, B4), labial (B2, B5) and lingual (B3, B6) views; **C**, SNSB-BSPG 2020 XCIV-1552, left M1 (original specimen and screenshots of its 3D model) in occlusal (C1, C4), labial (C2), lingual (C3), mesial-occlusal (C5) and mesial (C6) views. **Abbreviations**: **meta**, metacone; **metal**, metaconule; **lp**, lingual platform; **para**, paracone; **paral**, paraconule; **prot**, protocone; **protl**, protoconule.

The available upper carnassial (GPIT/MA/17347; Fig. 2B) is complete, with a moderately developed wear facet on its carnassial blade and a strong cingulum through the whole perimeter of the tooth. The paracone is high and acute, forming a fine crest with the metastyle, without a carnassial notch. It has a small parastyle at the mesial cingulum. A large valley-shaped shelf is present between the labial and lingual cusps. The protocone is wide and high, standing mesially to a hypocone of similar size and morphology. The two lingual cusps are connected by two small crests that merge in an indistinct notch. The protocone is situated between the planes of the paracone and the parastyle, while the hypocone is situated slightly distally to the plane of the paracone. In terms of height, paracone is the highest cusp, followed by the metastyle, the lingual cusps, and lastly the parastyle.

TABLE 1. Comparison of the upper teeth dimensions of *Vishnuonyx neptuni* sp. nov. with other species of *Vishnuonyx*. The parentheses indicate measurement taken at the alveolus. Data from: Grohé et al. (2020).

Species	Code	P3L	P3W	P4L	P4W	M1L	M1W
Vishnuonyx neptuni sp. nov.	BSPG 2020 XCIV-1022	7.8	6.0				
	GPIT/MA/17347			13.4	10.4		
	GPIT/MA/10505					(7.9)	13.3
	BSPG 2020 XCIV-1552					7.6	14.0
Vishnuonyx chinjiensis	GSI D 223			11.5	9.1		
	GSP-Y 2108			10.2	7.8		
	KNM-BN 1730			11.6	9.4		
Vishnuonyx maemohensis	MM-36			12.2	8.6		
	MM-37					5.3	11.1
	MM-78 left	6.5	4.5	11.9	8.3	5.9	11.5
	MM-78 right	6.7	4.6	11.7	8.4	5.0	
Vishnuonyx? *angololensis*	KNM-LT 23948			15.3	12.9		

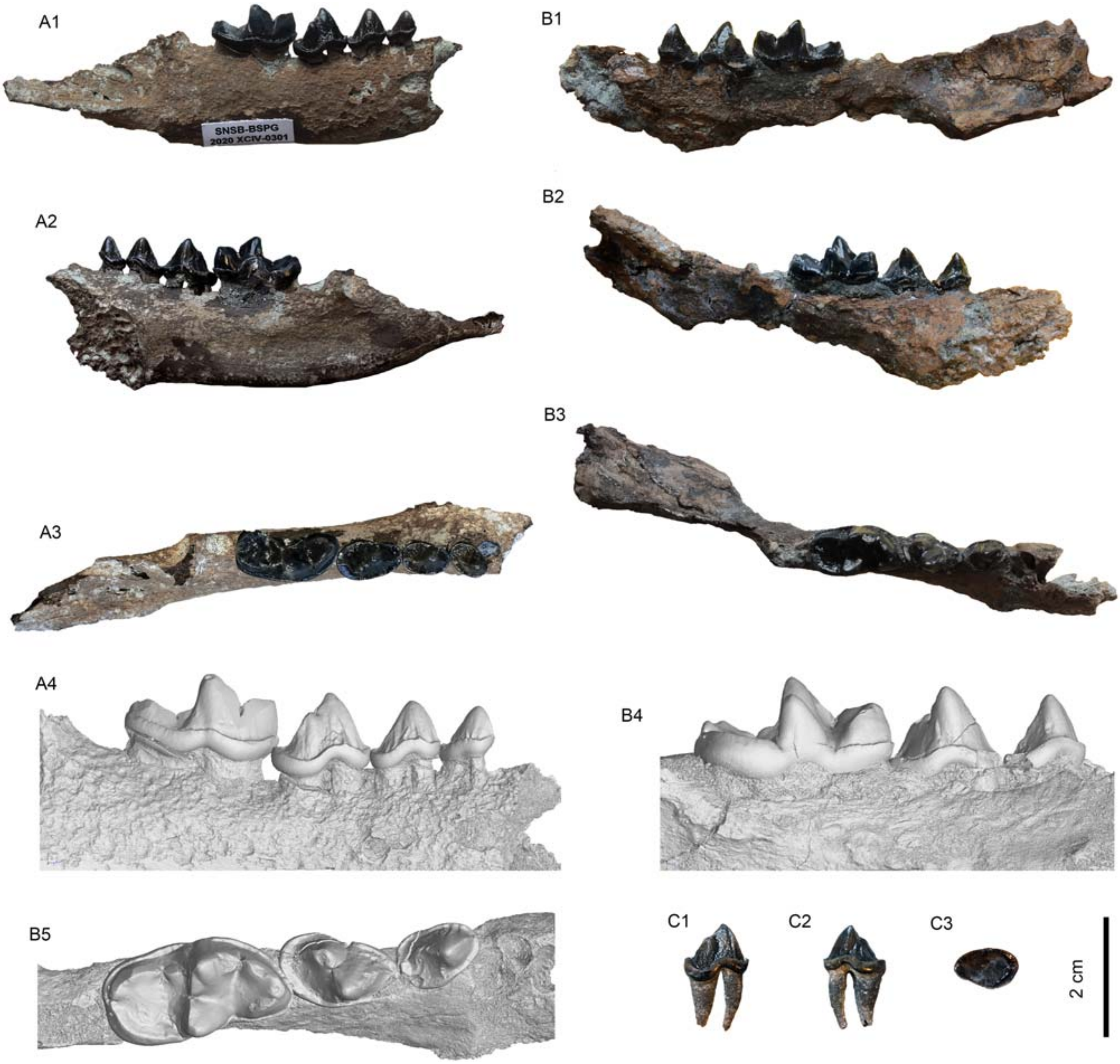

FIGURE 3. The lower dentition of *Vishnuonyx neptuni* sp. nov. **A**, SNSB-BSPG 2020 XCIV-0301, right hemimandible (holotype; original specimen and screenshots of its 3D model) in labial (**A1**, **A4**), lingual (**A2**) and occlusal (**A3**) views; **B**, GPIT/MA/16733, left hemimandible in labial (**B1**), lingual (**B2**, **B4**) and occlusal (**B3**, **B5**) views; **C**, SNSB-BSPG 2020 XCIV-1301 right p4 in labial (**C1**), lingual (**C2**) and occlusal (**C3**) views. Screenshots of the 3D models not in scale.

The upper molar (SNSB-BSPG 2020 XCIV-1552; Fig. 2C) is complete and slightly worn at the lingual side of the paracone and the metacone. A developed cingulum is present in the perimeter of the tooth, being less developed in its mesial part. The outline of the tooth is slender and almost rectangular. The labial border of the tooth is more enhanced at the paracone level than in the metacone level. The paracone and the metacone are approximately of equal height, but the paracone is considerably wider. They are connected with a low crest that forms a small notch in its center. Lingually to these two cusps there is a shallow valley, where a metaconule and a well-developed protoconule (bordered by two clear notches) are located. A postmetaconular crista is present, as well as a postprotocrista (almost reaching the metaconule) and a preparaconular crista reaching the mesial cingulum and hosting a small crest-like paraconule. The lingual platform is mesiodistally short, in relation to the extant lutrines.

None of the two preserved hemimandibles is complete. SNSB-BSPG 2020 XCIV-0301 preserves part of the alveolus of the canine, part of the angular process and part of the masseteric fossa (Fig. 3A). The masseteric fossa is deep cranially and shallow caudally. The caudal part of the mandible is bent labially, while the angular process is small and hook-like. The hemimandible GPIT/MA/16733 is heavily damaged (Fig. 3B), so only the cheek teeth, part of the canine alveolus and part of the masseteric fossa are preserved. Over the ventral part of the masseteric fossa, it exhibits a large area for the insertion of M. masseter pars superficialis and M. pars profunda. The mandibular ramus of SNSB-

TABLE 2. Comparison of the lower teeth dimensions of *Vishnuonyx neptuni* sp. nov. with other species of *Vishnuonyx*. The parentheses indicate measurements taken at the alveolus. Data from Grohé et al. (2020).

Species	Code	p1L	p1W	p2L	p2W	p3L	p3W	p4L	p4W	m1L	m1Ltr	m1W	m2L	m2W
Vishnuonyx neptuni sp. nov.	GPIT/MA/16733					6.6	4.8	8.9	6.2	14.6	10.4	7.7		
	BSPG 2020 XCIV-0301	(4.0)	(3.3)	5.7	4.1	6.6	4.6	9.0	5.7	14.1	9.6	(7.3)	(3.5)	(3.2)
	BSPG 2020 XCIV-1301							9.9	6.5					
Vishnuonyx chinjiensis	GSI D 245							7.3	4.2	11.7			5.0	3.3
	WIHG FR 24/18							7.2	4.3					
	GSP-Y 40764									12.2	7.5	5.9		
Vishnuonyx maemohensis	MM-30 left					6.2	3.7	8.3		11.8	7.8	6.2	4.5	4.2
	MM-30 right	3.5	2.6	5.3	3.1	6.1	3.7	8.2	4.6	11.9	7.8	6.0	4.5	4.2
	MM-32									12.1	7.8	6.4		
	MM-33							7.6	4.1	10.6	6.7	5.8		
	MM-34			5.1	2.9	5.3	3.1	6.7	3.5	10.5	7.1	5.2		
	MM-35					5.2	3.4	7.7		11.1	7.3	5.8		
	MM-79							7.1	3.5	10.7		4.8	3.4	2.3
Vishnuonyx sp.	GAW-VP-1/1									13.5	8.2	7.2		

BSPG 2020 XCIV-0301 is moderately robust and it has one large mental foramen, below the p2. The mandibular symphysis is inclined cranially.

The canine is absent, but its alveolus is enlarged in both hemimandibles. One small alveolus for the p1 is also present and in proximity to the p2. The p2 is two-rooted, unicuspid and asymmetrical, with a well-developed cingulum, especially in its labial and distal part. The long axis of the tooth is not aligned with the long axis of the whole toothrow. Both p3 and p4 are high and pointed premolars, with their main cuspids being mesially located and distally inclined. The p3 is relatively high, unicuspid with a rough labial surface with many small wrinkles. The p4 is much larger than p3 and higher than the m1 paraconid. It also possesses a developed cingulum (mesially crowned) and a large distal accessory cuspid, situated at the distolabial ridge of the main cuspid. The m1 is significantly broad, with the talonid covering almost one third of the length of the tooth. The trigonid is slightly wider than the talonid. A strong cingulum surrounds the entire tooth. The trigonid exhibits small wear facets on the carnassial blade in GPIT/MA/16733, whereas in SNSB-BSPG 2020 XCIV-0301 the wear is more evident. The protoconid is the highest cusp. It is separated by the much smaller paraconid by a shallow notch. The metaconid is very developed. It is robust, slightly inclined lingually and it has approximately the same height as the paraconid. The talonid valley is large and deep. Two small labial cuspids (hypoconid and hypoconulid) are present on the talonid. They have approximately the same height, the hypoconid is continued mesially by a relatively long crest and the hypoconulid is labiodistally situated. A small cuspid (protoconulid/mesoconid) is located between the protoconid and the hypoconid. The distal cristid of the protoconid (also called mesoconid in literature) and the mesial cristid of the hypoconid form a carnassiform notch between them. The entoconid is absent. The lingual wall of the talonid is V-shaped. The alveolus for m2 is heavily damaged, but it is evident that it is of a relatively moderate size and a nearly circular outline.

DISCUSSION

Comparison

The material exhibits considerable differences with the typical morphology of the Lutrini sensu Willemsen (1992). The developed P4 hypocone, the mesiodistally slender M1, the more developed distal accessory cuspid of p4, the relatively short m1 talonid, the high m1 trigonid cuspids and especially the protruding m1 protoconid are traits that differentiate the Hammerschmiede material from the Lutrini (van Zyll de Jong, 1987; Willemsen, 1992; Pickford, 2007; Peigné et al., 2008).

Regarding the differences of the studied specimens from the tribe Aonychini (sensu Willemsen 1992, comprising the genera *Aonyx*, *Amblonyx* Rafinesque, 1832, *Cyrnaonyx* Helbing, 1935, *Limnonyx* Crusafont Pairó 1950, and *Megalenhydris* Willemsen and Maletesta, 1987), the members of this group have a wide M1, P4 hypocone reduced or absent, p4 with reduced or absent accessory cusp, and a very wide m1 talonid and m1 trigonid with low cuspids in relation to the Hammerschmiede specimens (van Zyll de Jong, 1987; Willemsen, 1992; Pickford, 2007; Peigné et al., 2008).

The genera *Siamogale*, *Mionictis*, and *Lartetictis* form a diverse group of otter-like mustelids from the middle to late Miocene, found in several localities of Eurasia and North America (e.g., Matthew and Gidley, 1904; Matthew, 1924; Ginsburg and Morales, 1996; Peigné, 2012; Wang et al., 2018; Grohé et al., 2020; Valenciano et al., 2020). They represent a group with uncertain affinities both among them and with other mustelid groups, being colloquially named as badger-like otters, because of their robust and bunodont dentition (Wang et al., 2018). *Vishnuonyx neptuni* sp. nov. undoubtedly differs from these species in the more developed protocone area of P4, the mesiodistally slenderer M1, the more labially situated distal accessory cuspid in p4 and the higher m1 trigonid cusps. These differences are more evident particularly with *Siamogale* spp. and *Lartetictis* spp.

The group of *Potamotherium* is also compared here because of its morphological affinities with the lutrines, regardless of its exact phylogenetic position. This genus has been reported with two species, the smaller *Potamotherium valletoni* Geoffroy, 1833 from the upper Oligocene and the lower Miocene (Savage, 1956; Mödden and Wolsan, 1993; Mörs and von Koenigswald, 2000) and the larger *Potamotherium miocenicum* (Peters, 1869) from the early middle Miocene, both from France and Germany (Thenius, 1949; Fahlbusch, 1967; Ginsburg, 1968). This genus has a very primitive dentition, and therefore several traits distinguish it from the otter from Hammerschmiede. Among them are a P4 with a carnassial notch, a distinct angle between the two parts of the carnassial blade, the absence of the P4 hypocone, the absence of paraconule, protoconule and metaconule in M1, the much more developed M1 parastyle, the more acute M1 lingual platform, the lower premolars are shorter, having a more bunodont aspect, both p3 and p4 have mesial and distal accessory cuspids with the distal one being more detached from the main cuspid and the m1 talonid is sharper (Thenius, 1949; Savage, 1956; Fahlbusch, 1967; Ginsburg, 1968; Mörs and von Koenigswald, 2000).

Compared with the Enhydrini, the post-canine dentition of *V. neptuni* sp. nov. is far slenderer with no distinct crushing surfaces (sensu Pickford, 2007, containing the genera *Enhydra* and *Enhydritherium*). The genus *Enhydriodon* also has far more developed occlusal surfaces and bunodont cusps in each cheek tooth (Pickford, 2007 and references therein). A similar morphology of the cheek teeth is also evident in *Paludolutra* (Hürzeler, 1987; Pickford, 2007).

The genus *Sivaonyx* is known from several species from Africa and Eurasia. The first record of *Sivaonyx* was made by Lydekker (1884), who identified the species *Sivaonyx bathygnathus* (as *Lutra bathygnathus*) from the Late Miocene of Punjab (India). The only representative of the genus in Europe is *Sivaonyx hessicus* from Eppelsheim firstly described by Lydekker (1890) as *Lutra hessica*. The genera *Vishnuonyx* and *Sivaonyx* have been proposed to have close affinities (Pickford, 2007). The specimens from Hammerschmiede differ from this genus by the less developed lingual shelf of P4, the far more restricted m1 talonid (both in length and in width), the lesser development of the m1 entoconid-cristid, the smaller m1 metaconid and the smaller m2, while most *Sivaonyx* species are far larger than *Vishnuonyx* (Pilgrim, 1931, 1932; Pickford, 2007; Grohé et al., 2013).

The African genus *Torolutra* from the early Pliocene is scarcely known and shares several traits with *Vishnuonyx*, making the distinction between the two genera intricate (Werdelin and Lewis, 2007; Haile-Selassie, 2008; Grohé et al., 2020). However, it differs from the Hammerschmiede material in the following traits: P4 hypocone smaller than the protocone, P4 protoconule present, p4 distal accessory cuspid less robust and more robust m1 trigonid (Petter et al., 1991; Morales et al., 2005; Haile-Selassie, 2008; Grohé et al., 2020).

The morphological features of the described specimens from Hammerschmiede fit perfectly with the diagnostic characters of the genus *Vishnuonyx*. The moderately developed protocone region of P4, the presence of a P4 hypocone of comparable size with the P4 protocone, the mesiodistally slender M1 with a reduced lingual platform, the strong and labially situated distal accessory cuspid in p4, the high m1 protoconid and the short m1 talonid suffice for the attribution of the Hammerschmiede material to this genus.

Metrically, the type species *V. chinjiensis* is significantly smaller than *V. neptuni* sp. nov. (Tables 1 and 2). The relative proportions of the lower premolars seem to be higher in the type species, than in the Hammerschmiede hemimandibles (Table 3). The morphological comparison is made based on the material published by Pilgrim (1932), Morales and Pickford (2005b) and Grohé et al. (2020). The upper carnassial of *V. chinjiensis* is more slender than that of *V. neptuni* sp. nov., with a less developed hypocone (both in width and in height), a fainter cingulum and a considerably smaller parastyle. The lower dentition of the two species is very similar. However, the m1 metaconid is relatively lower in *V. chinjiensis* and the talonid is wider than the trigonid. The lower carnassial of this species lacks the notch between the distal cristid of the protoconid and the mesial cristid of the hypoconid.

TABLE 3. Comparison of the relative lengths of the lower premolars in relation to m1L in *Vishnuonyx neptuni* sp. nov. with other species of *Vishnuonyx*. Data from: Grohé et al. (2020).

Species	Code	p2L/ m1L	p3L/ m1L	p4L/ m1L
Vishnuonyx neptuni sp. nov.	GPIT/MA/16733	35.4	44.2	60.5
	BSPG 2020 XCIV-0301	40.4	44.7	63.8
	BSPG 2020 XCIV-1301			62.4
Vishnuonyx chinjiensis	GSP-Y 40764		52.5	70.3
Vishnuonyx maemohensis	MM-30 left	44.5	51.3	68.9
	MM-32			71.7
	MM-33	48.6	50.5	63.8
	MM-34		46.8	69.4
	MM-35			66.4

Similarly, *V. maemohensis* is smaller than *V. neptuni* sp. nov. (Tables 1 and 2), while its premolars are relatively longer (Table 3). The morphological comparisons are based on the specimens published by Grohé et al. (2020). The P3 of the Thai species is very similar to that from Hammerschmiede, but the lingual root of the tooth is partially fused to the distal root. However, this trait, based on the slenderness of the lingual root, can be considered as an abnormality (Fig. 2). The upper carnassial is more slender than that from Hammerschmiede, with a less developed hypocone (both in width and height), less robust cingulum and a smaller parastyle. The M1 morphology of *V. maemohensis* is very similar to that of *V. neptuni* sp. nov., but, apart from the size difference, it lacks a protoconule, the paraconule and metaconule are considerably smaller, the labial expansion of the paracone area is less enhanced and the lingual platform is relatively more reduced. The lower teeth of *V. maemohensis* exhibit a distinct outline compared with the ones of *V. neptuni* sp. nov., due to their blunt and convex ridges that create a more robust profile. The mental foramen in *V. maemohensis* is located below p3, in contrast to that of *V. neptuni* sp. nov., which is located below p2, while the p3 is lower and blunter in the Thai species. Additionally, the lower carnassial in *V. maemohensis* lacks the notch between the distal cristid of the protoconid and the mesial cristid of the hypoconid.

The species *V.*? *angololensis* is known only by an upper carnassial from the Lower Nawata Formation in Lothagam (Werdelin, 2003). The metrical comparison exhibits that this specimen is considerably larger than the P4 from Hammerschmiede (Table 1). In terms of morphology, the African specimen does not have a parastyle, the hypocone is smaller than the protocone, the protocone is situated more mesially (reaching the level of the mesial border of the tooth), and the cingulum is less prominent in the mesiolabial side of the paracone and the distal end of the metastyle.

A fragmentary hemimandible assigned to *Vishnuonyx* sp. by Haile-Selassie (2008), from the lower Pliocene of the Haradaso Member of the Middle Awash, Ethiopia, differs from *V. neptuni* sp. nov. in having a more robust m1.

Thus, both overall morphology and dental proportions of the specimens from Hammerschmiede differ from all the known forms of *Vishnuonyx*, and accordingly the erection of *V. neptuni* sp. nov. is well justified.

Paleobiogeography

The new taxon described herein is of great interest, not only in terms of taxonomy, but also in terms of paleobiogeography. The record of the genus *Vishnuonyx* is characterized by sporadic occurrences in East Africa and Southern Asia (Thailand and the Indian subcontinent), while *V. neptuni* sp. nov. represents the westernmost and northernmost occurrence and the first European representative of the genus (Fig. 1). The Asian record of the genus includes its oldest known occurrence in the Middle Miocene (14.2–13.2 Ma) from Mae Moh in Thailand (Grohé et al., 2020), but also the slightly younger Middle Miocene (13.8–12.7 Ma) material from the Siwaliks, India (Pilgrim, 1932; Sehgal, 2013; Grohé et al., 2020). In Africa, the genus seems to have a stratigraphically longer fossil record from the late Middle Miocene at 12 Ma (Loc. 2/11 of Ngorora

D; *V. chinjiensis*; Morales and Pickford, 2005b) to the Late Miocene (Lower Nawata, Lothagam; 7.3–6.6 Ma, Böhme et al., 2021; *V.*? *angololensis*; Werdelin, 2003) and finally to the earliest Pliocene (Haradaso; 5.2–4.85 Ma; *Vishnuonyx* sp.; Haile-Selassie, 2008). The age of the HAM 4 fossiliferous layer (11.44 Ma; Kirscher et al., 2016) is slightly younger than the records from Siwaliks and Ngorora D.

Considering the oldest known record of *Vishnuonyx* from Thailand as the most ancestral in its evolutionary line (in terms of morphology and biogeography), the radiation of the genus from Southeast Asia towards the Indian subcontinent, East Africa and Europe was completed by the end of the Middle Miocene. Particularly, the radiation event from southern Asia to Africa (where the genus persisted until the early Pliocene) occurred before 12 Ma (Grohé et al., 2020). Similarly, if the significant morphological differences of *V. neptuni* sp. nov. from the other species of the genus are considered, a relatively long period of genetic isolation seems justified. Therefore, we consider that the dispersal of *Vishnuonyx* to Europe must be noticeably older than 11.5 Ma.

Given the supposed semi-aquatic lifestyle of *Vishnuonyx*, the dispersal path of this otter must be searched for in a water connection between South Asia, East Africa, and Central Europe. The lutrines are a group that lives in proximity to both seawater and fresh water (e.g., Hung and Law, 2016), while some taxa, like *Enhydra lutris* (Linnaeus, 1758), are primarily marine (Estes, 1980). Therefore, the pathway of the genus between South Asia and Europe could possibly include either seawater or fresh water. Thus, the biogeography of *Vishnuonyx* can be understood considering marine gateways.

A marine water connection between these two regions was potentially present during the Konkian Eastern Paratethys regional chronostratigraphic stage (late Badenian, early Serravalian; 13.4–12.65 Ma; Palcu et al., 2017). During the Konkian, the Eastern Paratethys was connected to the Central Paratethys (Studencka et al., 1998; Kovac et al. 2007; Palcu et al., 2017) and, via the Araks Strait, probably to the Eastern Mediterranean and the Mesopotamian Basin (Fig. 4). The existence of the Araks Strait has been proposed on the basis of marine benthos (echiniids, scaphopods, gastropods, bivalves) found in Konkian sediments of the southeastern part of the Eastern Paratethys (see Studencka et al., 1998 and Iljina, 2003 for discussion and references). However, it remains yet unresolved if this gateway connects the Eastern Paratethys only to the Eastern Mediterranean via northern Syria or in addition via the Mesopotamian Basin to the Indian Ocean (Rögl 1998, 1999; Popov et al., 2004, Palcu et al., 2017). However, the last possibility is supported by Indo-Pacific affinities of late Badenian Radiolaria (Dumitrică 1978). Furthermore, the terminal marine influence in the Mesopotamian Basin, marked by the top of the marine Lower Fars, respectively Gahsaran Formations, has been dated in the Zagros foreland to 12.3 Ma (Homke et al., 2004; Böhme et al., 2021). In any case, a marine dispersal of *Vishnuonyx* from Asia to Europe via Mesopotamia could have happened only around 13 Ma during the Konkian, since the Araks Strait was closed before 13.4 (Karaganian regional stage) and after 12.65 Ma (Volhynian regional stage) (Studencka et al. 1998).

This approach, concerning the dispersal path of *Vishnuonyx* towards Central Europe, fits very well with the age of Hammerschmiede, the degree of differentiation in morphology, as well as the combination of the otter semi-aquatic lifestyle and the potential water connection between the Mesopotamian Basin and the Paratethys around 13 Ma. Similarly, a possibly

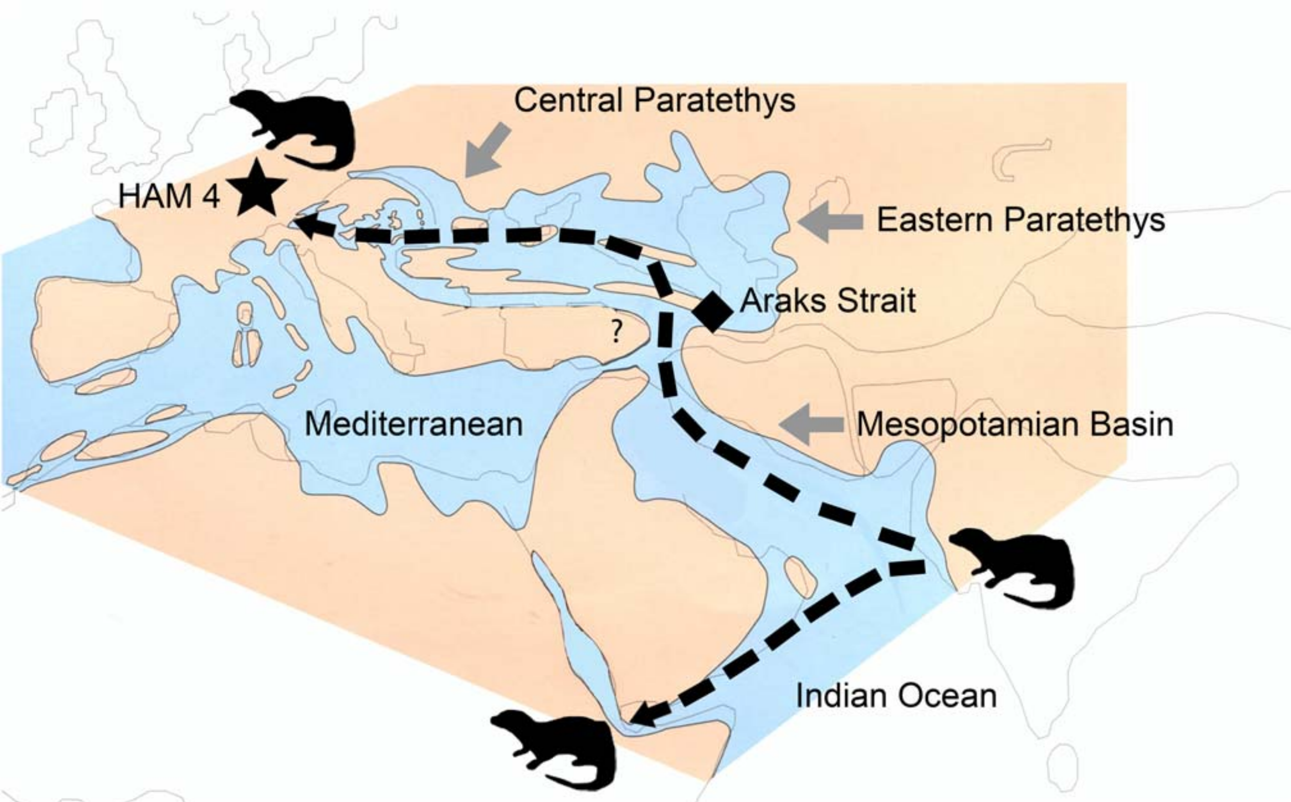

FIGURE 4. The proposed dispersal path of *Vishnuonyx* from South Asia towards Central Europe and East Africa during the Konkian around 13 Ma (late Badenian, early Serravalian). Modified after Rögl (1998) and Popov et al. (2004).

contemporaneous dispersal along the northwestern shorelines of the Indian Ocean into the East African Rift seems plausible.

Dietary Specialization of *Vishnuonyx*

Overall, the jaws and teeth of lutrines are adapted to fulfill two tasks: catching slippery fish and crushing hard items (such as bivalves or crustaceans), and all the extant members of the subfamily feed on both types of food (Friscia et al., 2006; Christiansen and Wroe, 2007). However, the percentages between the two types can fluctuate significantly and this variability can be correlated with the morphology of the post-canine dentition. Commonly, crushing bivalves requires a large occlusal area with several cusps that can create cracks in the shells (e.g., Lucas, 1979; Popowics, 2003; Friscia et al., 2006; Constantino et al., 2011; Hartstone-Rose, 2011). Conversely, catching fish inside the water requires pointy, blade-like teeth that can hang on to the prey (Lucas, 1979; Popowics, 2003; Friscia et al., 2006; Hartstone-Rose, 2011). Some extant lutrines exhibit adaptations that tend more to the former morphology (e.g., the Aonychini or *Enhydra*), while others to the latter (e.g., *Lutra* Brünnich, 1772, *Lontra* Schreber, 1777 or *Pteronura* Gray, 1837) (e.g., Willemsen, 1992; Popowics, 2003; Friscia et al., 2006). In fact, cases of extant otters of these two ecological groups living in the same region have been recorded. A fine example of this dietary partition has been reported from Thailand, where the extant *Lutra perspicillata* (Geoffroy Saint Hilaire, 1826) and *Lutra lutra* (Linnaeus, 1758) are feeding mainly on fish and amphibians, whereas *Aonyx cinereus* (Illiger, 1815) is particularly specialized on crabs (Kruuk et al., 1994). Following this ecomorphological distinction between more piscivorous and more durophagous otters, the teeth of *V. neptuni* sp. nov. seem to be better adapted to the former. Several traits point towards this direction: the mesiodistally narrow M1, the pointed premolars with high and curved main cuspids, the developed accessory cuspid in p4, the high m1 trigonid cusps, the narrow and short m1 talonid, the restricted m1 talonid cusps and the presence of a carnassiform notch between the distal cristid of the protoconid and the mesial cristid of the hypoconid (Crusafont-Pairó and Truyols-Santonja, 1956; Lucas, 1979; Van Valkenburgh, 1989; Van Valkenburgh and Koepfli, 1993; Popowics, 2003; Friscia et al., 2006; Hartstone-Rose, 2011). Additionally, the lower carnassial of SNSB-BSPG 2020 XCIV-0301 exhibits significant horizontal wear in its carnassial blade while the talonid is almost unworn. These hints suggest a diet based mostly on soft tissue/flesh (in that case fish) and less on hard material such as bivalves, crustaceans, or plants (Van Valkenburgh, 1989; Gipson et al., 2000; DeSantis et al., 2017; Schultz et al., 2020). However, extant lutrines exhibit a wide range of diet preferences and no definite suggestions can be made without a multiproxy approach.

Therefore, the attribution of *Vishnuonyx* spp. to the group of bunodont otters is not supported in an ecological sense. On the contrary, it shares several similarities with the living giant otter *Pteronura brasiliensis* (Zimmermann, 1780): strong P4, reduced M1, pointed lower premolars and relatively strong m1. *Pteronura* feeds mostly on fish (Noonan et al., 2017), supporting the indication of a comparable dietary specialization for *Vishnuonyx*.

CONCLUSIONS

The lutrine material from Hammerschmiede published herein, represents a new species of the genus *Vishnuonyx*, *V. neptuni* sp. nov. This record is the westernmost and northernmost occurrence of the genus and the first in Europe. The dispersal event of this South Asian otter is proposed to have happened during the Konkian (13.4–12.65 Ma) through a water connection between the Mesopotamian Basin and the Eastern Paratethys. The dietary specialization of *V. neptuni* sp. nov. is suggested to be focused more on piscivory and less on durophagy.

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Hyaenidae (Carnivora) from the Late Miocene hominid locality of Hammerschmiede (Bavaria, Germany)

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ABSTRACT
The present paper deals with new hyaenid material from the locality of Hammerschmiede (Bavaria, Germany). The described specimens are attributed to two forms: most of the specimens belong to the species *Thalassictis montadai*, whereas one I3 is attributed to a large bone-cracking hyena. The material comes from the layers HAM 5 (11.62 Ma) and HAM 6 (slightly younger than 11.44 Ma) of Hammerschmiede (base of Late Miocene). The species *Thalassictis montadai* is well-known from late Aragonian and early Vallesian localities of central and southern Europe and west Asia. The presented material enables us to make a short review of the state-of-the-art about the fossil record of this species and to discuss its intraspecific variability. A gradual replacement of *Thalassictis montadai, Thalassictis robusta* and *Hyaenictitherium wongii* in Europe is demonstrated, until the arrival of canids during the latest Miocene. Additionally, the upper incisor of the large hyaenid creates some interesting questions concerning the first appearance of the crocutoid hyenas in the fossil record and their dominance over the percrocutoids.

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Introduction

The locality of Hammerschmiede is situated at the Allgäu region at the southwest part of Bavaria, near the small town of Pforzen (Figure 1). The fossiliferous sediments are found in an active clay pit, and represent fluvio-alluvial flood plain deposits. Six different fossil bearing levels have been found in the clay pit, with the majority of the fossils being found at the levels HAM 4 and HAM 5. These levels have been dated to 11.44 and 11.62 Ma respectively (Kirscher et al. 2016). Therefore, the age of the locality is just at the base of the Late Miocene. A preliminary faunal list for the locality has been published by Kirscher et al. (2016) and Böhme et al. (2019), with the most famous taxon being *Danuvius guggenmosi* Böhme et al. (2019), a primitive hominid at the size of a small chimpanzee that included partial bipedalism in its locomotion (Böhme et al. 2019, 2020). The described carnivorans of the locality include *Proputorius sansaniensis* Filhol (1890), *Semigenetta sansaniensis* (Lartet 1851), *Semigenetta grandis* Crusafont Pairó and Golpe Posse (1981) and *Vishnuonyx neptuni* Kargopoulos et al. 2021b)(Mayr and Fahlbusch 1975; Kargopoulos et al. 2021a, 2021b).

The family Hyaenidae Gray (1821) is represented today only by four species: *Crocuta crocuta* (Erxleben 1777), *Hyaena hyaena* (Linnaeus 1758), *Parahyaena brunnea* (Thunberg 1820) and *Proteles cristatus* (Sparrman 1783). However, the fossil record of the family includes a very wide range of body sizes and dietary adaptations (Werdelin and Solounias 1991; Turner et al. 2008; Coca-Ortega and Pérez-Claros 2019). The most primitive hyenas are small-sized, viverrid/herpestid-like genera, like *Protictitherium* Kretzoi (1938), *Plioviverrops* Kretzoi (1938) and *Tungurictis* Colbert (1939). A considerable part of the fossil Hyaenidae consists of the ictitheres (subfamily Ictitheriinae Trouessart (1897) sensu lato), a group of canid-like species that covered the niche of the canids before their arrival in the Old World (Werdelin 1991; Werdelin and Solounias 1991; Wang and Tedford 2008; Coca-Ortega and Pérez-Claros 2019). Finally, the family includes large bone-cracking crocutoid species (subfamily Hyaeninae Gray 1821 sensu stricto), which are represented by three out of the four extant genera (*Crocuta* Kaup 1828; *Hyaena* Brisson 1762; *Parahyaena* Hendey 1974). The fourth extant genus, *Proteles* Geoffroy Saint-Hilaire (1824), is considered to be of more basal phylogenetic affinities, being associated with *Plioviverrops* (Werdelin and Solounias 1991).

The taxonomy and phylogeny of ictitheres have been a matter of debate since their first discovery in the 1840s. Several different schemes have been proposed during the past two centuries. The scheme of Werdelin and Solounias (1991), slightly modified by Turner et al. (2008), suggests a relatively linear phylogenetic tree for the fossil Hyaenidae, with different genera gradually diverging at different ages. On the other Semenov (1989, 2008) identified a split of two lineages: the Ictitheriinae sensu stricto (genera *Ictitherium* Wagner 1848, and *Thalassictis*; Gervais 1850, ex Von Nordmann) and the tribe Hyaenotheriini Semenov (1989) (genera *Hyaenotherium* Semenov 1989, *Hyaenictitherium*; Kretzoi 1938, and *Miohyaenotherium*; Semenov 1989).

The genus *Thalassictis* has been broadly used throughout nomenclatural history in order to describe nearly all the medium-sized canid-like hyenas. The close affinities of the genera *Ictitherium* and *Thalassictis* (discussed in detail by Kurtén 1982) have led to the attribution of the material of *Ictitherium viverrinum* Roth and Wagner (1854), to *Thalassictis robusta* Gervais (1850), ex Von Nordmann, for more than a century (Gaudry 1861; Pilgrim 1931; Viret 1951; Thenius 1966; Schmidt-Kittler 1976). Plenty of material from Europe and Near East, which is now attributed to the genus *Hyaenictitherium*, had also been included to the genus *Thalassictis* (Solounias and de Beaumont 1981; Kurtén 1982; Werdelin 1988). A

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major part of this material was specifically attributed to the species "*Thalassictis hipparionum*' (Gervais 1846) or '*Ictitherium hipparionum*' (Gervais 1846) (Gaudry 1861; Pilgrim 1931; de Beaumont 1964; Crusafont Pairó and Petter 1969; Schmidt-Kittler 1976), a taxon now considered as nomen dubium, because of its missing holotype (Werdelin 1988; Werdelin and Solounias 1991). Even some members of the more derived cursorial hyenas (the group of *Hyaenictis* Gaudry 1861, *Lycyaena* Hensel 1862, and *Chasmaporthetes*; Hay 1921) had been included to the genus *Thalassictis* (Solounias and de Beaumont 1981; Werdelin 1988).

Another genus that had been considered as similar to *Thalassictis* is *Progenetta* Depéret (1892). This genus was used to include the small-sized *Progenetta gaillardi* Forsyth Major (1903), and *Progenetta crassa* (Depéret 1892) (Crusafont Pairó and Petter 1969), which are now attributed to *Protictitherium* (Werdelin and Solounias 1991; Turner et al. 2008; Koufos 2011; Mayda et al. 2015). Additionally it included the medium-sized *Progenetta certa* Forsyth Major (1903), *Progenetta proava* (Pilgrim 1910) and *Progenetta montadai* Villalta Comella and Crusafont Pairó (1943) (Viret 1951; Crusafont Pairó and Petter 1969; Crusafont Pairó and Golpe Posse 1973) that have now been attributed to *Thalassictis* (Werdelin and Solounias 1991; Turner et al. 2008; Mayda et al. 2015).

After years of obscurity, it is now accepted that the genus *Thalassictis* belongs to the Ictitheriinae (sensu Semenov 2008) with *Thalassictis robusta* being its type species (Semenov 1989, 2008; Werdelin and Solounias 1991). However, the subgeneric status of the genus is still problematic. Given the distinction of the genus *Thalassictis* with the Hyaenotheriini, *Ictitherium* and *Lycyaena*, several schemes have been suggested. Werdelin and Solounias (1991) and Turner et al. (2008) included six species in the genus *Thalassictis: T. robusta* Gervais (1850), ex Von Nordmann, '*Thalassictis*' *certa* (Forsyth Major 1903), '*Thalassictis*' *montadai* (Villalta Comella and Crusafont Pairó 1943), '*Thalassictis*' *proava* (Pilgrim 1910), '*Thalassictis*' *sarmatica* (Pavlow 1908) and '*Thalassictis*' *spelaea* (Semenov 1988). On the other hand, Semenov (2008) considered that *T. robusta* is the only species of *Thalassictis*, attributing *T. spelaea* to the genus *Ictitherium*.

The latter form has been attributed to the genus *Ictitherium* by Semenov (1988, 1989, 2008). However, Werdelin and Solounias (1991), Turner et al. (2008) and recently Coca-Ortega and Pérez-Claros (2019) attributed it to the genus *Thalassictis*. The small M1 and M2, reduced M1 metastyle, reduced internal angle between P4 and M1-M2 differentiate this form from *T. robusta*, as described by Kurtén (1982) (Werdelin and Solounias 1991). However, a closer look to the material also indicates a relatively small m1 talonid, with no valley and high m1 paraconid and protoconid cusps, which are characteristics of *Thalassictis*. Herein, this form is referred to as *Thalassictis spelaea*, but a more thorough revision of this material is considered to be essential for the clarification of this form's status.

In this paper, new material of *Thalassictis montadai* and of a large-size hyaenid from the locality of Hammerschmiede is presented. These specimens expand the temporospatial range of both forms in the fossil record of Europe, enabling us to discuss some aspects of intraspecific variability and faunal replacement.

Material and methods

The material was found in the layers HAM 5 and HAM 6 of the Hammerschmiede clay pit. The HAM 5 fluvial channel has been dated to 11.62 Ma (Kirscher et al. 2016). The HAM 6 layer corresponds to a fossiliferous horizon that was excavated by the private collectors Sigulf Guggenmos and Manfred Schmid in the late 1970s and early 1980s and it has been entirely mined today. However, based on their personal communications and the preserved photos and notes from this period, it is reasonable to suggest that this layer had a lens-like structure, it was dominated by proboscidean remains and it was situated slightly above the HAM 4 fluvial channel (11.44 Ma; Kirscher et al. 2016), just below the topmost coal layer (see Figure 1 in Kirscher et al. 2016). Based on general sedimentation rates calculated for the Hammerschmiede locality, the age can be given as 11.42 Ma. More information concerning the location of Hammerschmiede and the detailed stratigraphy of the locality can be found in Kirscher et al. (2016, Figure 1) and Böhme et al. (2019, Extended Data Figure 1). The specimens from HAM 5 come from the ongoing excavations of the University of Tübingen that started in 2011. The studied material is currently stored in the Palaeontological Collection of the University of Tübingen, Germany (GPIT) and is inventoried with numbers of GPIT.

All measurements were taken with a digital calliper and rounded to the first decimal point. Individual measurements in parenthesis indicate approximate measurements. Individual measurements in brackets indicate measurements taken in the

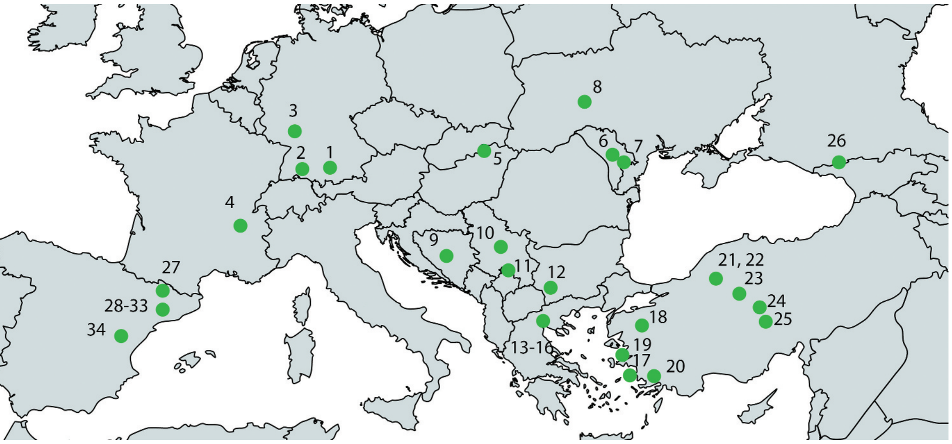

Figure 1. Map depicted the localities of: 1 – Hammerschmiede, 2 – Höwenegg, 3 – Dorn-Dürkheim, 4 – La Grive-Saint Alban, 5 – Rudabánya, 6 – Kishinev, 7 – Kalfa, 8 – Gritsev, 9 – Gračanica, 10 – Brajkovac, 11 – Prebreza, 12 – Oranovo, 13 – Diavata, 14 – Xirochori, 15 – Ravin des Zouaves, 16 – Ravin de la Pluie, 17 – Samos, 18 – Paşalar, 19 – Mordoğan, 20 – Yeni Eskihisar, 21 – Sinap, 22 – Yassiören, 23 – Çandir, 24 – Karain, 25 – Akkaşdaği, 26 – Belometchetskaja, 27 – Ballestar, 28 – Hostalets de Pierola, 29 – Abocador de Can Mata, 30 – Can Ponsic, 31 – Barranc de Can Vila, 32 – Can Barra, 33 – Mars Bernich and 34 – Masia del Barbo.

alveolus. In cases of multiple specimens per element, the description concerns all available material. In the tables, in cases of multiple data, the range, the average and the number of specimens are mentioned. The taxonomic scheme of Turner et al. (2008) was used for intraspecific comparison. The dental nomenclature of Werdelin and Solounias (1991) was used for the descriptions.

Systematic palaeontology

Family Hyaenidae Gray (1821)

Subfamily Ictitheriinae Trouessart (1897)

Genus *Thalassictis* Gervais (1850), ex Von Nordmann

Thalassictis montadai (Villalta Comella and Crusafont Pairó 1943)

Material

HAM 6: associated right p2 and p3 (GPIT/MA/10802). They were found together with some mandibular fragments of no descriptive value. Minimum Number of Individuals = 1. HAM 5: one left p3 (GPIT/MA/12164), one right p3 (GPIT/MA/13726), one left m1 (GPIT/MA/09634) and one right m2 (GPIT/MA/10506). Minimum Number of Individuals = 1.

Description

The second premolar (GPIT/MA/10802; Figure 2A) has two roots with a strong cingulum that ends in two small cuspulids at its mesial and distal ends. The distal cingulum is stronger than the mesial one, with a larger surface of attachment for the following tooth. A blunt distal accessory cuspid is present just mesially to the distal cingulid. A mesial cuspid is absent, but there is a small cingular bulge in the mesiolingual corner of the tooth. The tooth is asymmetrical, as the distal part of the tooth is slightly longer, the mesial cingulum is more developed lingually and the distal cingulum is more extended buccaly. The enamel surface of the tooth is finely wrinkled.

The third premolars (GPIT/MA/10802, GPIT/MA/12164 and GPIT/MA/09634; Figure 2A–C) considerably resemble the morphology of p2, but they are larger. GPIT/MA/12164 is much worn in its main cuspid, whereas GPIT/MA/10802 and GPIT/MA/13726 are unworn. They have two roots with a high main cuspid (which is higher than that of p3), a distal accessory cuspid (slightly lower than that of p3) and a distinct cingulum that surrounds the tooth. The cingulum is stronger in its lingual and distal sides forming two small cuspids in its mesial and distal edges. The position of the mesial cingulid is variable: in GPIT/MA/12164 it is almost in line with the main cuspid and the distal accessory cuspid, in GPIT/MA/13726 it is slightly inclined lingually, whereas in GPIT/MA/10802 it is situated even more lingually. Additionally, the distal crest of the main cuspid in GPIT/MA/10802 is damaged, but an enamel remnant is present close to the tip of the main cuspid, resembling an accessory cuspid.

The only available m1 (GPIT/MA/09634; Figure 2D) is complete, lacking only its roots. It is slightly worn in its shearing blade. It bears a strong cingulum, which is stronger in its mesiobuccal side. The protoconid is the highest cusp. It is distally oriented and separated from the paraconid by a deep notch that reaches approximately the middle of the cuspids height. The paraconid is long and

Figure 2. Material attributed to *Thalassictis montadai*: A – GPIT/MA/10802 right p2 (A1, A3) and p3 (A2, A4) in occlusal (A1, A2) and buccal view (A3, A4); B – GPIT/MA/12164 left p3 in occlusal (B1) and buccal view (B2); C – GPIT/MA/13726 right p3 in occlusal (C1) and buccal view (C2); D – GPIT/MA/09634 left m1 in buccal (D1), lingual (D2) and occlusal (D3) view; E – GPIT/MA/10506 right m2 in occlusal view.

robust and its mesial tip is slightly bent distally. The metaconid is developed, slender and slightly lingually bent. It is situated at the distolingual edge of the protoconid. The talonid is short, hosting a large hypoconid, a smaller entoconid and a reduced hypoconulid. The latter two cuspids are situated at the distal cingulum. A small valley is formed between the entoconid and the metaconid. The enamel surface of the tooth is more wrinkled in its buccal part.

The second lower molar (GPIT/MA/10506; Figure 2E) is subtrapezoidal in shape. Its lingual part is semi-circular, whereas its buccal side is almost straight. Four cuspids are present and the buccal cuspids are far larger than the lingual ones. The protoconid is the largest cuspid, situated in an elevation of the mesial cingulum. It is divided from the hypoconid by a wide opening. The hypoconid is the second-largest cuspid. It is situated in the distobuccal part of the cingulum and it is vertical. The metaconid is the smallest cuspid, situated slightly distally in relation to the protoconid. The entoconid is damaged and it is situated relatively close to the hypoconid. The two latter cuspid are separated distally by a notch in the cingulum. No signs of a paraconid or a hypoconid are present. A valley is formed at the centre of the tooth, being expanded between the protoconid and the hypoconid.

Comparison

The cheek teeth from Hammerschmiede are clearly larger than those of *Protictitherium, Plioviverrops* and *Tunguritis* (Colbert 1939; Schmidt-Kittler 1976; Torre 1989; Coca-Ortega and Pérez-Claros 2019). The specimens are relatively smaller in comparison to the genera *Lycyaena, Chasmaporthetes, Hyaenictis* and the crocutoid hyaenas (Werdelin 1988; Antón et al. 2007; Tseng et al. 2013; Vinuesa et al. 2017; Coca-Ortega and Pérez-Claros 2019). The premolars are relatively high, sharp and robust and the lower carnassial has a high and long blade and a short talonid, so the genus *Ictitherium* and the species *T. spelaea* are also excluded (Kurtén 1982; Semenov 2008). The relatively developed m1 talonid (with a hypoconid, a hypoconulid, an entoconid and a lingual valley) together with the not reduced m2 (with four cuspids and a central valley) differentiate the presented specimens from the group of *Hyaenotherium, Hyaenictitherium* and *Miohyaenotherium* (Semenov 1989, 2008). Therefore, the presented material is attributed to the genus *Thalassictis* (sensu lato; sensu Turner et al. 2008), given its resemblance in the form of the distal accessory cuspid of p3, the degree of development of the m1 talonid and the m2 as well as in the metrical characteristics.

The differentiation between the six described forms of this genus is not very clear. However, a metrical comparison is enough to demonstrate some distinctions (Tables 1 and 2; Figures 3 and 4). The species *T. certa* (based on material from La Grive-Saint Alban, France; Viret 1951), *T. proava* (based on material from Chinji and China; Pilgrim 1932), *T. spelaea* (based on material from Akkaşdaği, Turkey; de Bonis 2005) and *T. robusta* (based on material from Kishinev, Höwenegg and Dorn-Dürkheim, Ukraine and Germany; de Beaumont 1986; Semenov 1989; Morlo 1997) are considerably smaller than *T. montadai* (from the localities Hostalets de Pierola, Can Barra, Ballestar, Loc. 94 of Sinap and Yeni Eskihisar, Spain and Turkey; Crusafont Pairó and Golpe Posse 1973; Schmidt-Kittler 1976; Viranta and Werdelin 2003) and the specimens from Hammerschmiede (Tables 1 and 2). The holotype of *T. proava* is considerably worn (Pilgrim 1932, Pl. 5, Figure 6). However, it can be noted that the m1 talonid is relatively shorter than in GPIT/MA/09634, especially in the distance between the protoconid and the hypoconid. The type species, *T. robusta*, differs morphologically from the Hammerschmiede specimens in the larger distal accessory cuspid of p4, the higher m1 entoconid, the lower m1 paraconid,

Table 1. Metrical comparison of the *Thalassictis montadai* premolars from Hammerschmiede with other material of the genus. Data from: [1]Crusafont Pairó and Golpe Posse (1973), [2]Viranta and Werdelin (2003), [3]Schmidt-Kittler (1976), [4]Semenov (1989), [5]Wang et al. (1998), [6]Semenov (1988), [7]de Bonis (2005), [8]de Beaumont (1986) and [9]Viret (1951).

Premolar	Species	Locality	Code	L	W	W/L
p2	*T. montadai*	HAM 6	GPIT/MA/10802	16.5	8.5	52%
		Hostalets de Pierola[1]	-	14.5	8.0	55%
		Can Barra[1]	-	14.1	-	-
		Ballestar[1]	-	16.6	8.4	51%
		Loc. 94 Sinap[2]	AS.92.463	15.1	8.6	57%
		Loc. 94 Sinap[2]	AS.92.464	15.7	8.1	52%
		Yeni Eskihisar[3]	BSPM-1968 VI 772	17.0	8.0	47%
	T. robusta	Kishinev[4]	-	11.0	5.0	45%
	T. proava	Botamoyin[5]	IVPP V7733	9.8	5.0	51%
	T. spelaea	Gritsev[6]	-	9.6–11.7 10.8 (6)	4.7–5.8 5.3 (7)	-
		Akkaşdağı[7]	AKK-11	11.8	5.7	48%
p3	*T. montadai*	HAM 6	GPIT/MA/10802	18.3	10.2	56%
		HAM 5	GPIT/MA/12164	18.8	10.3	55%
		HAM 5	GPIT/MA/13726	18.5	9.8	53%
		Hostalets de Pierola[1]	No Nu	16.5	9.0	55%
		Can Barra[1]	No Nu	17.5	-	-
		Ballestar[1]	No Nu	17.5	10.0	57%
		Loc. 94 Sinap[2]	AS.92.463	17.4	10.0	57%
			AS.92.464	17.4	10.3	59%
		Yeni Eskihisar[3]	BSPM-1968 VI 772	19.4	10.3	53%
	T. robusta	Kishinev[4]	-	13.3–14.5 13.9 (3)	6.5–6.7 6.6 (3)	-
		Höwenegg[8]	Hö27	14.6	7.0	48%
	T. certa	La Grive[8]	LGr 1327	13.9	-	-
	T. proava	Botamoyin[5]	IVPP V7733	12.1	6.2	51%
	T. spelaea	Gritsev[6]	-	12.8–15.3 13.7 (8)	6.2–7.1 6.6 (8)	
		Akkaşdağı[8]	AKK-11	13.5	7.1	53%

Table 2. Metrical comparison of the *Thalassictis montadai* molars from Hammerschmiede with other material of the genus. Data from: [1]Crusafont Pairó and Golpe Posse (1973), [2]Viranta and Werdelin (2003), [3]Schmidt-Kittler (1976), [4]Mayda et al. (2015), [5]Semenov (1989), [6]de Beaumont (1986), [7]Morlo (1997), [8]Viret (1951), [9]Peigné (2016), [10]Wang et al. (1998), [11]Semenov (1988), [12]de Bonis (2005).

Molar	Species	Locality	Code	L	W	W/L
m1	*T. montadai*	HAM 5	GPIT/MA/09634	21.5	10.5	49%
		Hostalets de Pierola[1]	No Nu	20.5	10.2	50%
		Can Barra[1]	No Nu	19.4	10.0	52%
		Ballestar[1]	No Nu	22.1	9.8	44%
		Loc. 94 Sinap[2]	AS.92.463	23.4	10.5	45%
			AS.92.464	22.8	10.1	44%
		Yeni Eskihisar[3]	BSPM-1968 VI 772	23.3	10.1	43%
				23.3	10.2	44%
	T. cf. *montadai*	Çandır[4]	PV-2675	23.9	9.2	38%
	T. robusta	Kishinev[5]	-	16.7–18.3	7.5–8.2	-
				17.5 (4)	7.9 (4)	
		Höwenegg[6]	Hö27	17.2	7.8	45%
		Dorn-Dürkheim[7]	DD 3495	16.0	7.0	44%
			DD 3544a	(14.3)	(6.8)	48%
	T. certa	La Grive[8]	LGr 1330	17.8	8.9	50%
	T. proava	Chinji[9]	GSI D 126	15.6	8.1	52%
			GSI D 233	16.5	7.8	47%
		Ganqikair[10]	IVPP V7734	13.8	7.5	54%
		Duolebulejin[10]	IVPP V11499	16.6	8.1	49%
	T. spelaea	Gritsev[11]	-	15.0–18.1	7.5–9.1	
				16.8 (7)	8.3 (7)	
		Akkaşdağı [12]	AKK-11	18.6	8.8	47%
m2	*T. montadai*	HAM 5	GPIT/MA/10506	6.8	5.1	75%
		Hostalets de Pierola[1]	No Nu	[6.0]	[4.5]	75%
		Can Barra[1]	No Nu	[6.0]	[5.0]	83%
		Ballestar[1]	No Nu	[6.9]	[4.2]	61%
		Loc. 94 Sinap[2]	AS.92.464	5.6	5.2	93%
		Yeni Eskihisar[3]	BSPM-1968 VI 772	5.9	5.4	92%
	T. robusta	Höwenegg[6]	Hö27	[6.3]	-	-
		Dorn-Dürkheim[7]	DD 4697	7.0	5.6	80%
	T. spelaea	Gritsev[11]	-	5.6–6.7	4.6–5.5	-
				6.3 (7)	5.0 (7)	

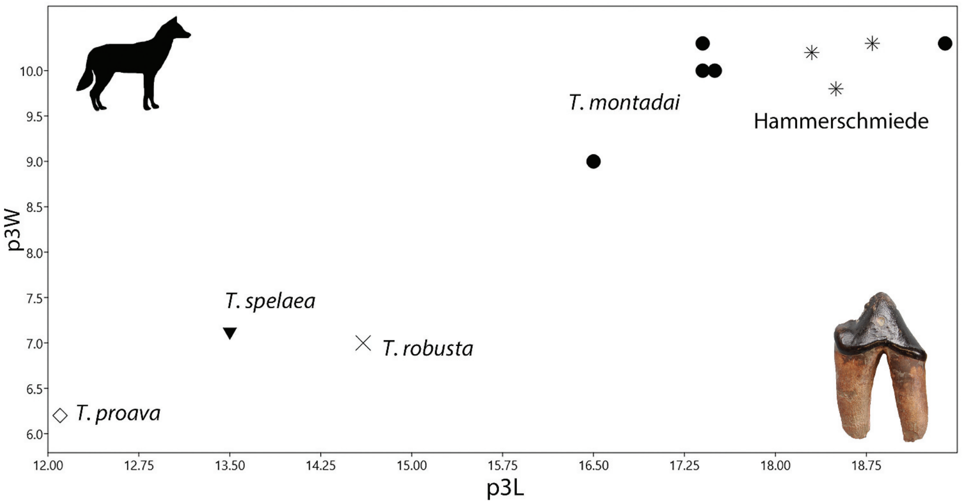

Figure 3. Comparison of p3 dimensions of several species of *Thalassictis*: stars – Hammerschmiede specimens of *Thalassictis montadai*; dots – other *Thalassictis montadai* specimens; X – *Thalassictis robusta*; Inverted triangle – *Thalassictis spelaea*.

the more vertical and robust m1 metaconid and the more enhanced lingual m1 cingulum (Kurtén 1982; Morlo 1997). Additionally, the species *T. certa* is characterised by higher and more robust cuspids (including the main and accessory cuspid of p3 and the trigonid and talonid cuspids of m1) resembling a more crocutoid-like morphology (Viret 1951, Pl. 1, figs. 12–15). The species *T. sarmatica* is known only from upper dentition from Kishinev (Pavlow 1908), but Pilgrim (1931) clearly states that this species is only slightly larger than *T. robusta*. Therefore, it can be deduced that it should be included in the size group of *T. certa*, *T. spelaea*, *T. proava* and *T. robusta*, thus, smaller than *T. montadai* and the present specimens. Therefore, the presented specimens are identified as *T. montadai*, based on their large size and the morphology of the preserved cuspids.

Hyaenidae indet.

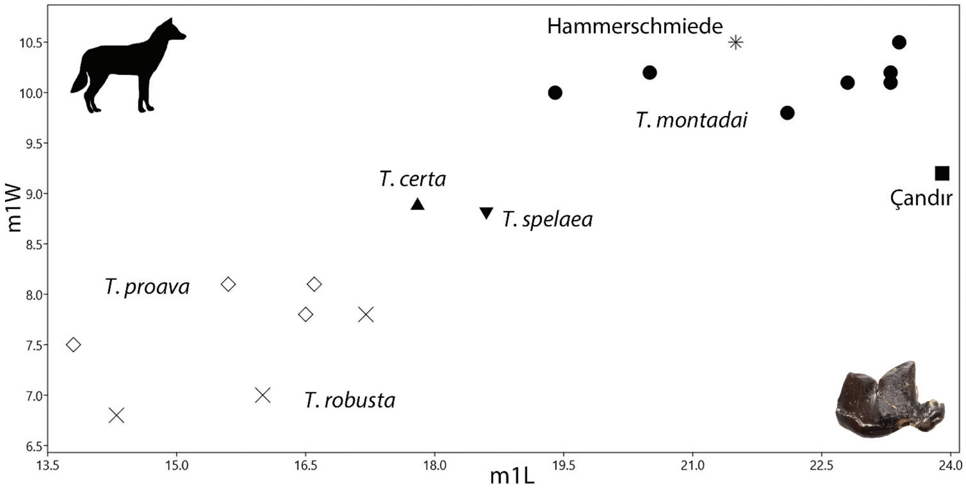

Figure 4. Comparison of m1 dimensions of several species of *Thalassictis*: star – Hammerschmiede m1 of *Thalassictis montadai*; dots – other *Thalassictis montadai* specimens; square – *Thalassictis* cf. *montadai* from Çandir; Triangle – *Thalassictis certa*; Inverted triangle – *Thalassictis spelaea*; Diamond – *Thalassictis proava*; X – *Thalassictis robusta*. Data sources as in. Table 2

Material: HAM 5: one left I3 (GPIT/MA/12147). Minimum Number of Individuals = 1

Description

The specimen GPIT/MA/12147 (Figure 5) is a complete left I3 of a crocutoid hyena. The root is robust ending mesially to a blunt hook. The crown is short and robust. It bears two facets of strong wear, a large one occupying a major part of its buccal surface and a small one in its lingual side, caused by the friction with c and I2 respectively. The larger facet is confluent with a facet at the tip of the tooth. The buccal facet also reveals well-developed Hunter-Schreger bands in the enamel of the tooth. No signs of a cingulum, crest or any other structure are exhibited.

Comparison

Unfortunately, this is the only element found so far in Hammerschmiede that can be attributed to this larger form, so its identification is problematic. However, the size of this tooth is larger than that of the extant spotted hyenas, based on the dataset

Figure 5. The described I3 of the large hyaenid form (GPIT/MA/12147).

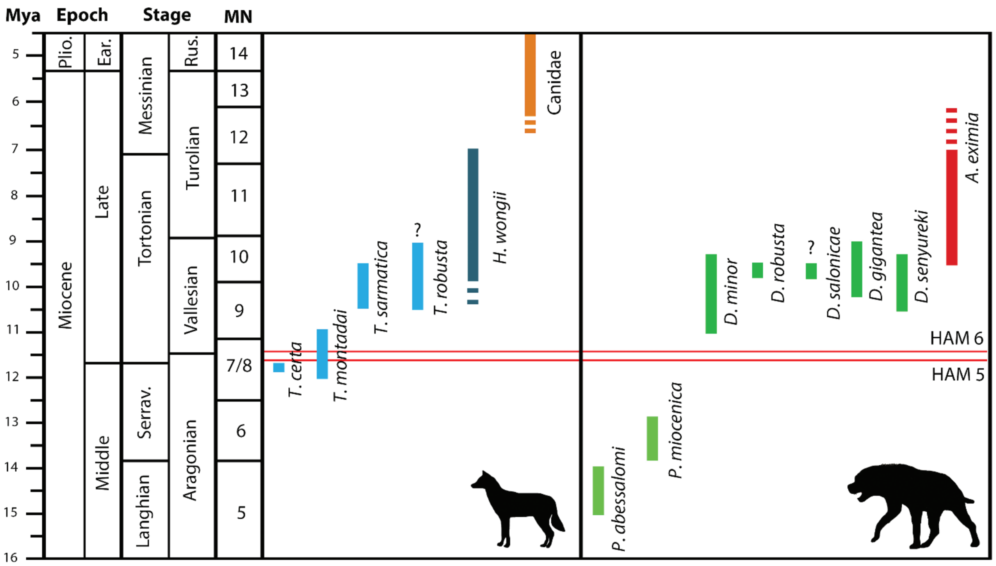

Figure 6. The stratigraphical replacements of the large ictitheres and crocutoid hyenas in Europe and Anatolia between the Middle Miocene and Early Pliocene. Data from: Schmidt-Kittler (1976), Werdelin and Solounias (1991), Spassov and Koufos (2002), Viranta and Werdelin (2003), Turner et al. (2008), Vangengeim and Tesakov (2013) and NOW (2021). Question marks indicate the doubtful identification in Dorn-Dürkheim for *T. robusta* and the unknown stratigraphy for *D. salonicae*. Dashed lines indicate sporadic occurrences.

of Beke (2010) (Table 3). *Thalassictis montadai* is in general smaller than *Crocuta*, so this incisor cannot be attributed to the previously discussed species. Additionally, the species *Allohyaena sarmatica* Semenov (1994), from Gritsev (Ukraine), is also smaller than *C. crocuta* based on m1L (24.8 mm for *A. sarmatica* and 27.3 ± 1.80 mm for *Crocuta*; Semenov 1994; Beke 2010). *Dinocrocuta gigantea* (Schlosser 1903) is a form that is known from China, Turkey, Greece, Bulgaria, Moldova, Georgia and Ukraine (Koufos 1995; Spassov and Koufos 2002; Vangengeim and Tesakov 2013; Koufos et al. 2018; Xiong 2019 and references therein). An incisor of this species from Oranovo (Spassov and Koufos 2002) is clearly larger than the present specimen, while a specimen from Laogaochuan (Zhang and Xiangxu 1996) is more similar to the Hammerschmiede specimen (Table 3). Additionally, the species *Dinocrocuta salonicae* Andrews (1918) (known only from upper dentition from the Vallesian of Diavata in Greece) is also similar in size with *D. gigantea* (Howell and Petter 1985). The dimensions of the Hammerschmiede incisor indicate that it most probably belongs to a hyena of intermediate size between *Crocuta* and *D. gigantea* from Oranovo (Table 3). An I3 published by Schmidt-Kittler (1976) as *Dinocrocuta senyureki* Ozansoy (1961), is of similar dimensions with GPIT/MA/12147 (Table 3). However, judging from P4L, *D. senyureki* is comparable in size to *D. gigantea* (Howell and Petter 1985), so a clear distinction is not possible. Additionally, the species *Dinocrocuta robusta* (Lungu 1978) (from Kalfa in Moldova) belongs to the same size group as *D. senyureki* (p4L = 27.0–28.0 mm; Lungu 1978; Radović et al. 2021), so it can also be considered as possible for the attribution of the described incisor. Finally, Ozansoy (1965) identified the species *Dinocrocuta minor* (Ozansoy 1965) at the late Aragonian localities of Yassiören and Yeni-Eskihisar in Turkey. This form is also relatively small in size (but smaller than *D. senyureki* and *D. robusta*; Radović et al. 2021) and it cannot be excluded from the comparison.

The genus *Percrocuta* Kretzoi (1938), is represented in the European fossil record by two species. The older species (known from the locality of Belometchetskaja in Georgia, MN 5; Gabunia 1973) is *Percrocuta abessalomi* (Gabunia 1973), whereas the younger species (known from several Anatolian and Balkans localities, such as Prebreza, Brajkovac, Gračanica, Mordoğan and Paşalar; Pavlović and Thenius 1965; Kaya et al. 2003; Bastl et al. 2020; Radović et al. 2021) is *Percrocuta miocenica* (Pavlović and Thenius 1965). However, both these species are relatively smaller in size than the middle-sized *Dinocrocuta* (Radović et al. 2021), so it is not very probable that the present specimen might belong to one of them.

The dimensions also fit with that of *Adcrocuta eximia* from Samos (Greece) (NHMW 1912/0004/0003, Table 3). This is one of the most common hyaenids in the Turolian of Europe (Werdelin and Solounias 1990, 1991). However, the first appearance of this form in the fossil record is at the late Vallesian (MN 10) of Xirochori (Greece; possibly the oldest occurrence of the species), Ravin des Zouaves 1 (Greece), Ravin de la Pluie (Greece), Karain (Turkey) and Masia del Barbo (Spain) (Koufos 1979, 2000, 2012; Turner et al. 2008). Therefore, due to the significant temporal

Table 3. Comparison of I3 measurements of the Hammerschmiede specimen with *Adcrocuta eximia, Dinocrocuta gigantea* and *Crocuta crocuta*. Data from: ^{1}personal data, ^{2}Spassov and Koufos (2002), ^{3}Zhang and Xiangxu (1996), ^{4}Schmidt-Kittler (1976) and ^{5}Beke (2010).

Tooth	Species	Locality	Code	L	W
I3	HAM5		GPIT/MA/12147	15.7	12.2
	A. eximia	Samos	1912/0004/0003^1	15.0	11.9
	D. gigantea	Oranovo	FM1500^2	18.0	13.5
		Laogaochuan	No Nu^3	16.2	12.3
	D. senyureki	Inönu	711^4	15.3	12.3
	Crocuta crocuta		summed^5	mean = 12.0 SD = 1.12 (26)	mean = 9.1 SD = 1.34 (26)

distance of over 2 million years between Hammerschmiede and MN10 (the best dated locality is Masia del Barbo of 9.3 Ma; van Dam 1997) and the presence of only one I3, it is not possible to attribute the specimen to *Adcrocuta*.

Until further remains of this form are found in Hammerschmiede, it is preferred to refer to it as Hyaenidae indet. ‘large form’.

Discussion

Since the original description of *T. montadai* by Villalta Comella and Crusafont Pairó (1943) based on material from Hostalets de Pierola, several new specimens have been published from other localities revealing a range of morphotypes. Crusafont Pairó and Golpe Posse (1973) were the first to notice a noteworthy intraspecific variability of *T. montadai*, creating three subspecies: *T. m. montadai* from Hostalets de Pierola, *T. m. vallesiensis* from Can Barra and *T. m. urgellensis* from Ballestar. Viranta and Werdelin (2003) published some large-sized material from the Loc. 94 (10.55 Ma) in Sinap (Turkey). Additionally, Schmidt-Kittler (1976) published some specimens from Yeni Eskihisar (Turkey), which are dated as Aragonian (Andrews et al. 1980). The species has also been reported in the faunas of Abocador de Can Mata (Spain; Alba et al. 2006), Can Ponsic (Spain; Crusafont Pairó and Kurtén 1976), Barranc de Can Vila 1 (Spain; Robles 2014), Mars Bernich (Spain; Robles 2014), Kalfa (Moldova; Lungu and Rzebik-Kowalska 2011) and Rudabánya (Hungary; as *T.* cf. *montadai*; Werdelin 2005). All these localities are characterised by their typical MN 7/8 and MN 9 faunas and their chronologic range can be given from 12 to 9.7 Ma.

The specimens described as *T.* cf. *montadai* from Çandir (Turkey) were dated as MN 5 or MN 6 (Mayda et al. 2015). Therefore, they represent the oldest report of a form that is related to *T. montadai*. However, Mayda et al. (2015) noted that the mandible from Çandir has more slender teeth (W/L ratio was 41% for p4 and 38% for m1) than the Spanish material (56% and 50% respectively for the holotype). It must also be noted that this specimen is the largest known specimen related to *T. montadai*, with a very long p4 in relation to m1 and that the accessory cuspids of p4 are far more developed than in the holotype and the Hammerschmiede material. Therefore, given also the age of the material, its attribution to the species is (as also Mayda et al. 2015 suggest) doubtful.

The specimens from Hammerschmiede are relatively large-sized fitting better to the specimens from Ballestar (Tables 1 and 2). The latter material has been attributed by Crusafont Pairó and Golpe Posse (1973) to the subspecies *T. m. urgellensis*, which is characterised by the long and narrow p2, long and wider p3, the longer m1 talonid, the absent distal cingulum in m1 and the longer and narrower m2. The characteristics of p2 and the significant length of p3 and m2 are evident in the Hammerschmiede material. However, the p3W/p3L seems to be variable in the three described specimens, the m1 talonid is relatively short (30% of m1L), the m1 distal cingulum is present (although faint) and m2 is relatively wide. Therefore, the attribution to this subspecies is doubtful. On the contrary, the variability seen in the Hammerschmiede specimens (even in the specimens only from HAM 5) indicates that the differentiation of the three aforementioned subspecies is not very clear.

In general, this species seems to be present in the fossil record of Europe and West Asia during the late Aragonian and early Vallesian (Werdelin and Solounias 1991; Turner et al. 2008). Robles (2014) stated that in the fossil record of Valles Penedes Basin, the species *T. montadai* is replaced by *T. robusta* during the late Vallesian. The latter species remains the dominant *Thalassictis* in Europe until MN 11 (Dorn-Dürkheim, Germany; Morlo 1997; Turner et al. 2008). However, the presence of this form in Dorn-Dürkheim has been questioned, restricting its secure stratigraphic range in MN9 (Werdelin and Solounias 1991; Turner et al. 2008). In the Turolian, this niche (resembling more the niche of today’s coyotes and wolves) is mostly covered by the species *Hyaenictitherium wongii* (Zdansky 1924). This form has been reported mainly from the MN10–MN12 of Europe (Turner et al. 2008), with the addition of two specimens from Höwenegg (de Beaumont 1986). The comparison between Vallesian and Turolian forms is biased by the geographical distribution of the known localities, as the Turolian faunas of Europe are mainly known from the south (Greco-Iranian Province), whereas the fossil record for central Europe is far more restricted. Finally, by the end of the Late Miocene, the arrival of canids took place in Europe, leading to their permanent establishment during the Pliocene (Wang and Tedford 2008; Böhme et al. 2021, Suppl. p. 24).

Finally, despite the present incapability of attributing the large I3 to a known genus, it is noteworthy that a large species of hyena existed in Hammerschmiede. Until the Vallesian, the percrocutoid hyenas (together with the amphicyonids) were covering the niche of the bone-cracking scavengers-hunters (Werdelin 1991; Werdelin and Solounias 1991) and it is possible that the herein described incisor might belong to a species of this group (*D. senyureki, D. robusta, D. minor* or another species). In that case, the age of Hammerschmiede closes the gap in the fossil record of percrocutids in central Europe (Figure 4), as *D. minor* is known only from Anatolia.

The oldest form of a crocutoid hyaenid in the fossil record is *Adcrocuta* and, since then, a continuum of large bone-cracking forms relented until the caveF hyenas of the Late Pleistocene (Turner et al. 2008). However, the exact forces that led the replacement of percrocutids by the crocutoids are still unresolved. If future studies reveal that the herein described tooth belongs to a true hyaenid, and not to a new small form of a percrocutoid, it is reasonable to suggest that the root of the discussed replacement probably took place considerably before the late Vallesian. Additionally, the amphicyonids (vernacularly called as ‘bear-dogs’) also started to decline by the beginning of the Vallesian (Ginsburg 1999). These faunal changes can be interpreted as factors that enabled the dominance of crocutoid hyenas in Europe from the Vallesian until the Late Pleistocene.

A depiction of the aforementioned replacements on the ictitheres and crocutoid hyenas of Europe can be seen in Figure 4. It is demonstrated that a gradual sequence on the wolf niche includes: *T. montadai, T. robusta, H. wongii* and the canids, whereas the niche of the large-sized bone-crackers includes *P. abessalomi, P. miocenica, D. minor*, the four Vallesian *Dinocrocuta* species and finally *A. eximia*. It must be mentioned that Howell (1987) has reported the presence of a percrocutid from Sahabi as ‘*Percrocuta* aff. *senyureki*’. However, based on the very fragmentary nature of these two specimens and the considerable age difference between Sahabi (7.3–7.2 Ma; Böhme et al. 2021, Suppl. p. 15) and the oldest verified occurrence of percrocutids, this attribution is herein considered doubtful.

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Disclosure statement

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PLOS ONE

RESEARCH ARTICLE

The exceptionally high diversity of small carnivorans from the Late Miocene hominid locality of Hammerschmiede (Bavaria, Germany)

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Abstract

The present study deals with new material of carnivorans (Mustelidae, Mephitidae, Ailuridae, Potamotheriinae and Viverridae) from the basal Tortonian (Late Miocene, late Astaracian) hominid-bearing locality of Hammerschmiede (Bavaria, Germany). The small carnivoran fauna includes 20 species belonging to nine different subfamilies (Guloninae, Lutrinae, Mellivorinae, Potamotheriinae, Leptarctinae, Mephitinae, Simocyoninae, Genettinae and Viverrinae). The identified forms include: "*Martes*" *sansaniensis*, "*Martes*" cf. *munki*, "*Martes*" sp., *Circamustela hartmanni* n. sp., *Laphyctis mustelinus*, Guloninae indet., *Eomellivora moralesi*, *Vishnuonyx neptuni*, *Paralutra jaegeri*, *Lartetictis* cf. *dubia*, *Trocharion albanense*, *Palaeomeles pachecoi*, *Proputorius sansaniensis*, *Proputorius pusillus*, *Alopecocyon goeriachensis*, Simocyoninae indet., *Potamotherium* sp., *Semigenetta sansaniensis*, *Semigenetta grandis* and *Viverrictis modica*. The new species *Circamustela hartmanni* n. sp. is differentiated from the other members of the genus by its small size and the morphology of its dental cusps in the upper and lower carnassials. This is one of the highest reported taxonomic diversities for fossil small carnivorans in the Miocene of Europe, including also first and last occurrences for several genera and species. Additionally, the assemblage comprises some rare taxa such as *Palaeomeles pachecoi* and *Eomellivora moralesi*. An ecomorphological comparison of the discovered taxa reveals possible cases of competition and niche partitioning.

Introduction

The locality of Hammerschmiede, situated near the small town of Pforzen (southwest Bavaria, Germany), has been known for its Miocene fluvio-alluvial fossiliferous sediments for nearly

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half a century. At least six different fossiliferous levels have been found in the clay pit, with the majority of fossils being found at the fluvial channels HAM 4 and HAM 5. These two channel fillings have been dated to 11.44 and 11.62 Mya respectively [1]. During these fifty years of studies, several publications have been conducted, revealing an extraordinary faunal assemblage of mammals, birds, reptiles, amphibians, fish, molluscs, and plants [1–23]. The species *Danuvius guggenmosi* Böhme et al., 2019 [16], a great ape that is suggested to have practiced bipedalism in its locomotion, has brought the locality in the spotlight [16, 24, 25].

The datum of the carnivorans of the locality was firstly investigated by [4], who reported the presence of *Proputorius sansaniensis* Filhol, 1890 [26] and *Proputorius pusillus* (Viret 1951) [27] (as "*Martes pusillus*") in the HAM 1 layer. Later, [1] and [16] published a preliminary faunal list for the locality, reporting carnivorans of several families. The present article is a part of a detailed review of the carnivoran fauna of the locality that has started recently with the publications of [21–23], reporting the discovery of the viverrids *Semigenetta sansaniensis* [28] and *Semigenetta grandis* Crusafont Pairó & Golpe Posse, 1981 [29]; the new otter species *Vishnuonyx neptuni* Kargopoulos et al., 2021 [22]; the ictithere *Thalassictis montadai* Villalta Comella & Crusafont Pairó, 1943 [30] and a large hyaenid.

The aim of this article is to present new material of the groups Mustelidae Batsch, 1788 [31], Mephitidae Bonaparte, 1845 [32], Ailuridae Gray, 1843 [33], Potamotheriinae Willemsen, 1992 [34] and Viverridae Gray, 1821 [35] from the locality of Hammerschmiede. The specimens belonging to the genus *Circamustela* Petter, 1967 [36] are here attributed to a new species. An ecomorphological comparison between the discussed forms is conducted, in order to reveal the possible intraspecific interactions, such as competition or niche partitioning.

Material and methods

Material

The specimens studied herein come from the fluvial channels HAM 1, HAM 4 (11.44 Ma), and HAM 5 (11.62 Ma) of the locality of Hammerschmiede (Bavaria, Germany). The material from HAM 1 corresponds to the material published by [4]. This material has been reviewed and some specimens were attributed to different taxa. The incisors published by [4] were not included in the present manuscript, because determination on species level was not possible, due to the lack of diagnostic characters. The exact age of HAM 1 is not known, but based on the details given by [4] [the sediment description as greenish-grey marl with aquatic gastropods, the given thickness of the horizon (50 cm) and the topographic height (ca. 680 m a.s.l.)] a lateral correlation to HAM 5 can be assumed. The material from HAM 4 and HAM 5 has been unearthed during the excavations held by the Eberhard-Karls University of Tübingen between 2011 and 2021. All the material is currently stored in the Palaeontological Collection of the University of Tübingen, Germany (GPIT), and is inventoried with numbers of both GPIT (for excavations from 2011 to 2019) and SNSB-BSPG (for excavations of 2020 and 2021). No permits were required for the described study, which complied with all relevant regulations. More information about the geographic position and the stratigraphy of the locality can be found in [1, 16].

Methods

The term "small carnivorans" is used in the sense given by [37]. Dental nomenclature follows [38] and [39]. All measurements were taken with a digital caliper and rounded to the first decimal point. In cases of multiple skeletal specimens per element for a single species, the descriptions and comparisons concern all the available specimens. In cases of multiple data for a form in the tables, the range, average value and number of specimens are mentioned. Single measurements in square brackets indicate that they have been taken at the alveolus, whereas single measurements in a parenthesis indicate that they were taken in approximation due to specimen damage.

Institutional Abbreviations: **GPIT:** Palaeontological collection of the University of Tübingen, Tübingen, Germany; **ICP:** Institut Català de Paleontologia, Barcelona, Spain; **MHNL:** Muséum d'histoire naturelle de Lyon, Lyon, France; **MNHN:** Muséum national d'Histoire naturelle, Paris, France; **NHMUK:** Natural History Museum, London, United Kingdom; **NMA:** Naturmuseum der Stadt Augsburg, Augsburg, Germany; **NHMW:** Naturhistorisches Museum Wien, Vienna, Austria; **SMNS:** Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; **SNSB-BSPG:** Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **UCBL:** Université Claude-Bernard Lyon I, Villeurbanne, France.

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSID for this publication is: urn:lsid:zoobank.org:pub:B09DB8CD-3CA3-48F9-ACAA-B6AB27001A44. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central and LOCKSS.

Results

Order Carnivora Bowdich, 1821 [40]
Suborder Caniformia Kretzoi, 1943 [41]
Family Mustelidae Batsch, 1788 [31]
Subfamily Guloninae Gray, 1825 [42]
Genus *Martes* Pinel, 1792 [43]
Type species: *Martes foina* (Linnaeus 1758) [44]

Remarks: The genus *Martes* in its traditional sense includes several dozens of extant and fossil species (e.g., [38]). Recently, [45] demostrated that small marten-like mustelids from the Early and Middle Miocene of Eurasia show a dissimilar morphology with *Martes* and adscribed them to "*Martes*". These mustelids are: "*Martes*" *laevidens* Dehm, 1950 [46], "*Martes*" *sainjoni* (Mayet, 1908) [47], "*Martes*" *munki* Roger, 1900 [48], "*Martes*" *delphinensis* Depéret, 1892 [49], "*Martes*" *burdigaliensis* de Beaumont, 1974 [50], "*Martes*" *collongensis* Roth and Mein, 1987 [51], "*Martes*" *cadeoti* Mein, 1958 [52], "*Martes*" *sansaniensis* (Lartet, 1851) [28], "*Martes*" *filholi* (Depéret, 1887) [53], *Aragonictis araid* Valenciano et al., 2022 [45], "*Martes*" *woodwardi* Pilgrim, 1931 [54], "*Martes*" *jaegeri* (Schlosser, 1902) [55], "*Martes*" *lefkonensis* Schmidt-Kittler, 1995 [56], "*Martes*" *anderssoni* Schlosser, 1924 [57], "*Martes*" *melibulla* Petter, 1963 [58], "*Martes*" *basilii* Petter, 1964 [59], "and "*Martes*" *leporinum* (Khomenko, 1914) [60]. These forms are in need of a thorough taxonomical revision, which is beyond the scope of the present article. For practical issues we refer to all these Miocene forms as "*Martes*", following [61], although [45, 62] suggested that some Late Miocene forms can be classified as *Martes*. The species *Mustela transitoria* Gaillard, 1899 [63] has been considered as related to the aforementioned forms, but it has now been transferred to its own genus: *Gaillardina*

Ginsburg, 1999 [38]. The two most commonly discussed extant species of the genus are *Martes martes* (Linnaeus, 1758) [44] and *Martes foina* (Erxleben, 1777) [64].

"*Martes*" *sansaniensis* (Lartet, 1851) [28]

Lectotype: MNHN Sa 755, a left hemimandible with the roots of p3 and the p4 & m1.

Type Locality: Sansan (France).

Referred Specimens: HAM 4: GPIT/MA/10959, skull; SNSB-BSPG-2020 XCIV-4065, right P4; GPIT/MA/16963, right P4. HAM 5: GPIT/MA/16349, left P4; GPIT/MA/09882, left M1; GPIT/MA/12308, right M1.

Description: The specimen GPIT/MA/10959 (Figs 1A and 2A) is an almost complete skull, lacking only parts of the zygomatic arches and being dorsoventrally compressed at the palate and slightly damaged at the right auditory region and the postorbital processes. The skull is relatively long and narrow. The external narial aperture is deformed, but it seems to be high, wide and M-shaped. The anterior palatine foramina are short, extending posteriorly at the middle of the canines' plane. The mesial border of the orbit ends at the plane of the connection between P3 and P4. The infraorbital foramen is relatively large. The palate extends far beyond the plane of M1, ending to a relatively narrow choana. The postorbital processes are moderately developed and a strong postorbital constriction is present. Two faint temporal lines start at the postorbital processes and merge approximately at the level of postorbital constriction. A faint sagittal crest starts to develop at this point, ending at the nuchal crest, which is also not very robust. Most probably, the restricted size of these crests and the absence of teeth wear indicate that the skull belongs to a young adult individual. The braincase is relatively low and wide. The remaining parts of the zygomatic arch are relatively thin and the glenoid cavity is

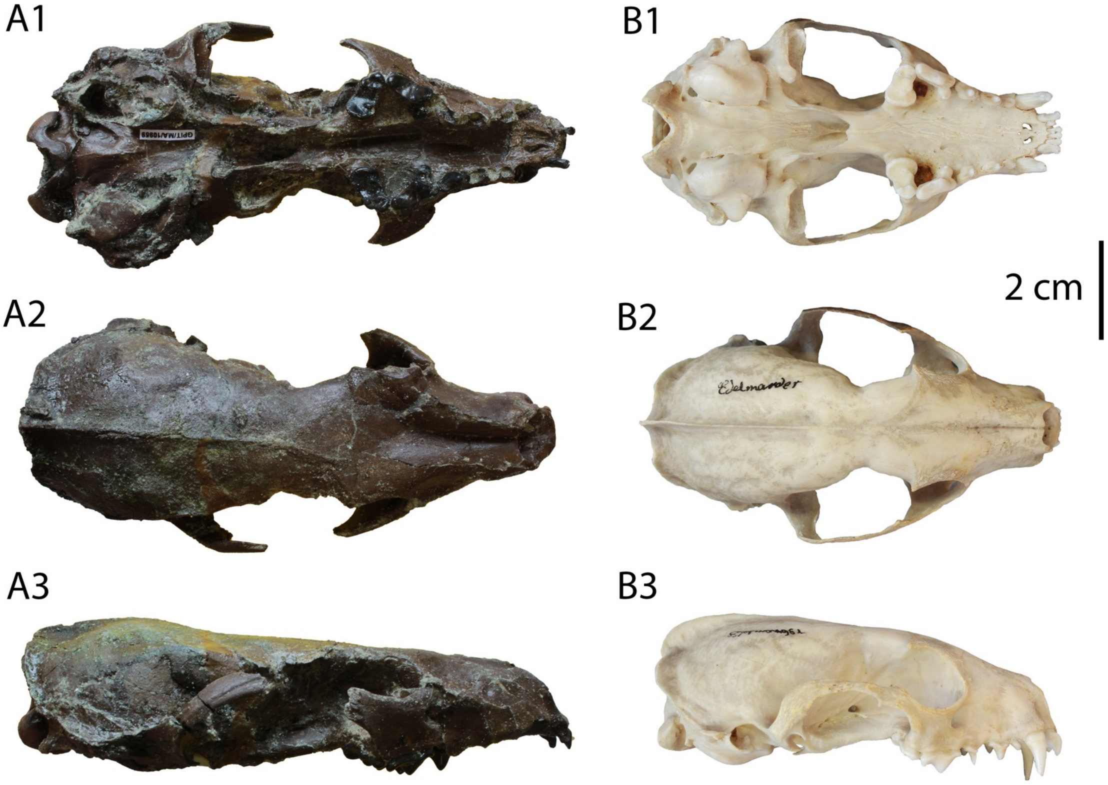

Fig 1. Skull of "*Martes*" *sansaniensis* from Hammerschmiede (A; GPIT/MA/10959) in comparison to that of the extant *Martes martes* (B; GPIT/MA/18609).

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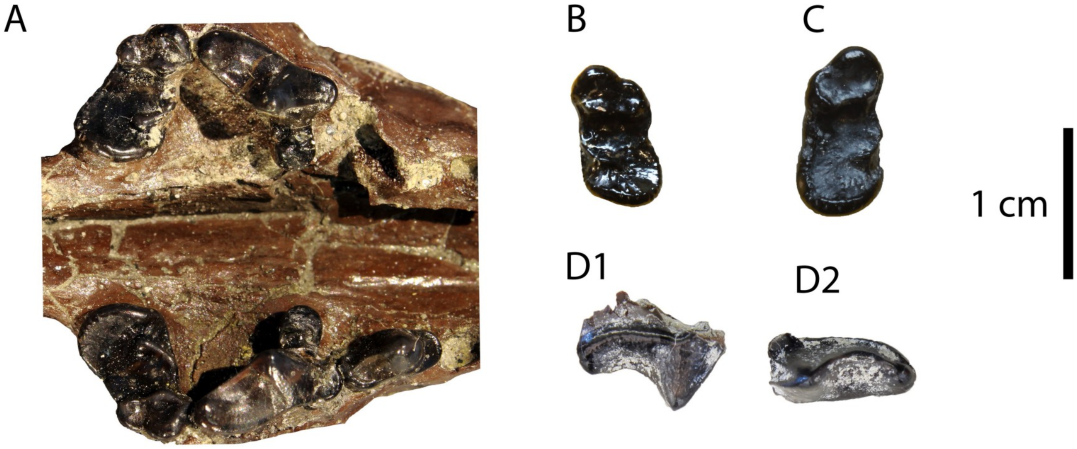

Fig 2. Upper dentition of "*Martes*" *sansaniensis* from Hammerschmiede: (A) GPIT/MA/10959 skull; (B) GPIT/MA/09882 left M1; (C) GPIT/MA/12308 right M1 (D) SNSB-BSPG-2020 XCIV-4065 right P4 in lingual (D1) and occlusal view (D2).

https://doi.org/10.1371/journal.pone.0268968.g002

anteriorly-oriented having a strong postglenoid process. The auditory region is damaged, not enabling a detailed description. However, the entotympanic is relatively large and elongated, chaperoned by a narrow and mesiolaterally placed ectotympanic. The mastoid process is small, while the paraoccipital process is developed. A hypoglossal foramen is present near the foramen magnum. The posterior lacerate and jugular foramina seem to be fused in one opening. The foramen magnum is oval in shape and the occipital condyles are laterally bent. The occiput is moderately high and U-shaped.

The first and second incisors seem to have approximately the same size, judging from their alveoli, while I3 is significantly larger. The preserved I2 and I3 have similar morphology, being peg-shaped and having a marked cingulum in their distal border. This cingulum covers only the distolingual part of I3, which also has a slight distal heel-like enhancement. Their measurements can be found in Table 1. The alveoli of C are large and oval-shaped. The alveolus of P1 is relatively large and in close contact to that of P2. The alveolus of P2 is two-rooted, large, in-line and in close contact with P3 and its distal root is significantly longer than the mesial one. The P3 is formed by a high main cusp (P3H = 4.1 mm) with no accessory cusps and a smooth cingulum in its perimeter. It is slightly asymmetrical with the main cusp being faintly distally bent and the distal part of the base of the tooth creating a small heel valley. The upper carnassial has a cingulum, which is more developed at its lingual-distal part. There are no signs of wear. The protocone is large, with a long and slightly compressed neck, situated between the planes of the paracone and the minute parastyle. The paracone is the largest cusp (P4H = 5.0 mm) and it hosts two fine crests, towards the low and robust parastyle and the mesial border of protocone's neck respectively. The metastyle is low, blunt and buccally bent. There is no carnassial notch between the paracone and the metastyle. The upper molar is large and oval-shaped, without signs of wear. The cingulum is faint. The buccal border over the paracone is distinctly more developed than over the metacone. The paracone and the metacone are of

Table 1. Dimensions (in mm) of the upper incisors of the "*Martes*" *sansaniensis* skull from Hammerschmiede (GPIT/MA/10959).

	L	W	H
I2	3.0	1.8	4.2
I3	3.9	2.8	5.2

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similar height and they are connected by the postparacrista and the premetacrista. The metacone is slightly sharper than the paracone. A preparacrista is also present, but there are no signs of a parastyle or a metastyle. A preparaconular crista connects the mesial cingulum with the low and blunt paraconule. There are no signs of other cusps or cristae. A similar morphology is exhibited at the two isolated M1.

Comparison: Size has been one of the main differentiating factors between the Miocene marten-like species. Tables 2 and 3 summarize the metrical comparison between all the forms in concern, based on upper and lower teeth respectively, demonstrating that there is a notable size difference between some groups.

Three main size groups can be seen when observing Tables 2 and 3 in comparison to the extant *Martes martes* and *Martes foina* (m1L≈8.5–10.5 mm; P4L≈7.5–9.0 mm; M1L≈3.5–4.5 mm). The small-sized forms include: "*M*". *delphinensis*, "*M*". *cadeoti*, "*M*". *laevidens*, "*M*". *jaegeri* and "*M*". *lefkonensis* (m1L≈5.0–7.5 mm; P4L≈6.5–7.5 mm; M1L≈3.0–4.0 mm). The species "*M*". *anderssoni*, "*M*". *collongensis*, "*M*". *burdigaliensis*, "*M*". *munki*, "*M*". *melibulla*, "*M*". *basilii and* "*M*". *sainjoni* occupy and intermediate position (m1L≈8.0–11.0 mm; P4L≈9.5–10.5 mm; M1L≈4.0–5.0 mm), whereas the species "*M*". *filholi*, "*M*". *sansaniensis*, "*M*". *woodwardi* and "*M*". *leporinum* are relatively large (m1L≈11.0–14.0 mm; P4L≈10.5–11.5 mm; M1L≈4.5–6.5 mm). The material from Rudabánya published by [65] as "*M*. cf. *filholi*" represents a smaller form with morphological differences from the type material of "*M*". *filholi* (e.g. the lower M1L/M1W ratio). These specimens most probably cannot be attributed to "*M*". *filholi*, but in the present paper the name "*M*. cf. *filholi*" is retained until more material can clarify its taxonomy.

The specimens GPIT/MA/10959, GPIT/MA/12308, GPIT/MA/09882 from Hammerschmiede belong to the large-sized species group, whereas the specimens GPIT/MA/10666, GPIT/MA/10636, GPIT/MA/18606 and GPIT/MA/16924 are clearly smaller, fitting between the small- and medium-sized forms. The latter material is discussed in detail further below.

Table 2. Comparison of the upper teeth of the "*Martes*" material from Hammerschmiede and the marten-like species from the Middle/Late Miocene indicating the source of data. In the "*M*". *filholi* specimen from La Grive-Saint-Alban, measurements were taken from a cast of the holotype and based on the figures of [27].

Species	Code/Locality	P3L	P3W	P4L	P4W	M1L	M1W
"*M*". *sansaniensis*	GPIT/MA/10959	7.0	3.4	10.2	7.3	5.0	10.2
	GPIT/MA/16349			9.8			
	GPIT/MA/16963			9.7			
	GPIT/MA/12308					5.1	10.6
	GPIT/MA/09882					5.3	9.4
"*M*". cf. *munki*	GPIT/MA/10666					4.5	7.3
	GPIT/MA/18606					4.4	7.4
"*Martes*" sp.	SNSB-BSPG-1973-XIX-34			4.1	2.2		
"*M*". *sansaniensis*	Sansan [72]	6.7	3.2	11.2	8.5	4.7–5.4 4.9 (5)	9.3–11.0 10.0 (5)
"*M*". *filholi*	La Grive [53], Vieux Collonges [52]	6.8	3.8	10.4–11.0 10.8 (3)	7.4–8.0 7.7 (3)	6.6–7.7 7.2 (2)	9.7–11.0 10.4 (2)
"*M. cf. filholi*"	Rudabánya [65]					4.4	8.0
"*M*". *munki*	Sandelzhausen [73], Sant Quirico [58], Vieux-Collonges [52]	5.0–7.4 6.2 (2)	2.1–3.7 2.9 (2)	9.6–10.0 9.8 (5)	5.0–6.2 5.8 (5)	3.9–5.0 4.4 (10)	7.8–10.2 9.2 (10)
"*M*". aff. *anderssoni*	Can Ponsic [36]					4.0	8.0
"*M*". *cadeoti*	Vieux-Collonges [52]			7.1–7.5 7.3 (3)	3.9–4.3 4.0 (3)	3.0–3.8 3.4 (4)	6.6–7.2 6.9 (4)
"*M*". *lefkonensis*	Maramena [56]			6.3		3.0	

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Table 3. Comparison of the lower teeth of the "*Martes*" material from Hammerschmiede and the members of the genus "*Martes*" in the Middle/Late Miocene indicating the source of data. The measurements of the material of "*M*". *filholi* from La Grive-Saint-Alban were taken based on the figures of [27].

Species	Code/Locality	p2L	p2W	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W
"*M*". *cf. munki*	GPIT/MA/10636							8.3	3.2		
	GPIT/MA/16924					4.6	2.2	7.6	3.1	3.3	2.7
"*M*". *sansaniensis*	Sansan [72]	4.4–5.9 5.4 (8)	2.5–3.3 2.9 (8)	5.5–7.0 6.6 (10)	2.7–3.4 3.2 (8)	8.0–9.0 8.4 (10)	3.6–4.2 3.9 (9)	11.8–13.8 12.9 (10)	4.8–5.9 5.3 (11)	4.3–5.6 5.1 (3)	4.1–4.5 4.3 (3)
"*M*". *woodwardi*	Pikermi [66]							11.4–12.0 11.7 (2)	4.6–5.0 4.8 (2)		
"*M*". *leporinum*	Taraklia [77]	5.0		6.5		8.8		13.5			
"*M*". *filholi*	La Grive & Vieux-Collonges [52]	6.0	3.0	7.0	3.3	6.0–8.0 7.0 (2)	3.0–4.0 3.5 (2)	10.0–11.5 10.8 (2)	4.4–5.3 4.9 (2)	4.6 (2)	3.8–3.9 3.9 (2)
"*M. cf. filholi*"	Rudabánya [65]					5.6	3.0	9.5–10.3 9.9 (2)	3.4–3.9 3.6 (3)		
"*M*". *munki*	Sandelzhausen [73], Erketshofen 2 [76] & Vieux-Collonges [52]	3.8–5.1 4.2 (5)	2.0–2.5 2.2 (5)	4.5–5.7 5.1 (9)	2.2–2.39 2.4 (9)	5.2–8.4 6.3 (11)	2.6–3.8 3.0 (11)	8.3–9.5 9.0 (10)	3.8–4.5 4.1 (10)	3.3 (2)	3.1–3.2 3.2 (2)
"*M*". *basilii*	Los Algezares [59]	4.1	2.7	5.8	3.0			11.0	4.0		
"*M*". cf. *basilii*	Can Ponsic [78]							9.8	4.5		
"*M*". *sainjoni*	Chilleurs-aux-Bois [47] & Artenay [47]			5.5		7.0 (3)		11.0	4.5		
"*M*". *melibulla*	Can Llobateres [58]					7.0	3.2	10.5	4.5		
"*M*". *anderssoni*	Can Ponsic [36]					5.5		9.0	3.4		
"*M*". *collongensis*	Vieux-Collonges [51]			4.4	2.2	5.3	2.5	8.3	3.5	2.2	1.6
"*M*". *burdigaliensis*	Vieux-Collonges [50]							7.4–8.3 (4)	3.3		
"*M*". *cadeoti*	Vieux-Collonges [52]			3.3 (2)	1.9–2.2 2.1 (2)	4.9–5.4 5.2 (2)	2.2–2.9 2.6 (2)	6.8–7.3 7.0 (4)	3.0–3.2 3.1 (4)		
"*M*". *jaegeri*	Salmendingen [55]			[2.5]		[3.0]		5.5			
"*M*". *laevidens*	Wintershof-West [46]	3.3–3.7 3.5 (2)		4.5–4.7 4.6 (2)		4.8–5.8 5.3 (4)		6.8–7.5 7.1 (5)		3.4	
"*M*". *delphinensis*	Hostalets de Pierola [30], Vieux-Collonges [52], Manchones [78] & La Grive [78]			3.5		3.7–4.5 4.1 (2)	1.7–1.9 1.8 (2)	5.3–6.7 5.9 (10)	2.1–2.6 2.4 (7)		
"*M*". *lefkonensis*	Maramena [56]					4.9	2.4	7.2–7.6 7.4 (4)	2.8–3.2 3.0 (4)		

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The former three specimens fit in the size group of "*M*". *filholi*, "*M*". *sansaniensis*, "*M*". *woodwardi* and "*M*". *leporinum*. The only species from the medium-sized group that is comparable to the larger specimens from Hammerschmiede is "*M*". *munki*, which is differentiated by its significantly narrower P4 (Table 2). The species "*M*". *woodwardi* and "*M*". *leporinum* are known only from lower teeth, so a direct comparison is impossible. However, a considerable stratigraphic difference must be taken into consideration as "*M*". *woodwardi* has been reported only from Pikermi [54, 66] and "*M*". *leporinum* only from Taraklia [60]. Both localities have been characterized as typical Turolian (MN 12) faunas [38]. Significant faunal turnovers have taken place during the Aragonian-Vallesian and Vallesian-Turolian transitions [67–71] making the unaltered survival of a marten species (known for being rather speciose) seem highly improbable. Therefore, the comparison is mainly focused on the species "*M*". *munki*, "*M*". *filholi* and "*M*". *sansaniensis*.

The species "*M*". *munki* is rather similar to "*M*". *sansaniensis*, but it exhibits considerably narrower upper carnassials (Table 2). This difference can be seen both metrically and in relation to M1L. Additionally, [52] mentions the presence of a protoconule and a metaconule in the M1, which are not present in the herein described specimens. The two remaining forms are similar in several characteristics of their dentition. However, the size of M1, both metrically and in relation to P4L, is far larger in "*M*". *filholi* (Table 2). Additionally, this tooth in "*M*". *filholi* is relatively long, having a M1L/M1W ratio of 68%, whereas in "*M*". *sansaniensis* this ratio ranges between 42% and 52%. The specimens published by [65] from Rudabánya as "*M*". cf. *filholi* represent a smaller form with a M1L/M1W ratio closer to that of "*M*". *sansaniensis* (55%). The Hammerschmiede molars are metrically smaller than the "*M*". *filholi* specimens from Vieux-Collonges and La Grive, being more similar to "*M*". *sansaniensis* (Table 2). Additionally, the M1L/M1W ratio ranges between 48% and 56% indicating closer affinities with the latter species. In terms of morphology, the two species are very similar [49, 53, 72]. [72] stated that the most considerable morphological difference between these two forms is that the M1 metaconule (when present) is not connected to the protocone in "*M*". *sansaniensis*, whereas these two cusps are always connected in "*M*". *filholi*. No sign of a metaconule is present in the described specimens, resembling more the morphology of "*M*". *sansaniensis*.

Therefore, the larger "*Martes*" specimens from Hammerschmiede are here considered to be closer to the species "*M*". *sansaniensis*. Some small differences can be traced with regard to the Sansan material, as the slightly more developed P4 parastyle and the mesiodistally shorter lingual platform of M1 in the Hammerschmiede specimens. However, we don't consider these differences to be of any taxonomic value and they can be interpreted as intraspecific variability.

The specimen GPIT/MA/10959 from Hammerschmiede is the first known skull of "*M*". *sansaniensis* and the youngest record of this form. Therefore, a comparison to that of the extant *M*. *martes* is here reported. [45] enumered several dental traits in common of "*M*". *sansaniensis* from Sansan with extant *Martes*. Among these are the presence of the p4 distal accessory cuspid, and the overall similarities in the carnassials and the M1 (large P4 protocone, a relatively elongated and basined m1 talonid with a conical hypoconid linking the metaconid by an entocristid; a non-reduced M1 lingual platform, and the posession of a narrow M1 crown at about mid-width). However, they also found differences, as the presence of a diastema between p2–3, a higher m1 protoconid, and M1 with distinct proportions (more elongated buccolingually) and morphology (larger M1 parastyle, stronger development of the metacone, metaconule more developed [when present], and a protocone located more buccally) compared to *Martes*. To these notes, we have observed the following differences. The skull and the dentition of the fossil species are larger than those of the extant marten. However, there is an inconsistency to the difference percentage between the two species (Table 4). The skull length, condylobasal length and palate length differences indicate that the skull of the extant species is approximately 82% as long as the fossil. However, other measurements that concern the width of the skull such as the rostrum width at the canines, the choana width, the braincase width and the mastoid width suggest that the two species are relatively more similar (94%). Some extreme differences (e.g. the palate width at P4 and the height of the foramen magnum) can be attributed to the diagenetic deformation of the fossil specimen. Additional cranial differences between the species are: the longer paraoccipital processes, the less inflated entotympanic (also possibly related to deformation), the stronger zygomatic arch and the longer anterior palatine foramina in "*M*". *sansaniensis*. Other cranial differences (such as the lesser development of the sagittal, nuchal and postorbital crests and the width of the zygomatic

Table 4. Comparison of the skull measurements of "*Martes*" *sansaniensis* from Hammerschmiede (GPIT/MA/10959) with that of *Martes martes* (GPIT/MA/18609).

Measurement	"*Martes*" *sansaniensis* (GPIT/MA/10959)	*Martes martes* (GPIT/MA/18609)	Difference %
Skull Length	108.4	88.7	82%
Condylobasal Length	101.4	81.9	81%
Rostrum Width at Canines	17.6	18.0	102%
Palate Length	54.4	45.4	83%
Palate Width at P4	(26.4)	28.3	107%
Choana Width	8.5	8.2	96%
Preorbital Constriction	(25.3)	21.3	84%
Postorbital Constriction	(20.8)	16.6	80%
Maximum Braincase Width	40.2	34.7	86%
Maximum Braincase Height	(26.3)	26.2	100%
Foramen Magnum Width	11.1	12.0	108%
Foramen Magnum Height	(6.6)	9.1	138%
Mastoid Width	43.7	40.3	92%

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arches) can be attributed to the relatively young age of the fossil individual, which is also supported by the absence of dental wear. The fossil species also exhibits some dental differences in comparison to the extant one: a more evident size difference between I2 and I3, the equal length of P2 and P3, the absence of the lingual expansion of P3, the less acute P4 protocone and paracone, the more developed cingulum in P4 and M1, the restriction of P4 parastyle to a faint elevation of the mesial cingulum, the higher M1 cusps, the slightly more homogenous connection between the M1 protocone and paracone, the more semi-circular buccal part of the tooth and the less developed lingual platform. The new skull of "*M*". *sansaniensis* from Hammerschmiede provides significant new evidence on the dentognathic morphology of this species, supporting the hypothesis of [45] of a generic split from the extant martens. A future detailed review of the heterogeneous group of "*Martes*" from the Miocene is expected to solidify this separation.

"*Martes*" cf. *munki* Roger, 1900 [48]

Holotype: NMA 80–39 a.S., right hemimandible with p3–m1.

Type Locality: Häder (Germany).

Referred Specimens: HAM 4: GPIT/MA/16924, right hemimandible with p4–m2. HAM 5: GPIT/MA/10666, right M1; GPIT/MA/18606, right M1; GPIT/MA/10636, left m1.

Description: The upper molar (GPIT/MA/10666; Fig 3B) exhibits a plesiomorphic mustelid morphology. There are no signs of wear and a moderately developed cingulum surrounds the tooth. The paracone is slightly larger than the metacone and there is not a high crista connecting them. The buccal side of the tooth is more enhanced over the paracone than over the metacone. A relatively high paraconule is present followed by both a preparaconular crista and a preprotocrista.

The hemimandible (GPIT/MA/16924; Fig 3A) is broken just mesially to p4 and at the centre of the masseteric fossa. It is relatively slender and no mental foramina are preserved. The masseteric fossa is deep and reaches the plane of the mesial part of m2. The fourth premolar is relatively high, with a developed cingulid and a large distal accessory cuspid. The lower carnassial is low, with developed wear facets and a smooth cingulid. The protoconid is the largest cuspid, connected with the paraconid through an obtuse angle. The metaconid is large and high, well separated from the protoconid and lingually inclined. The talonid is strongly worn, so no cuspids are exhibited. The talonid valley is moderately wide and shallow with a sagittal cristid

Fig 3. Material of "*Martes*" cf. *munki* from Hammerschmiede: (A) hemimandible (GPIT/MA/16924) in (1) buccal, (2) lingual and (3) occlusal views; (B) M1 (GPIT/MA/10666) in occlusal view; (C) m1 (GPIT/MA/10636) in buccal view.

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reaching the distal cingulid. The second molar is unworn, one-rooted and with a faint cingulid. Its buccal side hosts three similar-sized cuspids, the hypoconid, the protoconid and the paraconid, while its lingual side hosts only the metaconid. All the cuspids are situated in a perimeter ridge, and there are no other cristids connecting them.

Comparison: As mentioned before, these specimens' size can be better corresponded to that of the smallest members of the medium-sized group (Tables 2 and 3). In particular, this material can be attributed to a form that is smaller than most specimens of "*M*". *munki*, "*M*". *basilii*, "*M*". *sainjoni* and "*M*". *melibulla* and larger than "*M*". *cadeoti*, "*M*". *jaegeri*, "*M*". *lefkonensis*, "*M*". *laevidens* and "*M*". *delphinensis*. Therefore, only the species "*M*". *anderssoni*, "*M*". *collongensis* and "*M*". *burdigaliensis* are fitting this size-group.

The two latter species are known from very scarce material from the locality of Vieux-Collonges [50, 51]. The species "*M*". *burdigaliensis* (despite its relatively small size) is a considerably robust form, with wide trigonid and talonid and thick enamel and high hypoconid, being significantly different from the herein described specimens. The species "*M*". *collongensis* has an enlarged talonid, a relatively high metaconid (similar to that of "*M*". *cadeoti*) and developed hypoconid, hypoconulid and cuspid-like distal crest of the protoconid. Therefore, it is also considered to be significantly different from the present material.

The species "*M*". *anderssoni* was created by [57] based on dental and postcranial material from the latest Miocene/Pliocene of China. [36] published some dental remains (isolated p4, a broken m1 and a complete M1) from Can Ponsic (Late Miocene, MN 9) as "*M*". aff. *anderssoni*. The herein presented specimens are morphologically very close to the material from Can Ponsic. [36] described the specimens from this locality stating that they were resembling both "*M*". *munki* and "*M*". *anderssoni*. However, the author did not specify why the material was suggested to be closer to "*M*". *anderssoni*. Both of these forms exhibit some taxonomic problems concerning their holotype material. The mandibles of the original material of "*M*". *anderssoni* are lost (B. KEAR, pers. comm.). Therefore, the only comparable material with the herein described specimens is the M1 that [57] tentatively attributed to this species. This tooth differs from GPIT/MA/10666 in the following traits: the narrower outline, the larger metacone, the much shorter postprotocrista that ends at the plane of the paracone and the less expanded lingual platform. These differences are also evident between the material from Can Ponsic and the material from China. On the other hand, the holotype of "*M*". *munki* is a fragmentary and deformed mandible from Häder published by [48]. Therefore, this species is also not well-defined. However, this name has been used broadly (possibly as a wastebasket nomen) to include medium- to small-sized martens from all over Europe during the Middle Miocene [27, 38, 48, 52, 74–76]. Therefore, we are inclined to tentatively attribute the Hammerschmiede material to this species as "*Martes*" cf. *munki*, pointing out that a thorough revision of its taxonomic status is needed. A depiction of the dimensions of some of the discussed forms can be seen in Fig 4).

"*Martes*" sp.

Referred Specimens: HAM 1: SNSB-BSPG-1973-XIX-34, left P4.

Description: This specimen is identical to the upper carnassials described above, but it is considerably smaller (Fig 5).

Comparison: [4] figured two tiny carnassials of a small mustelid from Hammerschmiede as *Martes pusillus* (SNSB-BSPG-1973-XIX-34 left P4; and SNSB-BSPG-1973-XIX-32 right m1). However, the P4 does not have the typical P4 morphology of *Proputorius*, which is the currently accepted genus for this species (see below). [52] figured a P4 of *P. pusillus* from Vieux-Collonges (MN5, France). It has a mesially placed protocone, not separated from the parastyle area and with a reduced neck, a morphology typical for *Proputorius* spp. On the contrary, SNSB-BSPG-1973-XIX-34 has a very individualized protocone mesiolingually projected and buccodistally slender. In this sense, we confidently doubt the classification of this P4 as belonging to this taxon. Its morphology resembles other Early–Middle Miocene marten-like forms such as *Circamustela*? *laevidens* (Dehm, 1950) [46] from Wintershoft-West, *Circamustela hartmanni* n. sp. from Hammerschmiede (this paper) or *Aragonictis araid* from Escobosa [45]. Tough, it has a noticeable smaller size than the previously three mentioned taxa, even smaller than "*M*". *lefkonensis* and "*M*". *cadeoti* (Table 2). The only known species that have a smaller size than these two forms are "*M*". *jaegeri* from Salmendingen (MN 10) [55] and "*M*". *delphinensis* from several Middle Miocene sites of Europe (Table 3). However, only the lower dentition of these two taxa is known, so more complete and associate material is needed to test if they are present in Hammerschmiede. Therefore, we prefer to refer to this form as "*Martes*" sp.

Genus *Circamustela* Petter, 1967 [36]

Type species: *Circamustela dechaseauxi* Petter, 1967 [36]

Other included species: *Circamustela peignei* Valenciano et al., 2020 [62]; *Circamustela hartmanni* sp. n.

Remarks: The genus *Circamustela* is a rare hypercarnivorous member of the subfamily Guloninae (sensu [79], including martens, wolverines and their relatives). It was firstly

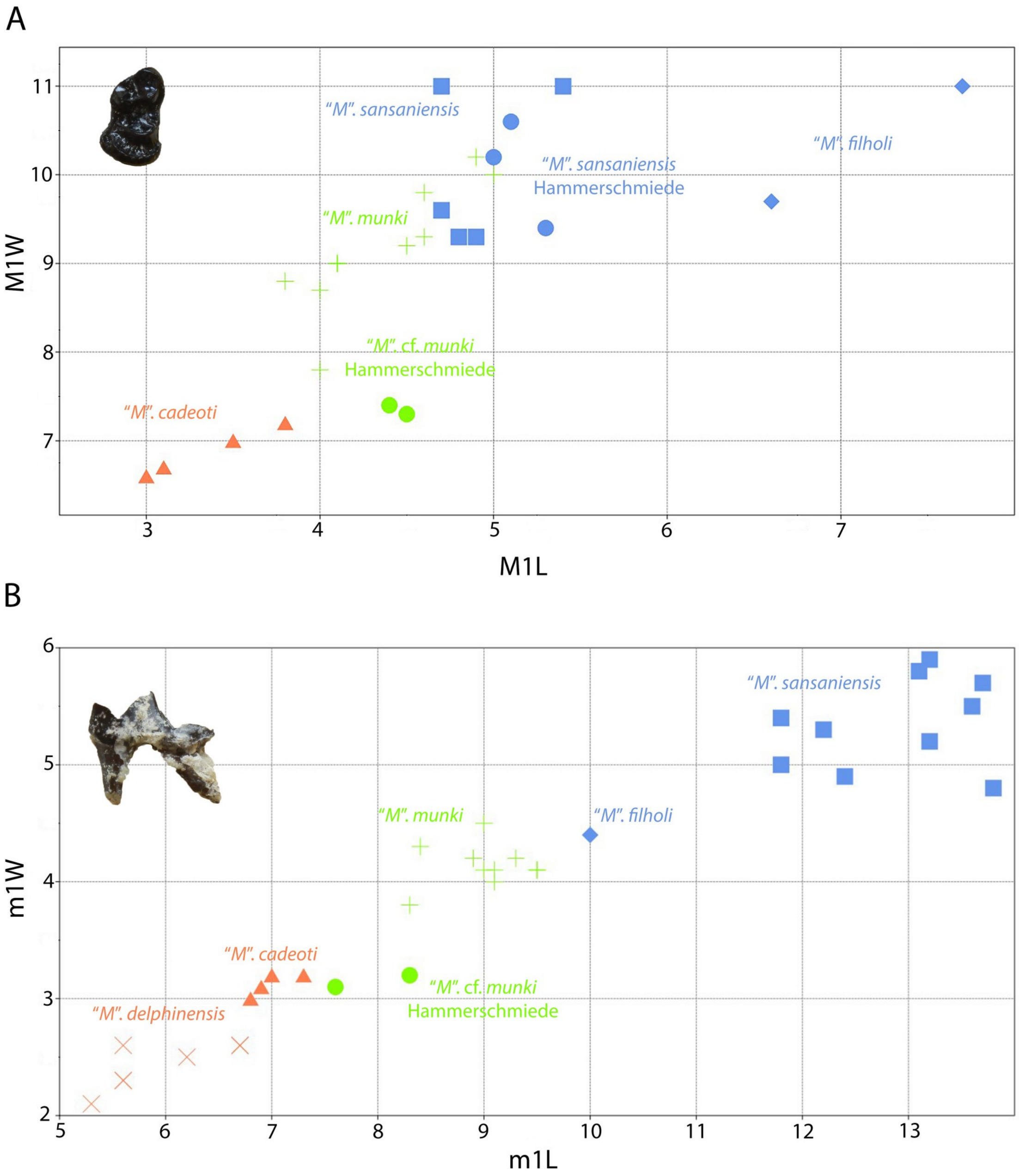

Fig 4. Comparison of the M1 (A) and m1 (B) of *"Martes"* from Hammerschmiede to that of other species of the genus. Data sources similar to that of Tables 2 and 3.

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described by [36] based on a mandibular fragment with m1 and a damaged p4 from the early Late Miocene (MN 9) Spanish locality of Can Llobateres. Some years later, the same author published an upper molar from the same locality [78]. Both specimens were attributed to the type species *Circamustela dechaseauxi*. Some years later, [80] published a fragmentary M1 (lingual platform) from the early Late Miocene (MN 9) locality of Los Valles de Fuentidueña in Spain that they also attributed tentatively to *C. dechaseauxi*. Another report of the genus was made by [81], who described an M1 and a p4 from the Turolian locality Dorn-Dürkheim (Germany) as? *Circamustela* sp. Recently, [62] published a second species of the genus,

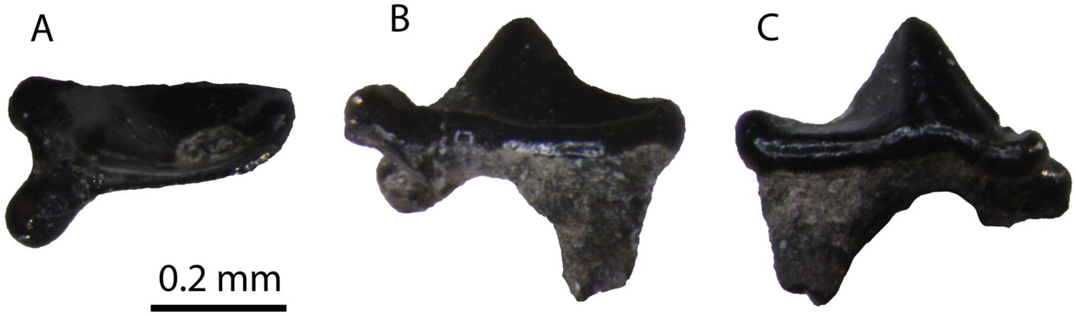

Fig 5. The P4 of "*Martes*" sp. from Hammerschmiede (SNSB-BSPG-1973-XIX-34) in (A) occlusal, (B) ventrolingual and (C) buccal view.

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Circamustela peignei, from the sites Batallones 3 and 5 (Late Miocene, MN 10, Spain) that differs from *C. dechaseauxi* mainly in the morphology of M1, but also in the more developed m1 metaconid and more conical m1 hypoconid. The herein presented material represents a new species for the genus, named as *Circamustela hartmanni* n. sp.

Circamustela hartmanni Kargopoulos et al. sp. nov. urn:lsid:zoobank.org:act:670F9140-2E0F-4F51-96A7-C4935B8A4FAA.

Holotype: GPIT/MA/17238, right hemimandible with p3–m1 and alveoli of p1, p2 and m2.

Hypodigm: HAM 1: SNSB-BSPG-1973-XIX-23, right P4. HAM 4: GPIT/MA/17033, left hemimandible with fragmentary m1 and complete m2. HAM 5: GPIT/MA/10388, right P4.

Etymology: The name *hartmanni* was chosen to acknowledge the help of Antonie Hartmann that has granted the permission for excavations in her land in Hammerschmiede for all these years.

Type locality: HAM 4 (Germany).

Other Localities: HAM 5 and HAM 1 (Germany).

Stratigraphy: Base of the Tortonian (11.44 Ma for HAM 4 and 11.62 for HAM 5).

Diagnosis: Species of the genus *Circamustela* with approximately 80% the size of *C. dechaseauxi* and *C. peignei* (P4L≈6.5 mm; m1L≈8.0 mm); P4 protocone slender with a long neck; p3 and p4 with developed distal accessory cuspids; lower carnassial with short crown and metaconid of intermediate development between *C. peignei* and *C. dechaseauxi*.

Differential Diagnosis: Differs from *C. dechaseauxi* in the smaller size (m1L 7.8 mm in contrast to the 9.7 mm for the Can Llobateres species) and the more developed m1 metaconid. Differs from *C. peignei* in the smaller size (P4L = 6.4 mm in contrast to 7.9–8.6 mm for the Batallones species), the presence of p3 distal accessory cusp, a much more developed p4 accessory cuspid (virtually absent in *C. peignei*), and a slenderer m1 talonid.

Description: The specimens GPIT/MA/10388 and SNSB-BSPG-1973-XIX-23 (Fig 6) are two complete P4, with signs of wear in their carnassial blades. They are three-rooted, with the roots under the mesial border and the protocone being in close proximity. The paracone is the largest cusp and it is connected with the metastyle via a crest without a notch. There is no parastyle. The protocone is low, has a long neck and it is mesially situated. Their only differences consist of the rougher enamel surface and the more developed lingual cingulum in SNSB-BSPG-1973-XIX-23.

The hemimandible GPIT/MA/17238 (Fig 7A) retains p3–m1 and the alveoli for p1, p2 and m2, whereas the specimen GPIT/MA/17033 (Fig 7B) retains the talonid of m1 and a complete m2. The mandibular body is slender and dorsoventrally short. Two mental foramina are present: one below the mesial half of p2 and one below the distal half of p3. The masseteric fossa ends at the plane of the distal end of m2. No developed cingula are present in any of the teeth.

Fig 6. The two P4 (GPIT/MA/10388) of *Circamustela hartmanni* sp. n. from Hammerschmiede: (A) GPIT/MA/10388 and (B) SNSB-BSPG-1973-XIX-23 in occlusal, buccal and lingual views.

https://doi.org/10.1371/journal.pone.0268968.g006

The second premolar is two-rooted and of similar size as the p3. The third premolar is relatively acute with a small distal accessory cuspid. The fourth premolar is damaged. However, it also seems to have been relatively high and it possesses a large and high distal accessory cuspid. The lower carnassial is long, with a low talonid and a high trigonid. The trigonid has clear wear facets in the carnassial blade and it overlaps with the distal part of the p4. The protoconid is the largest cuspid, clearly higher than the paraconid, divided from the latter by a deep notch. The metaconid is very small and blunt. The talonid covers approximately 25% of the tooth length. It is buccolingually reduced. It has a centrally placed hypoconid, which is blunt, conical and rounded by the cingulid. The second molar is reduced and almost circular in outline. It exhibits only one small protoconid and its trigonid covers approximately 1/3 of the tooth length.

Comparison: The plethora of marten-like mustelid taxa during the Middle and Late Miocene creates a relatively obscure taxonomic spectrum for the group. The genera *Martes* and *Mustela* have been used as wastebaskets for several fragmentarily known species, so the affinities of every taxon are not always clear (e.g., [45, 62]). However, the genus *Circamustela* can be easily distinguished from most of the other mustelids by considering its size and carnassial

Fig 7. Lower dentition of *Circamustela hartmanni* sp. n. from Hammerschmiede: (A) right hemimandible (GPIT/MA/17238; holotype) in (1) buccal, (2) occlusal and (3) lingual views and (B) m1 and m2 (GPIT/MA/17033) in (1) buccal, (2) lingual and (3) occlusal views.

https://doi.org/10.1371/journal.pone.0268968.g007

Table 5. Metrical comparison of the dimensions of P4 and M1 of *Circamustela hartmanni* sp. n., *Circamustela* sp., *C. dechaseauxi* and *C. peignei* indicating the source of data. Localities: HAM 5 (Hammerschmiede 5), LVF (Los Valles de Fuentidueña), DD (Dorn-Dürkheim), CLL (Can Llobateres) and BAT3 (Batallones 3).

Species	Code	Locality	P4L	P4W	M1L	M1W
Circamustela hartmanni n. sp.	SNSB-BSPG-1973-XIX-23	HAM 1	7.2	4.3		
	GPIT/MA/10388	HAM 5	6.4	4.3		
Circamustela sp.	LVF-55-y [80]	LVF			3.4	
	DD-14 [81]	DD			3.4	6.8
Circamustela dechaseauxi	IPS 28086 [3]	CLL			3.9	8.2
Circamustela peignei	BAT-3’10.1570 [62]	BAT3	7.9	4.9	3.8	8.5
	BAT-3’11.1041 [62]	BAT3	8.1	4.9		
	BAT-3’10.1246l [62]	BAT3	(8.6)			
	BAT-3’10.1246r [62]	BAT3	8.3	4.3	3.9	(8.8)

https://doi.org/10.1371/journal.pone.0268968.t005

morphology: the small dimensions, the low P4 metastyle, the high m1 protoconid, the low m1 metaconid and the mesiodistally enlarged p4 are herein considered sufficient enough for the attribution of the present specimens to the hypercarnivorous genus *Circamustela*. However, as noted in the past [45, 62, 81] the fossil record of the genus *Martes* is very problematic and a revision is needed in order to enable more secure attributions in the future.

It is evident from the metrical comparison with the upper (Table 5) and lower (Table 6) dentition, that the material described here is considerably smaller than that of *C. dechaseauxi* and *C. peignei*. In particular, most specimens seem to be approximately 20% smaller than the respective material of the other two species. Additionally, some morphological differences between the material from Hammerschmiede and that from Spain have been noted: the protocone of the upper carnassial is thinner and it has a longer neck than in *C. peignei*. The third lower premolar has a reduced distal accessory cuspid, which is absent in *C. peignei*. The distal accessory cuspid of the fourth lower premolar is much more developed than in *C. peignei*, which is absent in the majority of the specimens. The crown of the lower carnassial is in general shorter than in the other species of *Circamustela*, and the m1 metaconid is moderately reduced (intermediate between *C. peignei* and *C. dechaseauxi*). However, the slenderness of the m1 talonid of *C. hartmanni* is similar to that of the type species. The combination of metrical and morphological differences between the material from Hammerschmiede and that of Can Llobateres and Batallones are herein considered sufficient enough for its attribution to a

Table 6. Metrical comparison of the lower teeth of *Circamustela hartmanni* n. sp. from Hammerschmiede and other material of the genus *Circamustela* indicating the source of data. Localities: DD (Dorn-Dürkheim), and BAT3/5 (Batallones 3/5). Measurements on the holotype of *C. dechaseauxi* have been taken by the present authors.

Species	Code	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W
Circamustela hartmanni n. sp.	GPIT/MA/17238	4.0	1.9	5.4	2.1	7.8	3.0		
	GPIT/MA/17033						2.8	1.9	1.8
?*Circamustela* sp.	DD-15 [81]			5.0	2.4				
Circamustela peignei	BAT-3’10.1246l [62]	5.1	2.5	6.1	2.9				
	BAT-3’10.1246r [62]	5.0	2.5	6.2	2.8	10.0	4.1	(2.4)	(1.7)
	BAT-3’13.1056 [62]	4.8	2.5	6.0	2.9	9.2	3.8	3.5	2.8
	BAT-3’13.1048 [62]	5.3	2.4	5.8	2.9	9.4	3.9	3.4	2.7
	BAT-3’10.1570A [62]	-	-	6.5	3.0	9.4	3.6		
	BAT-3’10.1570B [62]	5.2	2.6	6.1	2.8	9.1	3.7		
	BAT-5’10.G14.129 [62]					9.0	4.1		
Circamustela dechaseauxi	IPS 2016					9.7	3.9		

https://doi.org/10.1371/journal.pone.0268968.t006

new species. The interpretation of this size difference as sexual dimorphism is presumed to be unfounded for the time being, since recently [62] studied material of several individuals of *C. peignei* without finding any sign of sexual dimorphism.

[80] published a fragmentary M1 from Los Valles de Fuentidueña, which they attributed to the type species *C. dechaseauxi*. However, the size of the tooth is considerably smaller (approximately 20%) than that published in [36] and [62]. Additionally, [81] published one M1 and one p4 from Dorn-Dürkheim as? *Circamustela* sp., based on their small size in comparison to *C. dechaseauxi*. The size of the material from Los Valles de Fuentidueña and Dorn-Dürkheim is similar to that of *C. hartmanni*. This could be interpreted as an indication for a common taxonomic attribution for all these forms, but, since the limited material does not enable a secure identification, it is herein preferred to retain the uncertain status of these specimens.

One further similar small marten-like mustelid is *Aragonictis araid* from the Middle Miocene of Spain (12.65–11.33 Ma) [45]. Both forms are similar at the first glance, but *C. hartmanni* clearly differs from *A. araid* in the presence of marked cingulids in the lower dentition, a distal accessory cuspid in p3 and p4, a relatively enlarged p4, m1 with more conical and rounded hypoconid and a higher entocristid, a reduced m2 with a single cuspid, as well as a relatively shorther P4 with a less individualized protocone. Lastly, *C. hartmanni* resembles the morphology "*M*". *jaegeri* from Salmendingen (MN 10) in some traits. However, it is much smaller (m1L = 5.5 mm; [55]) and the lower carnassial has a more marked buccal cingulid and a high bulbous hypoconid that makes it a more robust tooth. A metrical comparison of the species of Circamustela to Aragonictis can be seen in Fig 8.

Genus *Laphyctis* Viret, 1933 [82]

Type Species: *Laphyctis mustelinus* Viret, 1933 [82]

Other included species: *Laphyctis*? *comitans* Dehm, 1950 [46]

Remarks: *Laphyctis* Viret, 1933 [82] is very closely related to the Middle Miocene genus *Ischyrictis* Helbing, 1930 [83]. The latter has been used as a wastebasket of medium- to large-sized gulonines that are now distributed also to the genera *Dehmictis* Ginsburg & Morales, 1992 [84] and *Hoplictis* Ginsburg, 1961 [85]. This lineage also includes the genus *Iberictis* Ginsburg & Morales, 1992 [84]. The systematic position of the basal gulonine *Laphyctis* is unclear. It has been classified either as a subgenus of *Ischyrictis* (e.g. [76, 85]), as a valid genus [84] or as a junior synonym of *Ischyrictis* (e.g. [72]). Recently it has been re-validated [86, 87] and herein we follow this hypothesis.

Laphyctis mustelinus Viret, 1933 [82]

Holotype: UCBL-213784, right fragmentary maxilla with P3-4 and M1.

Type Locality: La Grive-Saint-Alban (France).

Referred Specimens: HAM 4: SNSB-BSPG-2020 XCIV-3395, right M1.

Description: The upper molar (SNSB-BSPG-2020 XCIV-3395; Fig 9) exhibits a relatively plesiomorphic gulonine morphology. The paracone is the largest cusp being significantly longer and higher than the metacone. The buccal part of the paracone is far more developed than that of the metacone. The border of the tooth is slightly constricted just lingually to the buccal cusps. A very small paraconule is present lingually to the paracone, followed by a moderately developed protocone. The protocone is mesially placed. The distal crest of the protocone ends at the plane of the paracone. No signs of any other cusps are present. The enamel surface of the tooth is wrinkled and the lingual platform is moderately developed, being circular in its lingual area.

Comparison: This relatively plesiomorphic upper molar differs from the specimens of "*Martes*" by its very large size (Table 7), the absence of any cusps in its distolingual part, the considerable difference in the buccal expansion of the paracone in comparison to that of the metacone, the restricted distal crest of the protocone and the outline constriction lingually to

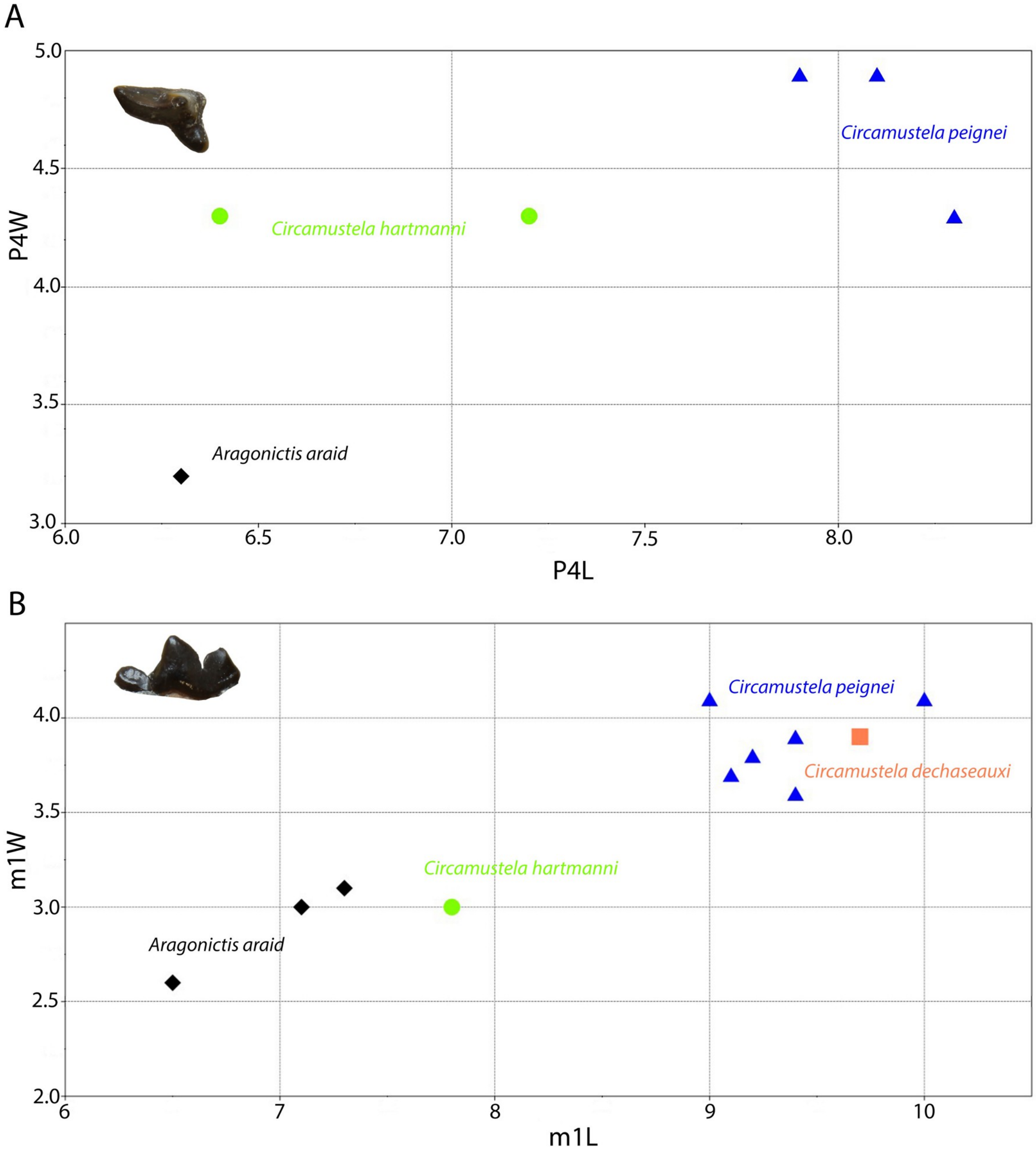

Fig 8. Comparison of the P4 (A) and m1 (B) of *Circamustela hartmanni* from Hammerschmiede to that of *Circamustela peignei*, *Circamustela dechaseauxi* and *Aragonictis araid*. Data sources: *C. peignei* [62], *C. dechaseauxi* (personal data) and *A. araid* [45].

https://doi.org/10.1371/journal.pone.0268968.g008

the buccal cusps. It differs from the genus *Iberictis* in the absence of a metaconule, a more reduced metacone and a more circular lingual platform, missing the incisure in its central area [88]. It differs from the genus *Hoplictis*, in the more developed lingual platform and the larger metacone [87]. It differs from *Dehmictis* by the more reduced protocone and metacone [84]. The morphology of the cusps and outline of the tooth seem to fit better with that of the genus *Ischyrictis* and *Laphyctis*. The genus *Ischyrictis* traditionally included three Middle Miocene species: the scarcely known *Ischyrictis bezianensis* Ginsburg & Bulot, 1982 [75], the better-known and larger form *Ischyrictis zibethoides* [17, 89], and *I. mustelinus* (herein considered as *Laphyctis mustelinus)*. The herein described specimen differs from the two species of *Ischyrictis*

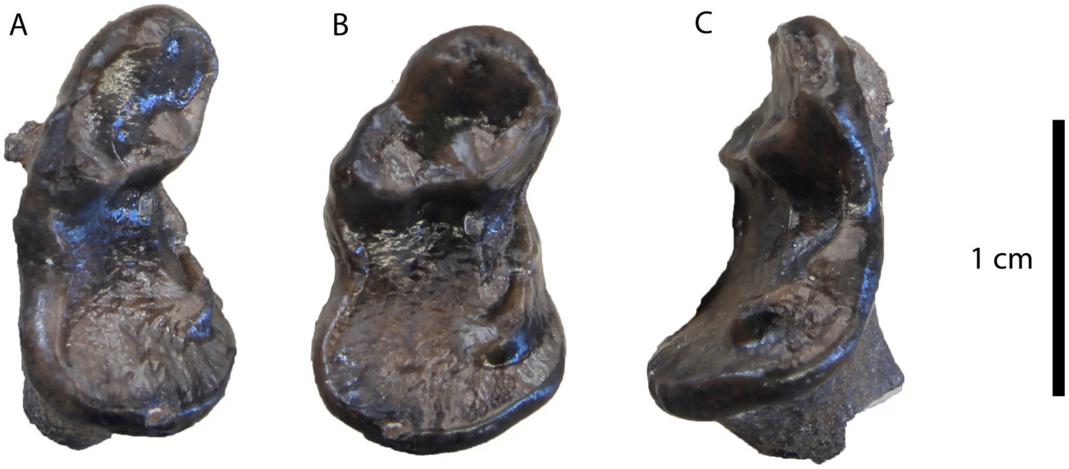

Fig 9. The right upper molar attributed to *Laphyctis mustelinus* (SNSB-BSPG-2020 XCIV-3395) in disto-occlusal (A), occlusal (B) and mesio-occlusal view (C).

https://doi.org/10.1371/journal.pone.0268968.g009

on the basis of the evident constriction lingual to the buccal cusps, the higher width of the tooth, the less developed paracone and metacone, the more developed buccal part of the paracone (in comparison to the metacone) and the larger lingual platform of *L. mustelinus* (e.g., [52, 75, 84]). Based on the previous described characters, the Hammerschmiede molar fits to the holotype of *L. mustelinus* from La Grive MN 7/8 [82]. Both forms share the same morphology of the parastylar area and the lingual platform. SNSB-BSPG-2020 XCIV-3395 only differs in a slightly lesser incisure below the paracone-metacone and in a more mesial position of the protocone. However, these differences can be explained by intraspecific variability. Additionally, this species has been found in Central Europe in the localities of Steinheim (MN 7; [90]), and Erkertshofen 2 (MN 4; [76]), as well as in Western Europe in Can Mata 1 (MN 7/8; [30, 58, 91]).

Guloninae indet.

Referred Specimens: HAM 5: GPIT/MA/10297, a left hemimandible with p2–m1 and the alveoli of p1 and m2.

Description: The hemimandible preserves p2–m1, as well as the alveoli of p1 and m2 (Fig 10). There are two mental foramina: one smaller below the distal part of p3 and one larger

Table 7. Comparison of the dimensions of SNSB-BSPG-2020-XCIV-3395 with that of other upper molars of Miocene gulonines indicating the data source.

Species	Code/Locality	M1L	M1W
L. mustelinus	SNSB-BSPG-2020 XCIV-3395	8.6	14.4
	Vieux-Collonges [52]	6.2–7.3 6.7 (4)	12.7–14.0 13.7 (4)
	La Grive [27]	6.5–8.0 7.3 (2)	12.2–15.4 13.8 (2)
	Hostalets de Pierola [30]	8.0	15.0
I. zibethoides	Sansan [72]	6.9–10.8 9.2 (5)	13.8–18.0 16.0 (4)
	Sandelzhausen [73]	7.6–9.1 8.6 (3)	14.4–16.3 15.4 (3)
	Artenay [52]	7.3	17.6
I. bezianensis	Bézian [75]	8.1	> 13.0

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Fig 10. The hemimandible attributed to Guloninae indet. (GPIT/MA/10297) from Hammerschmiede.

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below p2. The alveolus of p1 is small and circular, being in close contact with the alveolus of c and p2. All three remaining premolars have a smooth cingulid, which becomes stronger towards p4 and they also become more elongated and less high towards p4. The main cuspids are mesially located in the premolars. Both p2 and p3 are unicuspid. The p4 has a small damaged distal accessory cuspid. The lower carnassial is relatively long and low, with the talonid covering approximately 30% of the tooth length. There are signs of wear both in the carnassial blade and in the talonid valley. The trigonid is long with faint grooves at its buccal surface. The protoconid is the largest cuspid, slightly distally bent and separated from the slightly mesially bent paraconid by a shallow notch. The metaconid is clearly lower than the other two cuspids, being blunt and lingually bent. It stems from the base of the tooth and not from the middle height of the protoconid, of which it is slightly distally located. A small beveled hypoconid is present at the buccal border, as well as a very small hypoconulid. No other cuspids occur in the talonid. The talonid valley is shallow and wide with a marked distal border. Dental measurements of the specimen are given in Table 8.

Table 8. Dental dimensions of the hemimandible identified as Guloninae indet. (GPIT/MA/10297).

Code	p2L	p2W	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W
GPIT/MA/10297	5.5	2.8	6.2	3.1	7.5	3.5	11.8	4.8	[3.7]	[2.2]

https://doi.org/10.1371/journal.pone.0268968.t008

Comparison: The identification of this specimen is retained as Guloninae indet., because it exhibits significant differences with all the mustelid Miocene forms as far as we know. In general, it has a relatively plesiomorphic morphology, differentiating it from the more complex forms of mephitids (developed m1 entoconid, shortened rostrum), melines (more developed m1 talonid, small cuspules in the m1 cingulum) and lutrines (developed cingulum, sharp cuspids). It is also significantly smaller than *Plesiogulo* and *Eomellivora* and far larger than the small mustelines-gulonines like *Circamustela*. It also retains the p1, differentiating it from *Trochictis* and the mephitids. Usually, such characteristics fit better with the plesiomorphic gulonines such as "*Martes*" spp. However, it differs from "*Martes*" in the low height of m1 and the premolars, the elongated p4 and the small and ventrally situated distal accessory cuspid of p4. It differs from *Ischyrictis* and *Laphyctis* in the lower m1 trigonid, the longer m1 talonid and the slender premolars. The size, the low cuspids of the cheek teeth and the general morphology of the m1 cusps resemble *Martes melibulla* [58, 62]. However, the present mandible differs from that species by the shorter p2, the shape of the accessory cuspid in p4, the larger m1 talonid and the mesially inclined m2. The size, the low m1, the long p4, the accessory cuspid of p4 and the p2–p3 diastema are similar to that of *Sinictis pentelici* [92]. However, the Hammerschmiede specimen has a lower p4, not so distinct p2–p3 diastema, a lower m1 hypoconid and the p4 is only slightly overlapping with m1. Therefore, we suggest that this form is identified as Guloninae indet. until further findings clarify its affinities.

Subfamily Mellivorinae Gray, 1865 [93]

Genus *Eomellivora* Zdansky, 1924 [77]

Type species: *Eomellivora wimani* Zdansky, 1924 [77]

Other included species: *Eomellivora fricki* (Pia, 1939) [94]; *Eomellivora hungarica* Kretzoi, 1942 [95]; *Eomellivora ursogulo* (Orlov, 1948) [96]; *Eomellivora piveteaui* Ozansoy, 1965 [97]; *Eomellivora moralesi* Alba et al., 2022 [98].

Remarks: This genus includes Late Miocene giant mustelids from Asia, Europe and North America [98–100]. The Hammerschmiede material represents the earliest record of the genus (HAM 5; 11.62 Ma; [1]), given the fact that the type locality of *E. moralesi* from Abocador de Can Mata (ACM/PTA-A2) has been dated to 11.21 Ma [98]. The species *E. moralesi*, found in the MN 7/8 of Spain, has been considered as the most basal form of the genus, followed by the Vallesian *E. fricki* and *E. piveteaui* in the MN 9–10 that exhibit evolutionary trends towards the more derived *E. ursogulo* (MN 11), *E. wimani* (MN 12–13) and *E. hungarica* (MN 13) [98, 99]. It must be mentioned that [101] proposed an alternative, more simplistic approach, considering that only *E. wimani* is a valid species.

Eomellivora moralesi Alba et al., 2022 [98]

Holotype: ICP-IPS122262, palate with incisor, canine and left P1 alveoli, as well as left P2–M1 and right P1–M1 crowns.

Type Locality: ACM/PTA-A2, Abocador de Can Mata (Spain).

Referred Specimens: HAM 5: GPIT/MA/09877, left I3; GPIT/MA/12347, left p3; GPIT/MA/09875, right hemimandible with p4–m1; GPIT/MA/10302, left m1; GPIT/MA/09632, left m2.

Description: The specimen GPIT/MA/09877 (Fig 11A) is a left I3 without a root. It is robust, buccolingually compressed and it exhibits a strong lingual fold. Two crests start from the tip of the crown: one shorter, that meets mesially the lingual fold, and one longer, that ends to the distal border of a smooth cingulum. The buccal surface of the tooth is marked with very shallow grooves.

The only available p3 is complete, missing only its mesial root (Fig 11D). It is relatively worn. It is slightly asymmetrical as its distal part is slightly longer and wider than its mesial part. The distal base of the tooth is wide and slightly elevated. A faint cingulid is present in its

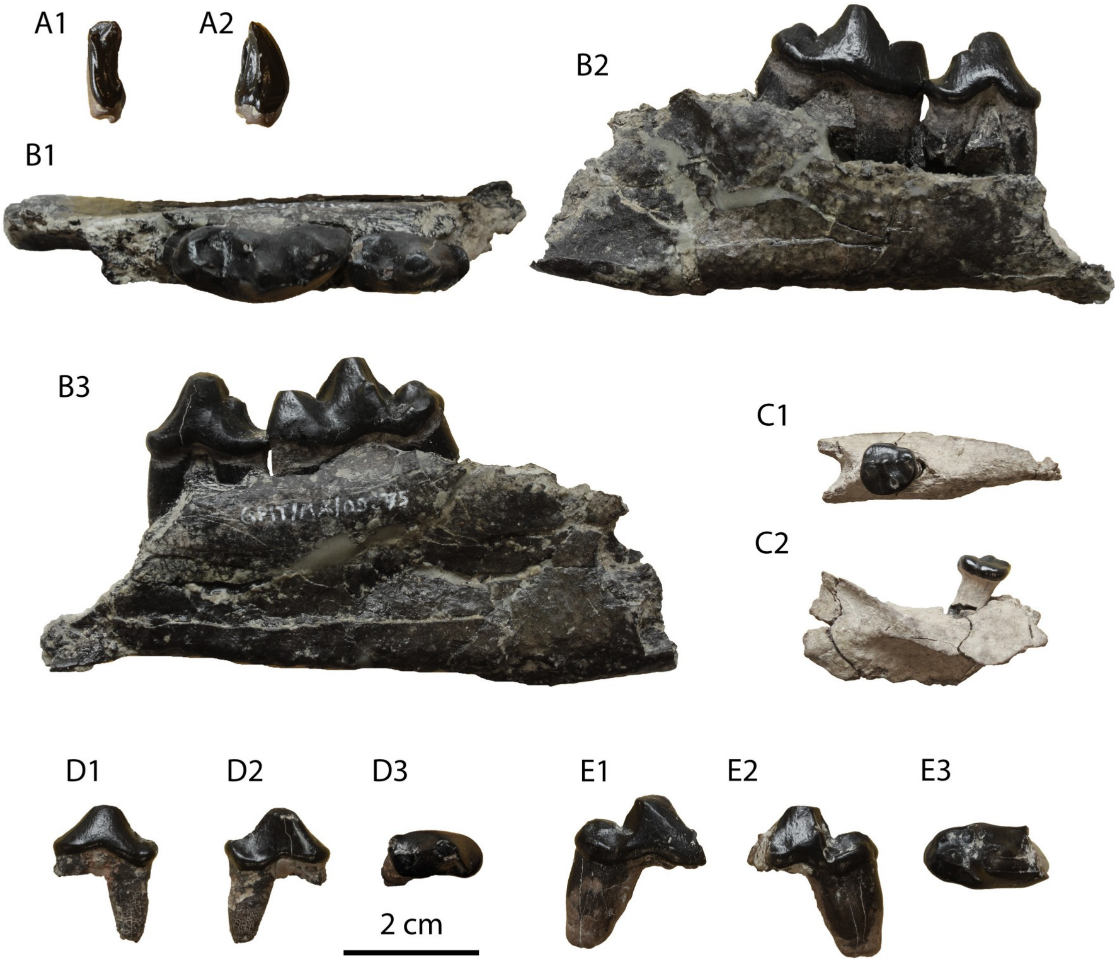

Fig 11. *Eomellivora moralesi* from Hammerschmiede: (A) GPIT/MA/09877 left I3, (B) GPIT/MA/09875 right p4–m1, (C) GPIT/MA/09632 left m2, (D) GPIT/MA/12347 left p3 and (E) GPIT/MA/10302 left m1.

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lingual side. There are no signs of accessory cuspids. The enamel is relatively thick with indistinct grooves.

The specimen GPIT/MA/09875 consists of a right partial hemimandible with p4 and m1 (Fig 11B). The description for m1 also applies to GPIT/MA/10302 (Fig 11E). The mandibular corpus is relatively high with a moderately deep masseteric fossa. The mesial end of the masseteric fossa is at the plane of the distal border of m1. The fourth premolar is worn and asymmetrical with its distal side being longer and wider than its mesial side. There is no mesial accessory cuspid. A strong distal accessory cuspid is present close to the main cuspid. The tooth is not inclined distally. The height of the main cuspid is higher than that of the paraconid of m1 and comparable to the one of m1 protoconid. The enamel is strong and faintly wrinkled in its surface. The lower carnassial is long and robust. It is moderately worn in its trigonid and talonid cuspids. A faint cingulid surrounds the tooth, being slightly more distinct in the talonid. The protoconid is the largest cuspid covering almost half of the tooth length. The paraconid is robust and vertical. A prominent carnassial notch is formed between these two cuspids. A small metaconid is present in the lingual side of the protoconid. The talonid is relatively short, covering approximately 25% of the tooth's length. Its valley is very short as it is restricted to the part distally to the metaconid. There is only one talonid cuspid present, the hypoconid, which is relatively long and high, being buccaly situated, close to the protoconid. However, the presence of a small hypoconulid cannot be excluded in the distal part of the talonid, which is affected by dental wear.

The m2 (Fig 11C) is still in its alveolus and it has a developed cingulid. It is slightly longer than broad (m2W/m2L = 92%). The trigonid is wider than the talonid, but they have approximately the same length. The mesiolingual part of the trigonid is slightly oblique ventrally. Four cuspids are present: a mesial paraconid, a central protoconid, a lingual metaconid and a small hypoconid at the distal end. All of them have approximately the same height and length. The protoconid is connected with all of the other cusps, resulting to a T-shaped structure of faint crests.

Comparison: The size of these specimens indicates that they must belong to a considerably large-sized mustelid. Given the already discussed presence of *Laphyctis mustelinus* in Hammerschmiede, a comparison with this species and the similar *I. zibethoides* is here attempted.

Unfortunately, the only reported I3 of *L. mustelinus* has been reported by [27] without providing description, measurements or figures. Therefore, a direct comparison based on this tooth is for the moment not possible. However, *L. mustelinus* has a comparable (and slightly smaller) size than *I. zibethoides* (Tables 7 and 9). Based on the dimensions given [72] for the Sansan material and by [73] for the Sandelzhausen material, the specimens from Hammerschmiede are significantly larger than those of *I. zibethoides* (Table 9). Therefore, it can also be deduced that the I3 of *L. mustelinus* would also be smaller than the Hammerschmiede incisor. [72] provided measurements for three mandibles of *L. mustelinus*, originating from La Grive-Saint-Alban, Steinheim and Erkertshofen. Additionally, [27] reported measurements for an m2. Comparing these measurements with the values for the present material, it is again clear that all the Hammerschmiede specimens are far larger than *L. mustelinus* (Table 9). Additional differences based on the descriptions of [27] and [90] include: the smaller p4 distal accessory cuspid, the larger m1 metaconid, the wider m1 talonid basin, the smaller m1 hypoconid and the more elongated m2.

As mentioned before, the specimens from Hammerschmiede are significantly larger than those of *I. zibethoides* (Table 9). Additionally, there are considerable morphological differences between this form and the Hammerschmiede material: the third upper incisor of *I. zibethoides* is relatively small and plesiomorphic, without any ridges and grooves [72]. As in *L. mustelinus*,

Table 9. Comparison of dental dimensions between the material of *Eomellivora moralesi* from Hammerschmiede and other relatable forms indicating the data source.

Species	Code	I3L	I3W	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W
E. moralesi	GPIT/MA/09877	7.4	5.4								
	GPIT/MA/12347			14.6	7.1						
	GPIT/MA/09875					17.3	8.7	24.7	10.7		
	GPIT/MA/10302								10.3		
	GPIT/MA/09632									7.6	7.0
E. moralesi [98]		[6.0]	[7.4]	[12.4]	6.4					7.6	6.4
E. piveteaui [100]		7.2	5.5	10.7–11.8 11.4 (3)	7.3–8.4 8.0 (3)	13.7–16.1 15.2 (5)	7.3–8.8 8.1 (5)	19.7–24.5 22.5 (7)	8.1–9.4 8.7 (6)	6.9–7.3 7.1 (2)	4.9–5.8 5.4 (2)
E. fricki [99]						17.9	8.7	26.5	10.5	[9.0]	[5.6]
L. mustelinus [27, 72]				8.1–8.3 8.2 (2)	4.3–4.6 4.5 (2)	9.7–11.1 10.2 (3)	5.1–5.2 5.1 (3)	14.5–15.5 15.1 (3)	6.3–6.6 6.5 (3)	6.5	5.5
I. zibethoides [72, 73]		5.0	3.6	9.2–10.3 9.8 (15)	4.4–5.2 4.8 (15)	11.0–12.9 11.8 (19)	5.0–6.3 5.7 (21)	15.7–18.9 16.9 (19)	6.5–8.7 7.2 (19)	6.0–6.3 6.2 (2)	5.6–6.0 5.8 (2)
I. bezianensis [102]						9.1	4.3	14.1	6.0		

https://doi.org/10.1371/journal.pone.0268968.t009

I. zibethoides differs from the present specimens in the lower p4 accessory cuspid, the m1 protoconid that is much higher than the m1 paraconid, the larger m1 metaconid, the lower m1 hypoconid and the wider and flatter m1 talonid basin [72]. Finally, the cuspids of the m2 of *I. zibethoides* are situated closer to the borders of the tooth, creating a central valley in the middle of the molar [72].

Eomellivora moralesi is known based on a complete maxilla with P2–M1, and fragmentary hemimandibles including complete p2 and m2, and a broken p3 from the locality of Can Mata, dated to 11.21 Ma [98]. Consequently, only the alveolus of the I3, part of the p3, and the complete m2 are directly comparable.

The dimensions of the described specimens fit only to that of the two large-sized mustelid genera typical from the Middle-Late Miocene: *Eomellivora* and *Plesiogulo*. Morphological differences between the Hammerschmiede material and the genus *Plesiogulo* include: the presence of grooves and ridges in I3, the longer p3, the presence of a distal accessory cuspid in p4, the higher trigonid cuspids of m1 and the more developed cuspids of m2 [77, 103–105].

On the contrary, the overall morphology of the presented material fits perfectly with the genus *Eomellivora*. The identification of the incisor is based on the remarkable similarity of the described specimen with the I3 of *Eomellivora piveteaui* from the Late Miocene of Batallones 3 (BAT-3'09.688; [99]). This specimen has the same morphology as the Hammerschmiede incisor (lingual fold, the pair of ridges and buccal grooves). The measurements of the I3 alveolus of *E. moralesi* [98] are to some extent different from those of GPIT/MA/09877 (Table 9), but as seen in [98] the alveolus is clearly mediolaterally compressed. Therefore, the measurements given in [98] do not fit with the depicted morphology. This fact is herein interpreted as metrical bias and the measurements are considered only as indicators of the approximate size of the tooth, which is relatively similar to that of GPIT/MA/09877.

The dimensions of the p3 indicate that it is larger and relatively slenderer than that of *E. piveteaui* (Table 9). Additionally, this species is characterized by the presence of a distal accessory cuspid in p3 [100], which is absent in the present specimen. The size is also slightly larger and slenderer than that of the paratype of *E. moralesi*, but the dimensions of the latter were taken in the alveolus, so it can be expected that the real length of the tooth must have been slightly larger.

The p4 is of intermediate size between *E. piveteaui* and *E. fricki* (Table 9). The p4 of *E. piveteaui* is much more robust, exhibiting a mesial accessory cuspid and also having a stronger distal accessory cuspid [98]. The p4L in relation to m1L is slightly longer in comparison to *E. fricki*. Additionally, this species is characterized by a relatively smaller p4 distal accessory cuspid [99].

The lower carnassial is also intermediate in size between *E. piveteaui* and *E. fricki* (Table 9), being a similar proportion to that of *Eomellivora* sp. from Gritsev [99]. It differs from that of *E. piveteaui* in the presence of a metaconid, the non-buccolingually compressed hypoconid and the possible absence of the hypoconulid. Though, [100] stated that the presence of the hypoconulid is evident only in one unworn specimen, so it is possible that this trait might have been present in *E. moralesi* too. It differs from the m1 of *E. fricki* in the shorter talonid, the larger metaconid and the more buccaly situated hypoconid. However, the preserved m1 of *E. fricki* (NHMW-2016/0065/0001) is extremely worn [99], not enabling a solid comparison.

The m2 of *E. piveteaui* has a relatively long trigonid (75% of the total length) and it does not have a metaconid [100]. In contrast, the second lower molar of *E. moralesi* has a more symmetrical ratio between trigonid and talonid and it possesses a metaconid [98], fitting to the present specimens. However, there is a difference in the width/length ratio between the two specimens, as the lectotype of *E. moralesi* has a ratio of 84%, whereas the molar from Hammerschmiede has a ratio of 92%. Finally, the m2 of *E. fricki* (judging from its alveolus) is far more elongated and larger than GPIT/MA/09632 [99]. Therefore, due to the same temporal range and similar morphology of the Hammerschmiede *Eomellivora* with the late Aragonian *Eomellivora moralesi*, we assign it to this taxon. These findings confirm the validity of this species, and undoubtedly differentiate it from the Vallesian *E. fricki* and *E. piveteaui*. It represents the earliest record of the genus (HAM 5; 11.62 Ma; [1]) and the first report of its p4 and m1.

Subfamily Lutrinae Bonaparte, 1838 [106]

Genus *Vishnuonyx* Pilgrim, 1932 [107]

Type species: *Vishnuonyx chinjiensis* Pilgrim, 1932 [107]

Other included species: *Vishnuonyx*? *angololensis* Werdelin, 2003 [108]; *Vishnuonyx maemohensis* Grohé et al., 2020 [109]; *Vishnuonyx neptuni* Kargopoulos et al., 2021 [22].

Remarks: Four different species have been attributed to the genus *Vishnuonyx*. The oldest species is *V. maemohensis*, which has been described from the middle-late Middle Miocene locality of Mae Moh in Thailand [109]. The type species *V. chinjiensis* has been reported from the late Middle / early Late Miocene of India [105, 110–112] and Kenya [113, 114]. [108] described the species *V.*? *angololensis* based on an upper carnassial from the late Late Miocene of Lothagam, but the attribution of this form to the genus *Vishnuonyx* has been doubted [115, 116]. [115] published a mandible from the Early Pliocene of Haradaso (Ethiopia) as *Vishnuonyx* sp., which is the youngest known occurrence of the genus in the fossil record. Finally, the only report of this genus from Europe is that of [22] that erected the species *V. neptuni* based on material from Hammerschmiede. The present study includes additional material that was found in the recent excavations at the same locality.

Vishnuonyx neptuni KARGOPOULOS et al., 2021 [22]

Holotype: SNSB-BSPG-2020-XCIV-0301, a right hemimandible with p1 alveolus and complete p2–m1.

Type Locality: HAM 4 (Germany)

Referred New Specimens: HAM 4: SNSB-BSPG-2020 XCIV-5702, right M1; SNSB-BSPG-2020 XCIV-5700, right p4; SNSB-BSPG-2020 XCIV-4029, right m1; SNSB-BSPG-2020 XCIV-5701, left m1.

Description: The M1 (Fig 12A) is complete with slight signs of wear in the buccal cusps. Its outline is relatively rectangular with the mesial and distal border being parallel to each other. The paracone is longer and slightly higher than the metacone. A strong protocone followed mesiobuccally by a paraconule is evident in the mesial part of the tooth. A developed metaconule is present just lingually to the metacone. The cingulum is relatively strong, especially in its lingual part, and marked with small notches. The enamel surface is wrinkled.

The p4 (Fig 12B) is asymmetrical, being considerably wider distally. Its cingulid is strong, especially in its buccal side. The main cuspid is high and robust, followed distobuccally by a significantly developed distal accessory cuspid. The enamel surface of the tooth (especially on its buccal side) is wrinkled.

Both lower carnassials (Fig 12C and 12D) are fragmentary. A strong cingulid is present, being stronger mesiobuccally. The paraconid is not preserved in both specimens. The protoconid is the higher preserved cuspid (considerably higher than the metaconid) and it is followed distally by a marked hypoconid.

Comparison: The genus *Vishnuonyx* has been considered as member of the group of bunodont otters [117]. However, it exhibits some unique characteristics that differentiate it from more typical genera of this group (such as *Enhydriodon* Falconer, 1868 [118] or *Sivaonyx* Pilgrim, 1931 [54]) [22]. The upper molar is mesiodistally short and its lingual platform is reduced; the accessory cuspid of p4 is relatively fused mesially with the main cuspid and the talonid is shorter than the trigonid, surrounded by a crenulated rim [22]. All these characteristics fit perfectly with the herein presented specimens.

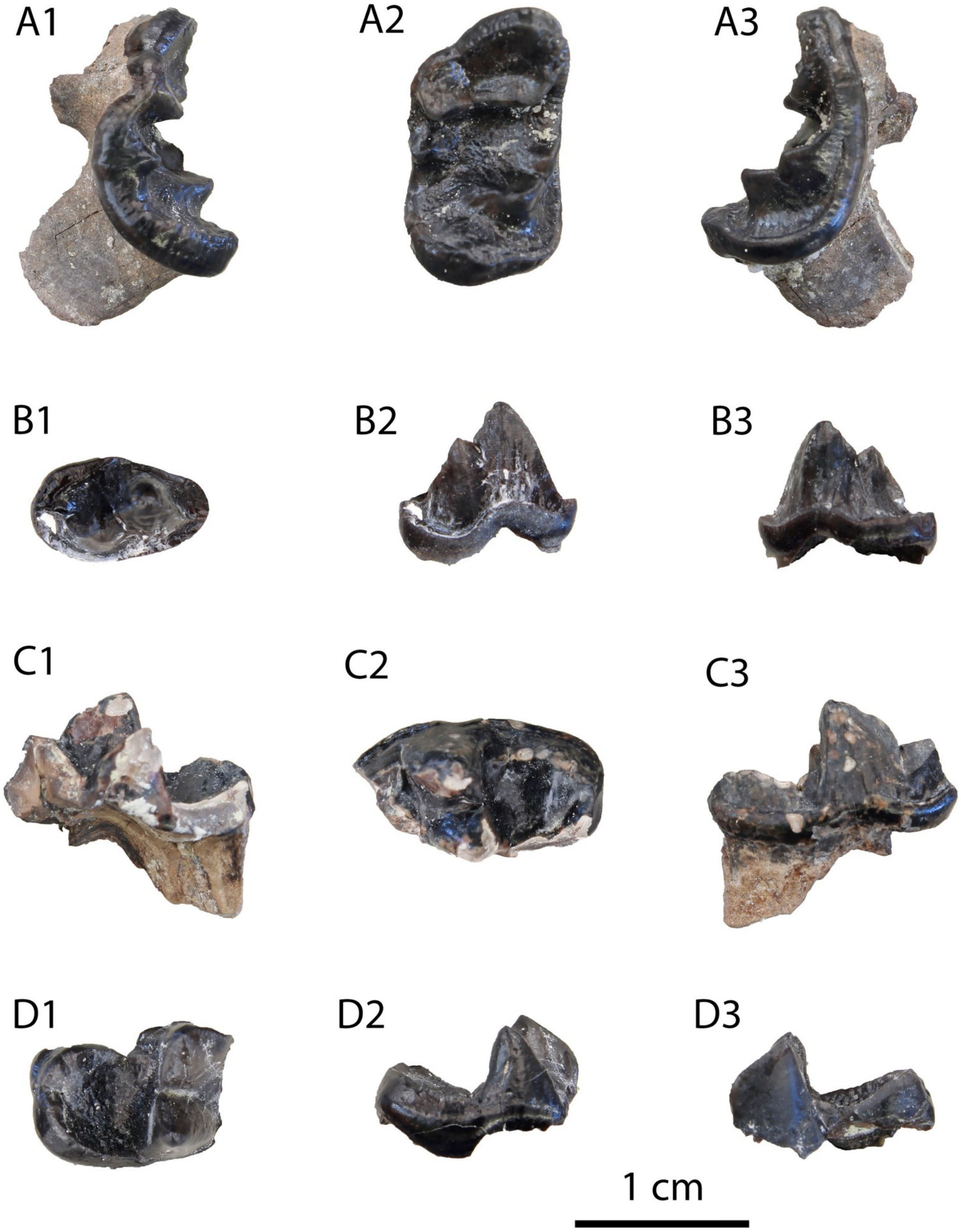

Fig 12. Material of *Vishnuonyx neptuni* from HAM 4: (A) SNSB-BSPG-2020 XCIV-5702 M1 in distal (A1), occlusal (A2) and mesial view (A3); (B) SNSB-BSPG-2020 XCIV-5700 p4 in occlusal (B1), buccal (B2) and lingual view (B3); (C) SNSB-BSPG-2020 XCIV-4029 right m1 in lingual (C1), occlusal (C2) and buccal view (C3); (D) SNSB-BSPG-2020 XCIV-5701 right m1 in occlusal (D1), buccal (D2) and lingual view (D3).

https://doi.org/10.1371/journal.pone.0268968.g012

The genus *Vishnuonyx* includes *V*. *neptuni* in Europe, *V*. *chinjiensis* in Asia and Africa, *V*. *maemohensis* in Asia and possibly *V*?. *angololensis* in Africa. These four species are differentiated based on their size (Table 10; [22]), as *V*. *chinjiensis* and *V*. *maemohensis* are relatively small, *V*. *neptuni* is of intermediate size and *V*?. *angololensis* is relatively large. Other morphological characteristics of *V*. *neptuni* that differentiate it from the other species of the genus include the small M1 paraconule, the large protoconule and metaconule, the more expanded buccal outline of the paracone, the shorter lower premolars and the m1 trigonid being slightly wider than the m1 talonid. All of these characteristics are clearly seen in the herein described

Table 10. Metrical comparison of the dimensions of M1, p4 and m1 from the herein presented specimens of *Vishnuonyx neptuni*, with previously published material from this species and other species of the genus indicating the source of data.

Species	Code	M1L	M1W	p4L	p4W	m1W
V. neptuni	SNSB-BSPG-2020 XCIV-5702	8.1	14.2			
	SNSB-BSPG-2020 XCIV-5700			9.2	5.5	
	SNSB-BSPG-2020 XCIV-4029					(7.2)
	SNSB-BSPG-2020 XCIV-5701					(7.7)
	SNSB-BSPG-2020 XCIV-1552 [22]	7.6	14.0			
	GPIT/MA/16733 [22]			8.9	6.2	7.7
	SNSB-BSPG-2020 XCIV-0301 [22]			9.0	5.7	(7.3)
	SNSB-BSPG-2020 XCIV-1301 [22]			9.9	6.5	
V. chinjiensis [109]				7.2–7.3 7.3 (2)	4.2–4.3 4.3 (2)	5.9
V. maemohensis [109]		5.0–5.9 5.4 (3)	11.1–11.5 11.3 (2)	6.7–8.3 7.6 (6)	3.5–4.6 3.9 (4)	4.8–6.4 5.7 (7)

https://doi.org/10.1371/journal.pone.0268968.t010

specimens, so they are attributed to the species *V. neptuni*, which is already known from HAM 4 [22].

Genus *Paralutra* Roman & Viret, 1934 [119]

Type species: *Paralutra jaegeri* (Fraas, 1862) [120]

Other included species: *Paralutra transdanubica* Kretzoi, 1951 [121].

Remarks: This genus is a typical member of the Middle Miocene assemblages of Europe, mainly represented by the type species *Paralutra jaegeri*, which was initially reported from Steinheim [90, 120]. However, the stratigraphic range of this species covers from the Early Miocene (Pellecahus; MN 4; [119]) to the early Late Miocene, as it has been found in Rudabánya (MN 9; [65]). The species "*Paralutra garganensis*" Willemsen, 1983 [122], was recently suggested to belong to a different genus [123].

Paralutra jaegeri (Fraas, 1862) [120]

Holotype: SMNS-4082, a left maxilla with P2–P4.

Type Locality: Steinheim (Germany).

Referred Specimens: HAM 5: GPIT/MA/10393, left P4; GPIT/MA/12322, left M1. HAM 4: SNSB-BSPG-2020 XCIV-5704, left M1; SNSB-BSPG-2020 XCIV-5703, left M1.

Description: The specimen GPIT/MA/10393 (Fig 13A) is a complete left P4, missing only part of its roots. It exhibits small facets of wear. The tooth is relatively short with no developed cingulum. The paracone is the highest cusp, but it is considerably low. The metastyle is extremely small and worn, forming a very low crest with the paracone. The parastyle is restricted to a tiny worn cusp at the preparacrista. The protocone is wide, high and acute, with a developed medial shelf that hosts a small hypocone. The mesial border of the protocone is in the same plane as the total distal tooth end. Two additional ridges are present: one connecting the protocone with the parastyle and one connecting the paracone with the hypocone. Two small basins are formed, medially and distally to the crest that connects the paracone with the hypocone. Another oblique basin is visible mesially to the crest that connects the protocone with the parastyle.

The upper molars (Fig 13B–13D) are surrounded by a developed cingulum, which is stronger in its lingual side. The paracone and the metacone are relatively low and a preparacrista is present mesially to the paracone. The protocone is not developed as a distinct cusp, but a crista is developed near the mesial end of the preparacrista and expanded until the lingual cingulum at the plane of the metacone. The lingual side is relatively wide creating a valley lingually to the buccal cusps.

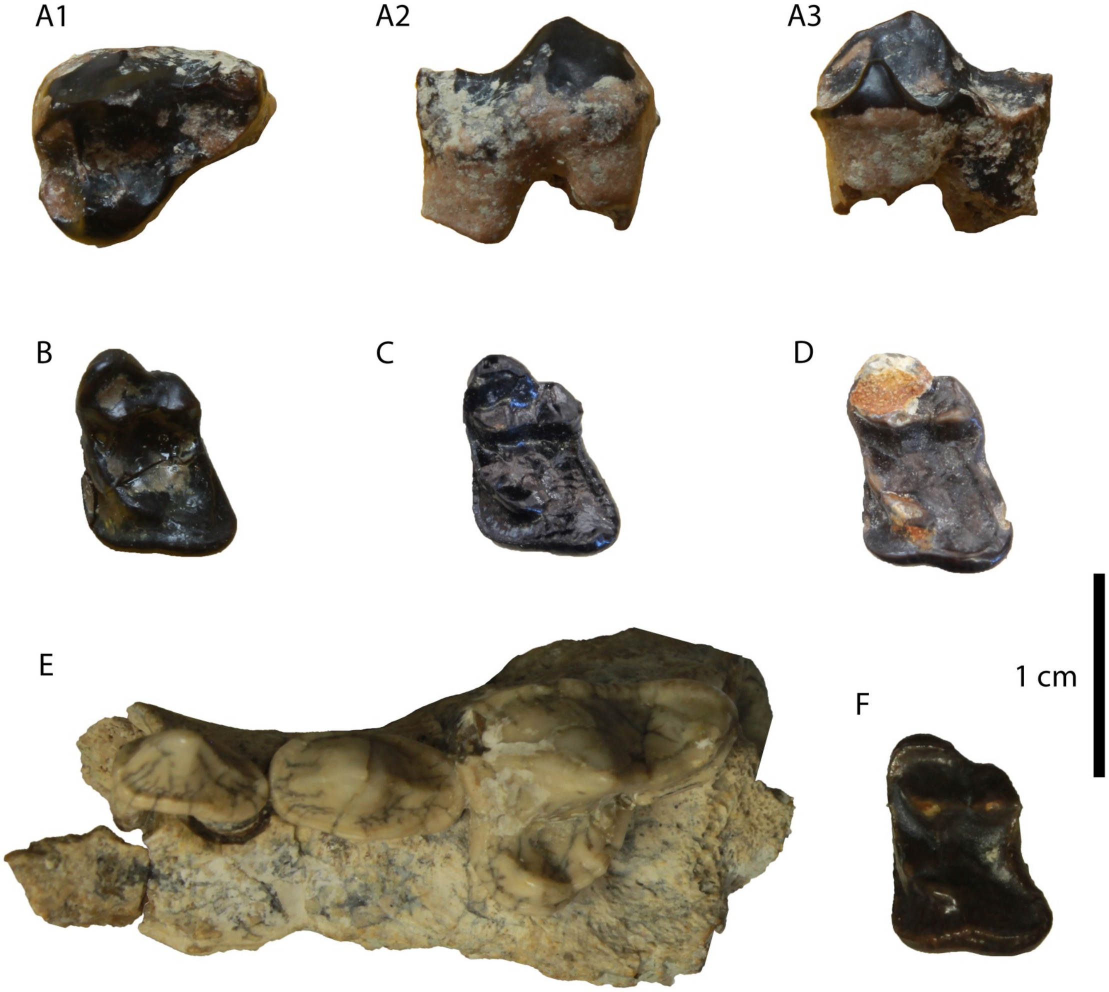

Fig 13. Material of *Paralutra jaegeri* from Hammerschmiede (A–D) and Steinheim (E–F): (A) GPIT/MA/10393 P4 in occlusal (A1), buccal (A2) and lingual view (A3); (B) GPIT/MA/12322 M1 in occlusal view; (C) SNSB-BSPG-2020 XCIV-5704 M1 in occlusal view; (D) SNSB-BSPG-2020 XCIV-5703 M1 in occlusal view; (E) SMNS-4082 left maxilla with P2–P4 in occlusal view, Holotype; (F) SMNS-16816 M1 in occlusal view.

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Comparison: The P4 does not belong to the subfamily Leptarctinae, because the medial shelf is not bent mesially and because of its larger size [124]. It cannot be attributed to the lineage of *Potamotherium*, since it has a relatively weak lingual cingulum [125]. Additionally, the presence of a hypocone is another character excluding Melinae [126]. On the contrary, general morphology of the specimen fits to that of the Miocene lutrines.

The subfamily Lutrinae is represented by the genera *Sivaonyx*, *Limnonyx* Crusafont Pairó, 1950 [127], *Lartetictis* Ginsburg and Morales, 1996 [128] and *Paralutra* at the Middle/Late Miocene of Europe. The genus *Sivaonyx* is represented by the species *Sivaonyx hessicus* (Lydekker, 1890) [129] in Europe, and no upper carnassial of it has ever been published. However, other members of the genus exhibit a far more developed medial shelf that results in a square outline in the carnassial [130]. It is reasonable to suggest that the morphology of *S. hessicus* would not have been significantly different from that of the other members of its genus. Concerning the genus *Limnonyx*, [34] considered it as a member of the tribe Aonyxini, which is characterized by an enlarged medial shelf, similar to extant *Aonyx* Lesson, 1827 [131]. The genus *Lartetictis* exhibits a slenderer and more mesially situated protocone [132].

The upper molars from the herein presented material are characterized by a moderately developed lingual platform and a significant width difference between the paracone and the metacone, resembling a plesiomorphic musteline-like profile. This morphology fits both to *Paralutra jaegeri* and *Marcetia santigae* Petter, 1967 [36]. The latter species has been described by [36] from the locality of Can Llobateres 1 by a left M1, a right M1, a right P3 and a left P4 (the right M1 was erroneously misspelled as a right m1 in [36], but it is clear from the descriptions and the figures that it is an upper molar). The author noted that the upper molars were extremely similar to that of *Paralutra jaegeri*, whereas the upper carnassial had a musteline-like morphology. Additionally, [133] stated that this form was referred to as "*Paralutra* sp." in publications concerning the fauna of Can Llobateres, before the publication of [36]. However, the new name, *Marcetia santigae*, was given to this material based on the fact that these four teeth were found together. Though, it must be noted that none of the four teeth published by [36] have been found in actual association with each other as no traits of connective bone is present [36]. Therefore, since exact taphonomic data from these excavations do not exist, there is no direct evidence indicating that these teeth actually belong to the same individual or to the same species.

The species *Paralutra jaegeri* has been found to have significantly high intraspecific variability as seen in the material from Steinheim [90]. Some specimens exhibit a relatively restricted lingual platform, whereas others a considerably developed one [90]. The three specimens from Hammerschmiede also exhibit a notable variability: GPIT/MA/12322 (as well as the upper molars of *Marcetia*) resemble more the morphology of SMNS-16814 [90], because of the non-evident constriction lingually to the buccal cusps, whereas the two other Hammerschmiede molars fit better with SMNS-16816 (Fig 13C; [90]). Unfortunately, the two molars described by [36] as "*Marcetia santigae*" are either lost or destroyed (Robles, pers. comm.), so a more detailed comparison is not possible. Therefore, we suggest that based on the similar variability of the M1s of Hammerschmiede and Steinheim the Hammerschmiede specimens belong to the species *P. jaegeri* (Table 11). This leads us to hypothesize based on the M1 that *Marcetia* could be a junior synonymy of *Paralutra*. Only new findings from Can Llobateres, especially complete and associated P4 and M1, would clarify the taxonomic status of *Marcetia*.

Genus *Lartetictis* Ginsburg & Morales, 1996 [128]

Type species: *Lartetictis dubia* (de Blainville, 1842) [89]

Other included species: *Lartetictis pasalarensis* Valenciano et al., 2020 [132].

Remarks: The genus *Lartetictis* is typical for the Middle Miocene faunas of Europe, as it has been reported in several localities ([132] and references therein). Its subfamily status is still

Table 11. Comparison of P4 and M1 dimensions between the Hammerschmiede specimens of *Paralutra jaegeri* and material from other localities indicating the data source.

Code/Locality	P4L	P4W	M1L	M1W
GPIT/MA/10393	11.1	9.4		
GPIT/MA/12322			6.7	11.0
SNSB-BSPG-2020-XCIV-5704			6.5	9.7
SNSB-BSPG-2020-XCIV-5703			6.8	9.8
Steinheim	10.9–12.7 11.8 (2)	8.0–10.8 9.4 (2)	7.6–8.1 7.9 (4)	10.2–10.4 10.3 (4)
Rudabánya [65]	10.3–12.0 11.2 (2)	9.7–10.3 10.0 (2)	9.3–9.6 9.5 (2)	12.1–12.4 12.3 (2)
Can Llobateres "*Marcetia santigae*" [36]	8.5		6.8	9.9

https://doi.org/10.1371/journal.pone.0268968.t011

Fig 14. Material of cf. *Lartetictis* cf. *dubia* from Hammerschmiede: (A) GPIT/MA/17790 hemimandible and (B) GPIT/MA/13749 m1.

https://doi.org/10.1371/journal.pone.0268968.g014

debatable as some authors consider it as a lutrine [132], while others as a musteline [74, 134]. However, its semi-aquatic adaptations have been widely accepted [134].

Lartetictis cf. *dubia* (de Blainville 1842) [89]

Holotype: MNHN Sa 801, right hemimandible with p2–m2.

Type Locality: Sansan (France).

Referred Specimens: HAM 4: GPIT/MA/17790, left hemimandible with p3–m1 and the alveoli of p2 and m2; SNSB-BSPG-2020-XCIV-2683, left m1.

Description: The specimen GPIT/MA/17790 (Fig 14A) is a left mandibular corpus with p3–m1 and the alveoli of p2 and m2. A mental foramen is present below p3 and the masseteric fossa ends at the level of m2. Both p3 and p4 are asymmetrical, they have a smooth cingulid and they don't have accessory cuspids. The fourth premolar is significantly higher and longer than the third one. The lower carnassial is long and relatively low, with the talonid covering approximately 30% of the tooth length. A relatively developed cingulid encircles the tooth, being more developed in its buccal part. There are faint signs of wear in the carnassial blade. The protoconid is the highest cuspid, separated from the paraconid by a shallow notch. The metaconid is high (approximately at the same height as the paraconid), acute and not lingually bent. The talonid valley is shallow and the only talonid cuspid is the large and conical hypoconid. The same description applies for SNSB-BSPG-2020-XCIV-2683, which is an isolated left m1 (Fig 14B).

Comparison: Two members of the genus *Lartetictis* have been described: the type species *L. dubia* (MN 5–MN 8 of central Europe) and *L. pasalarensis* (MN 5 of Turkey) (132)

Table 12. Metrical comparison of the lower teeth of the different forms of *Lartetictis*. Values in parentheses indicate measurements of the alveolus indicating the data source.

Code/Species	p3L	p3W	p4L	p4W	m1L	m1trL	m1W	m2L	m2W
GPIT/MA/17790	5.9	3.3	7.7	4.5	12.2	8.7	6.2	(4.2)	(3.5)
SNSB-BSPG-2020-XCIV-2683					10.4	8.1	5.4		
Lartetictis dubia [72, 132, 134]	6.8–8.1 7.4 (6)	3.8–4.5 4.2 (4)	9.0–10.8 9.9 (6)	4.7–5.6 5.1 (5)	12.2–17.2 15.6 (13)		6.5–8.3 7.5 (12)	6.9–7.2 7.1 (2)	6.3–7.0 6.7 (2)
Lartetictis pasalarensis [132]	7.8	4.4	9.7–9.9 9.8 (2)	5.0–5.1 5.1 (2)	15.2–17.0 16.0 (6)		7.2–8.4 7.7 (7)	6.4–6.6 6.5 (2)	5.9–6.0 6.0 (2)

https://doi.org/10.1371/journal.pone.0268968.t012

(Table 12). Therefore, the specimens from Hammerschmiede (together with those from Mörgen; [135]) consist of the youngest record of the genus. The two species have been differentiated on the basis of the morphology of P4, M1, m1 and m2. Consequently, only the lower carnassial can be used herein for the identification. The most distinct difference between the two species is the morphology of the m1 hypoconid, which is relatively higher and narrower in *L. pasalarensis*, whereas it is shorter and wider in *L. dubia*. The Hammerschmiede material is closer to the type species in this character, as well as in the absence of a hypoconulid and the lingual cuspulets of the m1 talonid. However, the talonid basin is relatively shallow and the trigonid cuspids are relatively high, so we prefer to refer to this specimen as *Lartetictis* cf. *dubia*.

Subfamily Leptarctinae Gazin, 1936 [136]

Genus *Trocharion* Forsyth Major, 1903 [137]

Type species: *Trocharion albanense* Forsyth Major, 1903 [137]

Remarks: The subfamily Leptarctinae includes five genera of small-sized mustelids, mainly from North America and Asia. The only genus that has been found in Europe is *Trocharion albanense*, which is a typical member of the late Early to Late Miocene faunas of central Europe, as it has been found in La Grive-Saint-Alban [137], Vieux-Collonges [52], Steinheim [90] and in several sites in the Vallès-Penedès Basin [124]. Regarding *Gaillardina*, recorded from La Grive (MN 7 and MN 8; [138]), it was classified into the Leptarctinae by [38], based on the possession of a double temporal crest. However, as noted by [139], the M1 of this taxon does not display the typically bunodont leptarctine morphology, but rather a derived mustelid condition, as shown by the expanded lingual cingulum around the protocone (a morphology more typical of the Guloninae and Melinae). On this basis, [139] considered it more likely that the double temporal crest of this taxon is an independent acquisition, so that it must be excluded from the Leptarctinae. As such, *Trocharion* remains as the only representative of the Leptarctinae in Europe [124].

Trocharion albanense Forsyth Major, 1903 [137]

Holotype: NHMUK 5307, a right hemimandible with p4–m2.

Type Locality: La Grive-Saint-Alban (France).

Referred Specimens: HAM 4: GPIT/MA/16579; partial skull; GPIT/MA/12553, right M1; SNSB-BSPG-2020-XCIV-2690, left M1. HAM 5: GPIT/MA/13462, right M1; GPIT/MA/13712, right M1; GPIT/MA/18601, right M1; GPIT/MA/18607, right M1.

Description: The subfamily is represented in the present material only by one partial skull and six upper molars. The partial skull (GPIT/MA/16579; Fig 15A) is part of the distal region of the braincase. It is convex dorsally and concave ventrally, indicating tha the braincase of the species was relatively globular. It is marked by two converging well-developed temporal crests that merge at their most distal point. Their medial profile is more marked than the labial one.

The molars are three-rooted, sub-trapezoidal with the lingual side being shorter than the mesial one. They have a faint cingulum and exhibit developed facets of tooth wear (especially

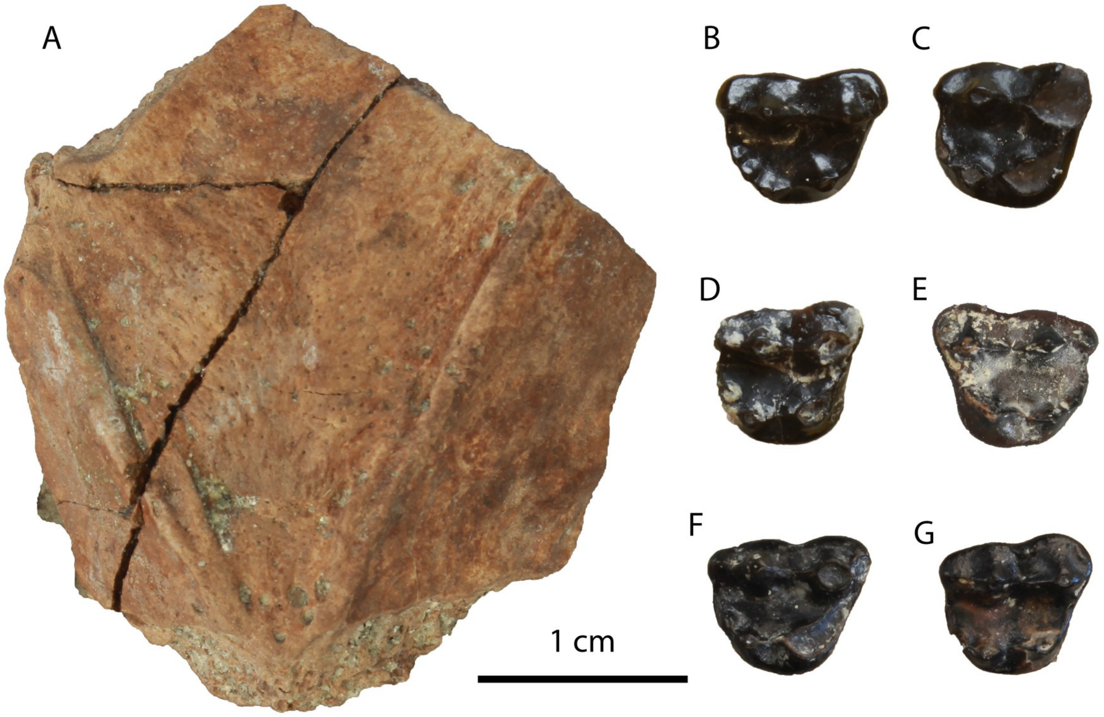

Fig 15. The material of *Trocharion albanense* from Hammerschmiede: (A) the partial skull GPIT/MA/16579 in dorsal view; (B–G) the M1 in occlusal view: (B) GPIT/MA/12553; (C) GPIT/MA/13462; (D) GPIT/MA/13712; (E) SNSB-BSPG-2020-XCIV-2690; (F) GPIT/MA/18601; (G) GPIT/MA/18607.

https://doi.org/10.1371/journal.pone.0268968.g015

in the mesial side) that restrict the detail of the description. The paracone is the longest cusp of the tooth, followed by the shorter and higher metacone, with which it is connected with a low crista. A postmetacrista connects the metacone with the distal cingulum that hosts a small accessory cusp (metastyle). The lingual part of the tooth hosts a large protocone mesially and two consecutive tiny cusps distally. The more mesially located one probably corresponds to the hypocone, while the second can be interpreted as a hypoconule. The most unworn specimen (GPIT/MA/12553; Fig 15B) exhibits another small cuspule, distobuccally to the other two.

Comparison: The described partial braincase is considerably fragmentary, which makes its identification problematic. However, the two well-defined temporal crests that converge distally are an apomorphy of the leptarctines [124]. Temporal crests are present in other groups of mammals through the Miocene, such as artiodactyles and primates, but in these cases they are now combined to a globular braincase or the absence of a sagittal crest.

The only subfamily that matches the rectangular outline, the cusp structure and the small size of the discovered M1 is Leptarctinae. Most leptarctine genera (except *Leptarctus* and *Trocharion*) are characterized by upper molars that are far wider than long [124, 139, 140]. Hence, the only comparable genus to *Trocharion* is *Leptarctus*, which has been found in Asia and North America. As aforementioned, the only European representative of the subfamily in Europe is *Trocharion albanense* (e.g. [124, 141]). Additionally, despite their overall similarity, the M1 of *Leptarctus* has a relatively similar lingual and buccal mesiodistal length [141–143], while that of *Trocharion* is clearly narrower lingually [124] (Table 13). Thus, based on the temporospatial range and morphological features, the material is assigned to *Trocharion albanense*.

Table 13. Metrical comparison of the Hammerschmiede material of *Trocharion albanense* to that from Vallès-Penedès and *Leptarctus* spp indicating the data source.

Species	Code	L	W	W/L
Trocharion albanense	SNSB-BSPG-2020-XCIV-2690	8.1	6.8	0.84
	GPIT/MA/12553	7.8	6.4	0.82
	GPIT/MA/13712	6.9	6.5	0.94
	GPIT/MA/13462	7.4	6.7	0.91
	GPIT/MA/18601	7.4	6.4	0.86
	GPIT/MA/18607	7.0	6.3	0.86
	Vallès-Penedès [124]	5.8–7.4 6.5 (12)	6.0–8.2 7.1 (14)	0.82–1.00 0.92 (11)
Leptarctus neimenguensis [142]		8.5	7.5	0.88
Leptarctus primus [142]		8.2	7.0	0.85

https://doi.org/10.1371/journal.pone.0268968.t013

Family Mephitidae Bonaparte, 1845 [32]

Subfamily Mephitinae Bonaparte, 1845 [32]

Genus *Palaeomeles* Villalta Comella & Crusafont Pairó, 1943 [30]

Type species: *Palaeomeles pachecoi* Villalta Comella & Crusafont Pairó, 1943 [30]

Remarks: *Palaeomeles pachecoi* is the only species of the genus *Palaeomeles*. It was originally described based on two associated fragmentary maxillas from Hostalets de Pierola in Spain [30]. One year later, the same authors published a mandibular fragment with a lower carnassial and the alveolus of the m2 from another site in the same region [144]. Several years later, [145] published additional dental material and some postcranial remains of this species from the locality of Castell de Barberá (early Vallesian, MN 9). In this study, the authors provided more details about the sites where the previous material was found. They stated that the material published by [30] was found "near Can Mata de La Garriga", while the material published by [144] comes from "the vicinity of Can Vila, near the local road of Can Mata". Therefore, it is registered in sediments of the late Aragonian to early Vallesian (MN 7/8 and MN 9) of Spain from Vallès-Penedès basin and potentially from Escobosa de Calatañazor [146].

Palaeomeles pachecoi Villalta Comella & Crusafont Pairó, 1943 [30]

Holotype: ICP-IPS697, a fragmentary maxilla including the right C alveolus, right P2 alveolus, right P3 and right P4, in addition to the left P4 and left M1.

Type Locality: Hostalets de Pierola (Spain).

Referred Specimens: HAM 5: GPIT/MA/12650, right P4; GPIT/MA/09884, right M1; GPIT/MA/09926, right M1; GPIT/MA/13711, right hemimandible with p3–m2; SNSB-BSPG-2020-XCV-0032, left hemimandible with p3–m1; GPIT/MA/13749, left m1. The hemimandibles were found in close proximity and they most probably belong to the same individual.

Description: The upper carnassial (GPIT/MA/12650; Fig 16A) is complete with faint signs of wear in the carnassial blade. A moderately developed cingulum surrounds the whole tooth. The paracone is the largest cusp and it is connected to the metastyle through a ridge. Mesially, there is a very small parastyle. The protocone region is long and distally situated. The protocone is relatively small and a slightly larger hypocone is also present.

The upper molars do not exhibit extensive signs of wear. However, the specimen GPIT/MA/09884 (Fig 16C) is partly damaged, so the description is based mainly on GPIT/MA/09926 (Fig 16B). The molars have an oval-trapezoidal shape and a strong cingulum in their perimeter, which is especially developed in the buccal and distal parts of the tooth. All the cusps are considerably low. The largest cusp is the paracone, which is slightly higher, longer and wider than the metacone. These two cusps are connected with a low and relatively

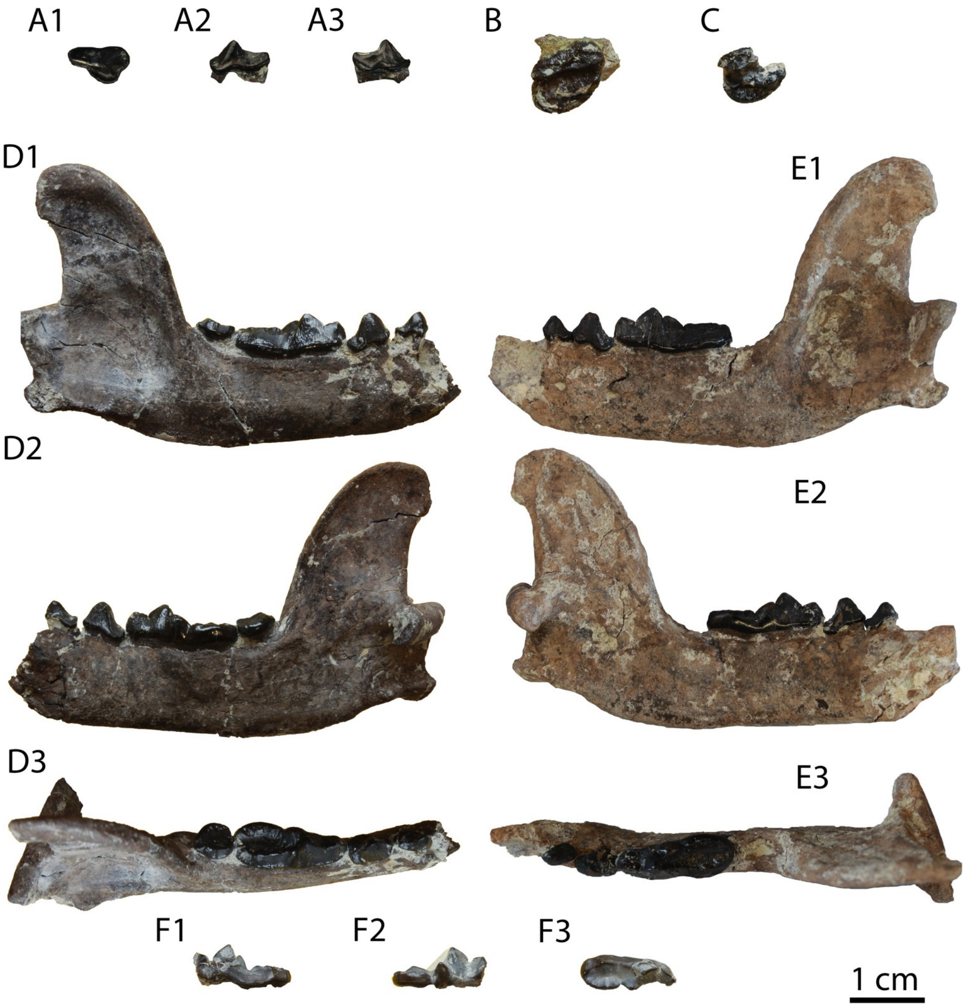

Fig 16. Material of *Palaeomeles pachecoi* from Hammerschmiede: (A) GPIT/MA/12650 P4; (B) GPIT/MA/09926 M1; (C) GPIT/MA/09884 M1; (D) GPIT/MA/13711 right hemimandible; (E) SNSB-BSPG-2020-XCV-0032 left hemimandible; (F) GPIT/MA/13749 m1.

https://doi.org/10.1371/journal.pone.0268968.g016

continuous crista. A small mesostyle is present in the buccal cingulum. A relatively large protoconule is also present, followed by a strong preprotocrista that ends at the plane of the metacone. This part is slightly worn, not enabling a detailed description. The distolingual part of the tooth is moderately enhanced, having a more robust cingulum, which is distally placed, in opposition to the mesial protocone. The surface of the tooth is marked by faint grooves.

Both hemimandibles are broken just mesially to the alveolus of p3 (Fig 16D, 16E). The mandibular body is thick and it hosts two mental foramina: one smaller and long under the distal root of p4 and one larger and circular under the distal root of p3. The mandibular corpus slowly becomes lower mesially. The masseteric fossa is deep and it reaches the level of m2's distal border. Both angular processes are broken. The mandibular condyle is considerably wide and it is situated quite dorsally to the angular process. The coronoid process is high and sigmoid-shaped with its tip placed distally, resembling that of the extant red panda (*Ailurus fulgens*). No diastemata are present.

The third and the fourth premolars have a similar simple morphology, without accessory cuspids, with a faint ridge extending disto-lingually of the main cuspid and a smooth cingulid.

They are both relatively robust, blunt and asymmetrical. However, the p4 is considerably larger than the p3. The lower carnassial has a stronger cingulid and its talonid is very long (especially in its buccal side), covering approximately 45–50% of the tooth length. It is very slightly worn in both the talonid cingulid and the carnassial blade. The buccal surface of the carnassial is rough. The trigonid cuspids are low. The protoconid is the largest one, while the metaconid and the paraconid have a relatively similar size, with the paraconid being longer and narrower. The protoconid is separated from the paraconid with a shallow notch. The metaconid is blunt and distolingually oriented. The talonid valley is long and shallow. All talonid cuspids are very small, especially the hypoconulid. Signs of wear are present between the hypoconid and the protoconid. Faint folds of the cingulid surface create tiny cuspules at its lingual part. The second molar is almost circular and the occlusal surface is not mesially bent. There is a strong cingulid that congregates several small cuspulids in its perimeter. The largest is located in its distobuccal part, and most probably corresponds to a hypoconid, whereas the protoconid is situated in its mesiobuccal region.

Comparison: This species is characterized by the derived features of its dentition towards a badger-like ecomorphotype. The upper carnassial has a developed, distally placed protocone region that hosts a developed hypocone. The upper molar is oval-like, much different than the rectangular molar of the intermediate fossil "badgers", such as *Promeles* (e.g. [66, 104]), *Taxodon* (e.g. [72]), *Trochictis depereti* (e.g. [147]) and *Ferinestrix* (e.g. [148]). All these taxa also have a relatively shorter m1 talonid and higher cusps in both M1 and m1 compared to *Palaeomeles*. The only genera with a comparable relative length of m1 talonid are the extinct *Melodon* and *Palaeomeles*. The genus *Melodon* exhibits some intrageneric variability, with the three species *Melodon incertum* Zdansky, 1924 [77], *Melodon major* Zdansky, 1924 [77] and *Melodon sotnikovae* (Tedford & Harington, 2003) [149] having some important differences. In comparison to *Palaeomeles*, *M. incertum* has a much more primitive M1 of rectangular shape, while *M. major* has a much more derived one, very similar to that of *Meles* (see [77]). On the other side *M. sotnikovae* has a M1 similar to that of *M. major* and an m1 with a relatively shorter talonid [149, 150]. All these species exhibit high cuspids in their m1 talonid. The only species that fits perfectly with the present specimens with an extremely derived molar morphology (enhanced lingual part of M1, very long m1 talonid and low m1 cuspids) and its moderate size is *Palaeomeles pachecoi*. The specimens of *P. pachecoi* from Hammerschmiede are the largest of this species in the fossil record (Tables 14 and 15).

Genus *Proputorius* Filhol, 1890 [26]

Type species: *Proputorius sansaniensis* Filhol, 1890 [26]

Other included species: *Proputorius pusillus* (Viret, 1951) [27]

Proputorius sansaniensis Filhol, 1890 [26]

Holotype: MNHN-Sa 776, left hemimandible with c and p3–m1.

Type Locality: Sansan (France).

Referred Specimens: HAM 1: SNSB-BSPG-1973-XIX-24, right p4; SNSB-BSPG-1973-XIX-25, right m1.

Table 14. Metrical comparison of the two M1 of *Palaeomeles pachecoi* from HAM 5 with that of *P. pachecoi* from Spain indicating the data source.

Code/Locality	P4L	P4W	M1L	M1W
GPIT/MA/12650	7.4	4.8		
GPIT/MA/09926			9.6	7.7
GPIT/MA/09884				(7.4)
Castell de Barberá & Hostalets [30, 145]	7.5	5.0	8.0–8.6 8.3 (3)	6.9–7.7 7.2 (3)

https://doi.org/10.1371/journal.pone.0268968.t014

Table 15. Metrical comparison of the lower dentition of *Palaeomeles pachecoi* from HAM 5 with that of *P. pachecoi* from Spain indicating the data source.

Code/Locality	p3L	p3W	p4L	p4W	m1L	m1trL	m1W	m2L	m2W
GPIT/MA/13711	4.2	2.6	5.4	3.8	14.2	8.4	5.7	5.0	4.7
BSPG 2020 XCV-0032	4.1	2.5	5.4	3.6	14.4	8.7	5.7		
GPIT/MA/13749					12.7	6.9	4.6		
Castell de Barberá & Hostalets [30]	4.1	2.3	5.2	3.0	10.8–11.0 11.0 (3)		4.0–4.5 4.3 (3)	3.8–4.5 4.3 (3)	2.5–3.9 3.4 (3)

https://doi.org/10.1371/journal.pone.0268968.t015

Description: The specimen SNSB-BSPG-1973-XIX-24 is a right p4 with no signs of wear (Fig 17A). It is asymmetrical with the distal part being longer and wider than the mesial part. It is unicuspid with a faintly rough enamel surface. The mesial and distal ridges of the main cuspid host a cristid. It is two-rooted and with a faint cingulid.

The lower carnassial (SNSB-BSPG-1973-XIX-25; Fig 17B) exhibits distinct signs of wear in the carnassial blade. The protoconid is the highest and longest cuspid. It is separated from the paraconid by a deep notch. The metaconid is high (almost as high as the paraconid) and well-individualized from the protoconid. A small valley is formed between the metaconid and the paraconid. The talonid is long with a deep valley. The hypoconid is enlarged (height, width and length) and the rest of the talonid border hosts small cuspulids. The talonid is relatively developed in the mesiobuccal part of the tooth, but more reduced in the rest of the dental border.

Comparison: The known dentition sample of this species from Sansan is quite complete. [4] described some teeth of *P. sansaniensis* from Hammerschmiede including the I3, P4, p3, m1 and m2. The isolated incisor does not exhibit any diagnostic features, so it is not attributed to any group herein. The P4 clearly differs to the P4 of *P. sansaniensis* in being more elongated and having an enlarged and mesiolingually projected protocone to that of the specimen from Sansan Sa 15668 [72], which is more reduced and closer to the paracone. As we mentioned

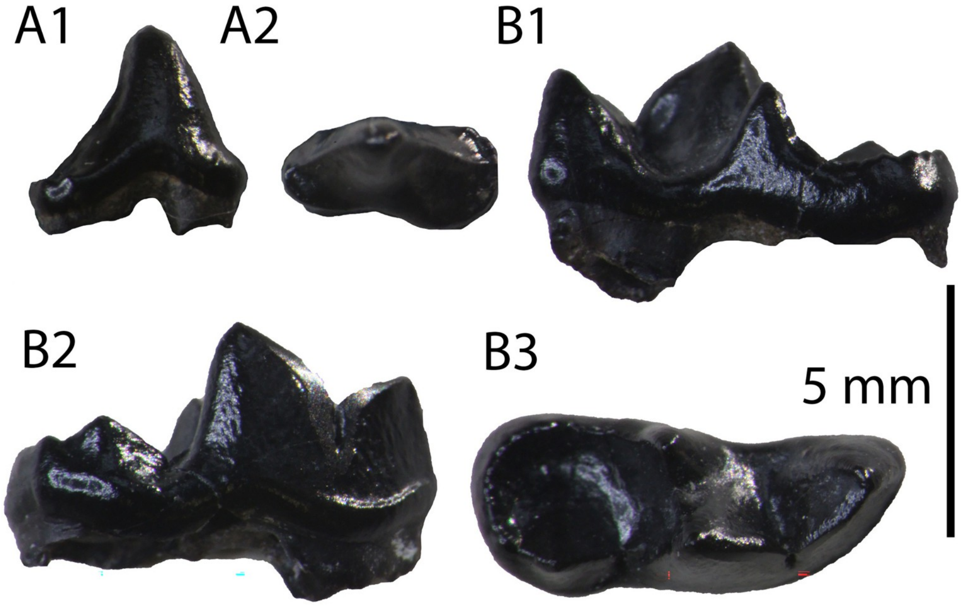

Fig 17. Material of *Proputorius sansaniensis* from Hammerschmiede: (A) SNSB-BSPG-1973-XIX-24: right p4 in buccal (A1) and occlusal (A2) views; (B) SNSB-BSPG-1973-XIX-25: right m1 in lingual (B1), buccal (B2) and occlusal (B3) views.

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Table 16. Metrical comparison of the upper and lower dentition of *Proputorius sansaniensis* and *Proputorius pusillus* from HAM 1 (the abbreviation SNSB-BSPG- was removed to save space) with other material of the genus indicating the data source.

Species	Code/Locality	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W
P. sansaniensis	1973-XIX-24			4.3	2.2				
	1973-XIX-25					8.3	3.6		
P. pusillus	1973-XIX-30	1.9	0.9						
	1973-XIX-31	2.1	1.0						
	1973-XIX-32					4.2	1.6		
	1973-XIX-33					4.5	1.7		
P. sansaniensis	Sansan [72]	3.7–4.3 3.9 (10)	2.0–2.3 2.1 (9)	4.1–5.3 4.9 (14)	2.2–2.9 2.6 (14)	8.0–10.4 9.4 (18)	3.6–4.7 4.1 (18)	3.4–4.0 3.7 (3)	2.7–3.2 3.0 (3)
P. pusillus	Vieux-Collonges [52]	2.3–2.3 2.3 (3)	1.2–1.4 1.3 (3)	2.7–2.9 2.8 (6)	1.4–1.5 1.5 (6)	4.4–5.4 4.9 (15)	1.9–2.4 2.1 (15)	1.9–2.3 2.1 (6)	1.5–1.7 1.6 (6)

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above, this tooth is herein re-classified as *Circamustela hartmanni* n. sp. The m2 of *Proputorius* spp. includes only one cuspid (protoconid) at its central-buccal side [52, 72]. On the contrary, the m2 described by [4] has two larger and one smaller cuspid in its border. As discussed below, this tooth is here attributed to a viverrid. The rest of the teeth are similar to that of *P. sansaniensis* from Sansan (Table 16).

Proputorius pusillus (Viret, 1951) [27]

Lectotype: [27] did not define a holotype. However, the first specimen mentioned by [27] is MHNL-Lg 1256, which is a right hemimandible with p3–m1. This is also the most complete specimen published by [27]. Therefore, it is proposed as the lectotype of the species by present designation under the provisions of ICZN Art. 74.

Type Locality: La Grive (France).

Referred Specimens: HAM 1: SNSB-BSPG-1973-XIX-30, right p3; SNSB-BSPG-1973-XIX-31, right p3; SNSB-BSPG-1973-XIX-32, right m1; SNSB-BSPG-1973-XIX-33, right m1.

Description: The p3 are of typical mephitid morphology. They are triangular in buccal and occlusal, unicuspid and distally enlarged with a complete cingulid rounded the tooth view (Fig 18A). The lower carnassials (Fig 18B) have an open m1 trigonid with very tall protoconid, and a metaconid almost reaches the height of the paraconid. The talonid shows some variability, being slenderer with a lower entocristid in SNSB-BSPG-1973-XIX-32. Both talonids are rhomboidal in occlusal view. The hypoconid is buccally located, relatively tall and crested-like, with a bevelled wall in its lingual part.

Comparison: This material was reported in [4], but it was never described. Both lower premolars are similar to the ones of *P. pusillus* in terms of morphology and dimensions [52] (Table 16). Among the two m1s, one is comparable to *P. pusillus* (SNSB-BSPG-1973-XIX-33) based on the specimens from La Grive and Vieux-Collonges, and the other one (SNSB-BSPG-1973-XIX-32) is close to "*Martes*" *jaegeri* in having similar metaconid and talonid morphology but slightly smaller and with a less marked cingulid. The sample of *P. putorius* from the type locality shows also some variability in the width of the m1 talonid, with some forms being more robust than others [27]. Consequently, until more material is available from Hammerschmiede we classify the smallest musteloid taxon as *P. pusillus*, with the exception of the P4 SNSB-BSPG-1973-XIX-34. This material fits to the smallest specimens of the species from La Grive [27], Vieux-Collonges [52] and Sandelzhausen [73].

Family Ailuridae Gray, 1843 [33]

Subfamily Simocyoninae Dawkins, 1868 [151]

Genus *Alopecocyon* Camp & Vanderhoof, 1940 [152]

Type species: *Alopecocyon goeriachensis* (Toula, 1884) [153]

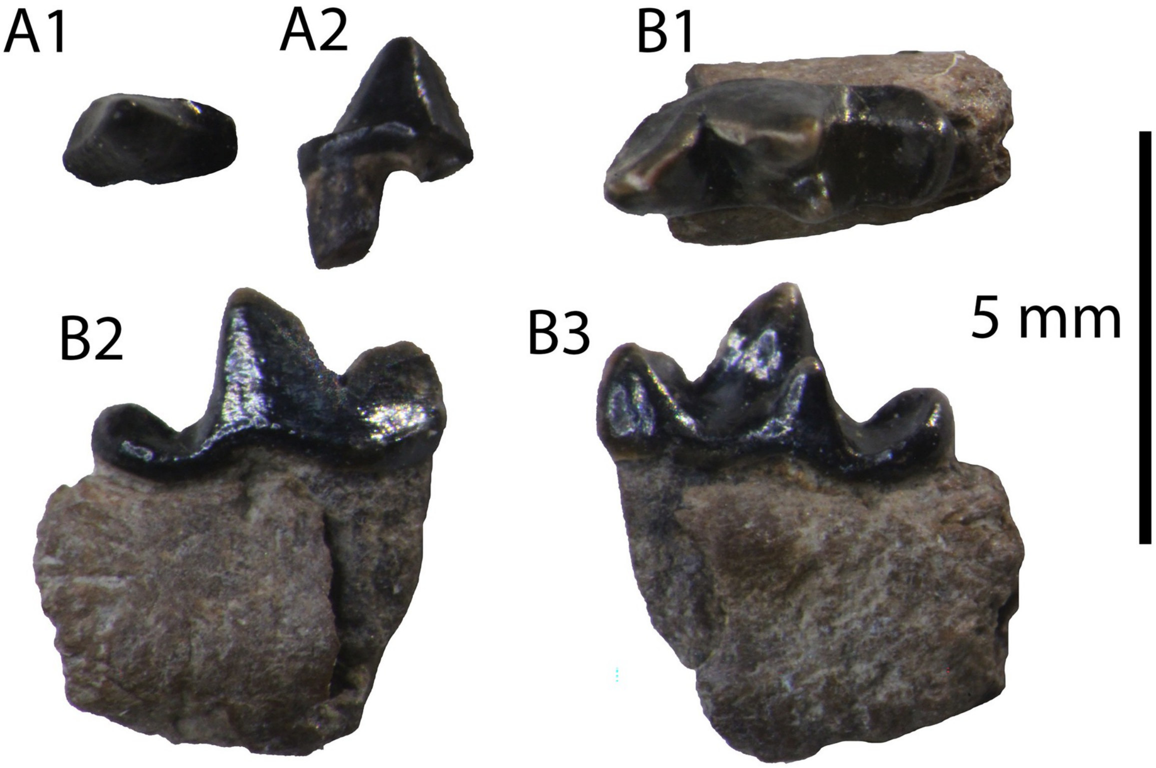

Fig 18. Material of *Proputorius pusillus* from Hammerschmiede: (A) SNSB-BSPG-1973-XIX-31, left p3 in (A1) lingual and (A2) occlusal views; (B) SNSB-BSPG-1973-XIX-32, right m1 in (B1) occlusal (B2) buccal and (B3) lingual views.

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Questionable other included species: *Alopecocyon getti* Mein, 1958 [52]; *Alopecocyon leardi* Stock, 1947 [154].

Remarks: The only well-known species of this genus is the type species, *Alopecocyon goeriachensis* (Toula, 1884) [153]. This form has been described from several localities in the Middle Miocene of Europe, such as Göriach [153], Sansan [72, 85], La Grive-Saint-Alban [27], but also from the locality Duolebulejin in China [155]. Some material from Vieux-Collonges has been considered to be a different form, *Alopecocyon getti* Mein, 1958 [52], but the taxonomic position of this species has been questioned by some scholars [156]. The species "*Alopecocyon*" *leardi* (Stock, 1947) [154] was originally described as a species of *Actiocyon* Stock, 1947 [154], but it was later transferred into *Alopecocyon* (Webb, 1969) [157]. However, once again, this attribution is not considered undoubtful [156]. The youngest record of *Alopecocyon* is from Rudabánya [65] as "*Viretius* sp.", but this form is far larger than *A. goeriachensis* (Table 17; Fig 21). Thus, the herein described molar consists of the youngest report of *A. goeriachensis* in the fossil record.

Alopecocyon goeriachensis (Toula, 1884) [153]

Holotype: NHMW 470/1963, an assemblage of specimens (possibly from the same individual; [27]) that includes right C, P4, M1 and M2, fragmentary left p4 and m1 and fragmentary right p4 and m1.

Type Locality: Göriach (Austria).

Referred Specimens: HAM 5: SNSB-BSPG-2020 XCV-382, right M1.

Description: The upper molar (Fig 19) is complete with no signs of wear. Its outline is triangular and it has a relatively strong cingulum on its buccal and mesial side. The lingual

Table 17. Comparison of M1 and m2 between the specimens from Hammerschmiede and other Miocene ailurids from Europe indicating the data source.

Species	M1L	M1W	M1W/M1L	m2L	m2W	m2W/m2L
Alopecocyon goeriachensis SNSB-BSPG-2020 XCV-382	8.1	10.1	124%			
Simocyoninae indet. (SNSB-BSPG-2020 XCIV-5705)				10.3	5.7	55%
Alopecocyon goeriachensis Göriach [168], Oppeln [168], Schlieren-Uetikon [168], La Grive-Saint-Alban [82], Sansan [72], Leoben [72]	8.2–9.3 8.8 (5)	9.5–10.5 9.9 (4)	107–118% 111% (4)	6.3–8.0 7.0 (3)	4.0–5.0 4.1 (3)	57%–63% 59% (3)
Protursus simpsoni Can Llobateres [159], Rudabánya [65]	11.8–11.9 11.9 (2)	12.9–13.1 13.0 (2)	109%–110% 110% (2)	11.8–12.4 12.1 (2)	6.8–6.9 6.9 (2)	55–58% 57% (2)
Magerictis imperialensis Madrid [167]				12.1	5.8	48%
Simocyon diaphorus Rudabánya [65], Eppelsheim [169]	14.8	18.8	127%	14.2	7.9	56%
Simocyon batalleri Batallones-1 [170]	15.7–17.0 16.4 (4)	18.6–20.0 19.3 (4)	115%–120% 117% (4)	15.9–16.0 16.0 (3)	7.6–8.4 8.1 (3)	48%–53% 51% (3)

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border of the tooth also forms a robust wall, which is bent distally. The cusps are relatively low. The paracone is the highest cusp, being slightly longer than the metacone. These two cusps are connected at their bases through their crests. A crest starts from the paracone and it ends just before the buccal crest of the protocone. A minute metaconule is present at the distal part of the tooth. No sign of a paraconule or any other accessory cusp is present. However, the lingual border of the tooth is marked by faint notches, creating very small cuspules in its occlusal surface.

Comparison: The fossil record of the ailurids includes several different forms during the Miocene of Europe. [156] made a comprehensive review of the fossil representatives of Ailuridae. The smallest genus (and the most basal after *Amphictis* Pomel, 1853 [158]) is *Alopecocyon*, which was erected for the species *Alopecocyon goeriachensis* from Göriach by [153]. This taxon is attributed to the subfamily Simocyoninae, which also includes the genera *Protursus* Crusafont Pairó & Kurtén, 1976 [159] (including *Protursus simpsoni* Crusafont Pairó & Kurtén, 1976 [159]) and *Simocyon* Wagner, 1858 [160] [including the smaller-sized *Simocyon diaphorus* (Kaup, 1832) [161] and *Simocyon batalleri* Viret, 1929 [162], as well as the larger-sized *Simocyon primigenius* (Roth & Wagner, 1854) [163] and *Simocyon hungaricus* (Kadic & Kretzoi, 1927) [164]]. This subfamily includes forms with relatively hypercarnivorous adaptations (reaching their climax in *S. primigenius*). The subfamily Ailurinae Gray, 1843 [33], characterized by hypocarnivorous adaptations, includes the extant genus *Ailurus* Cuvier, 1825 [165], as well as the fossil genera *Parailurus* Schlosser, 1899 [166] (morphologically close to *Ailurus*; Pliocene), *Pristinailurus* Wallace & Wang, 2004 [150] (latest Miocene/Pliocene of the USA) and *Magerictis* Ginsburg et al., 1997 [167] (including *Magerictis imperialensis* Ginsburg et al., 1997 [167] from the Middle Miocene of Spain).

The herein described specimen is relatively small in size and has a high M1W/M1L ratio (Table 17). These dimensions only fit to *A. goeriachensis* from La Grive-Saint-Alban. The species *Magerictis imperialensis* is known exclusively from an m2. However, based on its dimensions, the size of its M1 is expected to be similar or larger to the M1 described as "Simocyoninae indet." below (Figs 20 and 21). Therefore, it is also considerably larger than SNSB-BSPG-2020 XCV-382.

[65] published two upper molars from Rudabánya as "*Viretius* sp." and a partial hemimandible as *Ursavus brevirhinus*. However, these three specimens are herein considered to be of different taxonomic status. The upper molars are considerably larger than those of *A. goeriachensis* (Table 17; Fig 20) and they also exhibit some morphological differences, such as

Fig 19. The upper first molar of *Alopecocyon goeriachensis* from Hammerschmiede (SNSB-BSPG-2020 XCV-382) in (A) occlusal, mesial (B) and buccal view (C).

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the less evident constriction of the tooth at the lingual base of the buccal cusps, the deeper valley between the buccal and the lingual cusps, the more developed metaconule, the more restricted region between the protocone and the lingual cingulum, as well as the more developed cingulum around the tooth. The hemimandible from Rudabánya shares several similarities with the ailurids, such as the absence of m3, the high and separated paraconid and metaconid in m2, the simple talonid in m2 and the high m2L in relation to m2W that differentiate it from the ursids. In particular, the m2W/m2L ratio in the specimen is 55%, whereas the known range for the ursid genus is 59–67% [171]. Judging from the size (Table 17; Figs 20 & 22) and morphology, the mandible and upper molars from Rudabánya can be attributed to the species *Protursus simpsoni*. The preserved m2 (RUD/1989/142) is almost identical to the one from Can Llobateres, with the exception of stronger cingulum crests being present in the specimen from Rudabánya. Additionally, the age of the two localities is similar. Therefore, it is

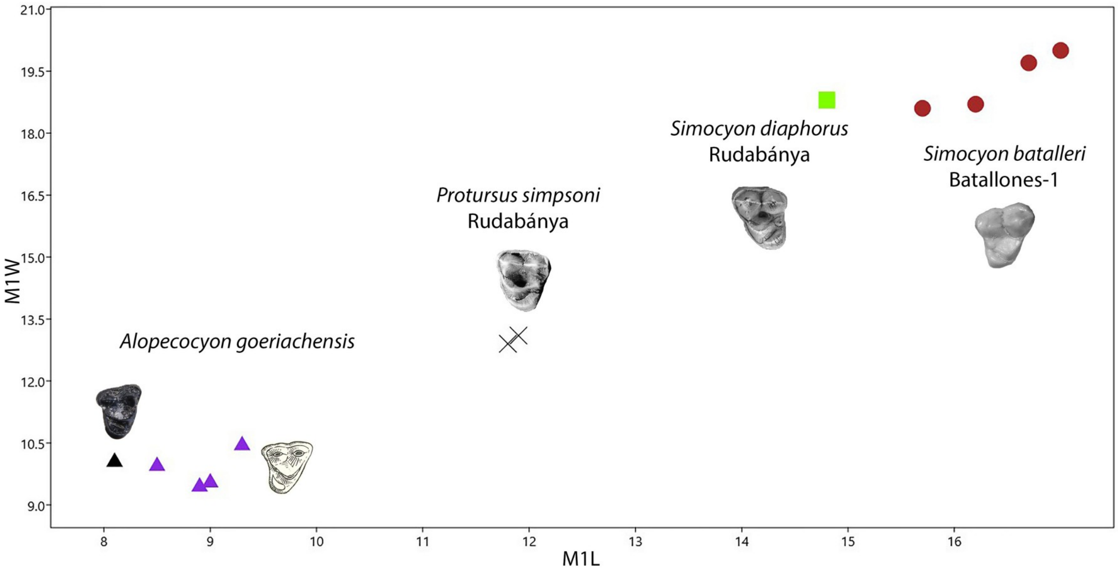

Fig 20. Scatter plot comparing the M1 dimensions of Middle and Late Miocene ailurids of Europe: black triangle = *Alopecocyon goeriachensis* from Hammerschmiede; violet triangle = *Alopecocyon goeriachensis* from other localities [82, 168], black X = *Protursus simpsoni* from Rudabánya [65], green square = *Simocyon diaphorus* from Rudabánya [65] and brown dots = *Simocyon batalleri* from Batallones-1 [170].

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herein suggested that this specimen belongs to *P*. *simpsoni*. Based on size, distinct morphology, correlated ecomorphological trends and taxonomic parsimony, we suggest that the two upper molars from Rudabánya also belong to this form.

In this new scheme, the Hammerschmiede molar differs from the Rudabánya in all discussed traits. The morphological characteristics typical for the genus *Alopecocyon* are evident in the present specimen, such as the relatively narrow and bent lingual part of the tooth, its short length in relation to its width, the absence of a cavity between the buccal and lingual cusps, the absence of accessory cuspules, the relatively small buccal cusps, the small metaconule and the moderately developed cingulum.

Simocyoninae indet.

Referred Specimens: HAM 4: SNSB-BSPG-2020 XCIV-5705, right m2.

Description: The specimen SNSB-BSPG-2020 XCIV-5705 is a complete right m2 with no sings of wear (Fig 21). It is two-rooted, with the distal root being more elongated and thinner than the mesial one. The talonid is very large, covering approximately 60% of the tooth's length. The overall shape of the tooth outline is bean-like with the buccal side being concave and the lingual one convex, while the tooth is most wide at the level of the protoconid-metaconid. A faint rounded cingulid can be seen in the distal part of the tooth. The trigonid hosts two large cuspids: the protoconid and the metaconid. Both of them are blunt, stemming from the buccal and lingual border of the tooth respectively and they are placed 1–2 mm from the corner of the tooth. They are connected with a transverse cristid that forms a small notch in its middle point. The protoconid is slightly higher and vertical, whereas the metaconid is lower and lingually inclined. The tooth border mesially to these cuspids is marked by four notches that create small cuspulids in the faint cingulid. The largest of them, placed at the buccal side of the tooth, can be tentatively interpreted as a small paraconid. The talonid valley is relatively shallow and long. Distally to the metaconid there is a cuspid just buccally to the lingual border of the tooth that corresponds to a small hypoconid. Again, four notches mark the distal part of the talonid creating cuspulids. The largest of them, at the distolingual part of the tooth, can be interpreted as a hypoconulid.

Comparison: The m2 of *A*. *goeriachensis* is considerably smaller than the specimen found in Hammerschmiede (Table 17; Figs 20 and 22). [85] noted that the second lower molar of *A*. *goeriachensis* has a developed paraconid, hypoconid, hypoconulid and entoconid. These structures are only faintly seen in SNSB-BSPG-2020 XCIV-5705 as intermediate regions between the cingulid's notches. Additionally, the distal part of that tooth in *A*. *goeriachensis* is more bent lingually than in the Hammerschmiede molar.

The lower second molar of *Magerictis* is slightly larger than the herein presented respective tooth and has a lower m2W/m2L ratio (Table 17; Fig 22). Additionally, this tooth differs significantly from SNSB-BSPG-2020 XCIV-5705 in several morphological traits: the outline of the tooth is not oblique, there are no connecting cristae between the metaconid and the

Fig 21. The right m2 of Simocyoninae indet. from Hammerschmiede (SNSB-BSPG-2020 XCIV-5705) in: (A) occlusal, (B) buccal and (C) lingual view.

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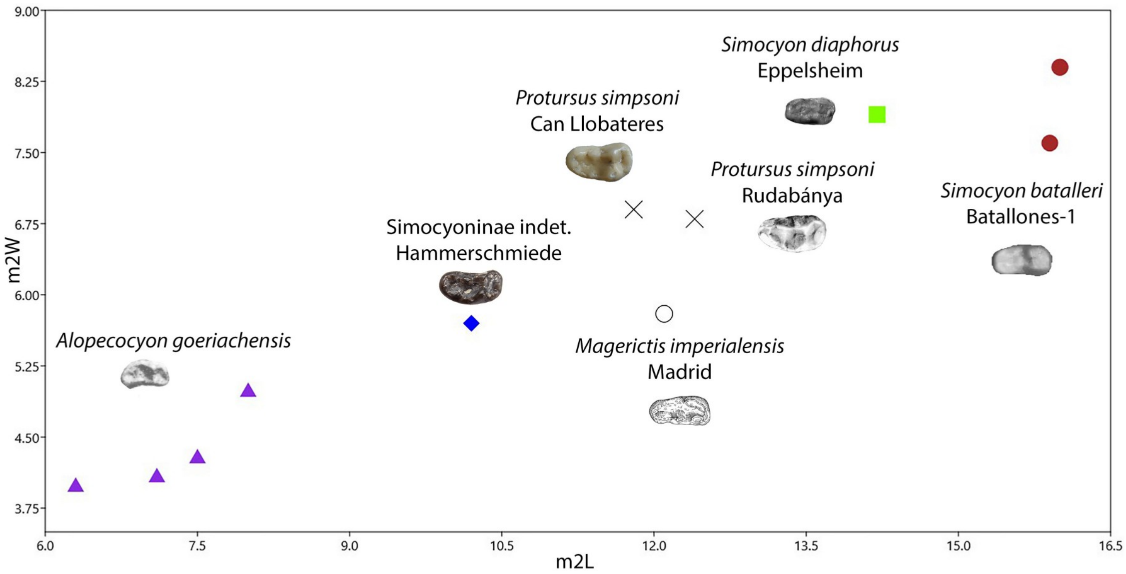

Fig 22. Scatter plot comparing the m2 dimensions of Middle and Late Miocene ailurids of Europe: violet triangles = *Alopecocyon goeriachensis* [27, 72, 168], blue rhombus = Simocyoninae indet. from Hammerschmiede (SNSB-BSPG-2020 XCIV-5705), black X = *Protursus simpsoni* from Can Llobateres [159] and Rudabánya [65], black circle = *Magerictis imperialensis* from Madrid [167], green square = *Simocyon diaphorus* from Eppelsheim [169] and brown dots = *Simocyon batalleri* from Batallones-1 [170].

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protoconid, the metaconid is more mesially positioned, the hypoconid is larger, the paraconid is considerably developed and several additional cuspulids can be seen in the distal part of the talonid [167].

The dimensions of the specimen from Hammerschmiede are significantly lower than that of *S. diaphorus* and *S. batalleri* (Table 17; Fig 22). *Simocyon diaphorus* exhibits a similar m2W/m2L ratio, whereas the values for *S. batalleri* are slightly lower (Table 17). The valley mesially to the metaconid-protoconid plane in the m2 is shallower and less marked in *S. batalleri* [170], whereas in *S. diaphorus* it is almost absent [169]. In both species no additional cuspids or cristids are seen creating a simpler overall morphology of the teeth than that of SNSB-BSPG-2020 XCIV-5705 [169, 170].

The genus *Protursus* is known from one m2 from the locality of Can Llobateres [159] and, as discussed above, from another mandibular specimen in Rudabánya. Both specimens are larger than SNSB-BSPG-2020 XCIV-5705 (Table 17; Fig 22). Furthermore, there are some morphological differences between these two specimens and the molar from Hammerschmiede, such as the less bent talonid, the more restricted valleys (mesially to the protoconid-metaconid and the talonid valley), the smaller cuspids (especially the protoconid) and the more bulbous (and less cristrid-like) border of the talonid.

Consequently, the taxonomic status of this form remains unclear. Its size is intermediate between *Alopecocyon* and *Protursus*, whereas its morphology is distinct from both genera. Given the aforementioned presence of a typical M1 of *A. goeriachensis* in Hammerschmiede (even though in a different layer), it is possible that this m2 is an abnormal specimen that follows the size increase tendency of the species through the Aragonian [168]. On the other hand, the morphological differences are important, in order to be interpreted through intraspecific variability. It is possible that this specimen corresponds to a primitive form of the Vallesian clade of *Protursus*. However, until further material comes to light, it is preferred to refer to it as Simocyoninae indet.

Family indet.

Subfamily Potamotheriinae Willemsen, 1992 [34]

Genus *Potamotherium* Geoffroy Saint-Hilaire, 1833 [172]

Type species: *Potamotherium valletoni* Geoffroy Saint-Hilaire, 1833 [172]

Other included species: *Potamotherium miocenicum* Peters, 1868 [173].

Remarks: This genus is known from the Late Oligocene to the Middle Miocene of Europe [125]. During the past decades it has been considered as member of the *Semantor* lineage that links the morphology of otters and pinnipeds (e.g. [38]). Different approaches consider this group as a distinct subfamily of Mustelidae (as Potamotheriinae e.g. in [38]), as part of the subfamily Lutrinae (e.g. [125, 174]), as part of the subfamily Oligobuninae [175], as a distinct subfamily of Phocidae [176] or as a sister group of Phocidae [177]. Unfortunately, very few specimens of this group have been described yet, limiting our capability to reconstruct solidly its phylogenetic affinities. Recent studies support the distinction of this lineage from the family Mustelidae, suggesting a basal connection to the pinnipeds [178, 179]. The present specimen is tentatively considered as the youngest report of the genus up to date.

Potamotherium sp.

Referred Specimens: HAM 4: SNSB-BSPG-2020-XCIV-3551, right P3. HAM 5: GPIT/MA/10505, left M1.

Description: The right P3 (SNSB-BSPG-2020-XCIV-3551; Fig 23A) is elongated, but distally broad. A well-developed distal accessory cuspid is present, as well as one small cusp in the mesial and distal borders of the tooth. There are signs of wear in both the main and distal accessory cusps. The available M1 (GPIT/MA/10505; Fig 23B) is broken in its mesiobuccal part, showing no signs of wear and a moderately developed cingulum. The specimen was erroneously added in the first table of [22]. It is relatively narrow and the lingual part is bent occlusally. The buccal border of the tooth is considerably more extended at the level of the paracone (parastylar area) than at the level of the metacone. The remaining buccal part of the tooth includes the narrow and moderately low paracone and metacone. There are no signs of a metastylid. The valley between the buccal cusps and the lingual cingulum does not host any cusps or crests. Only an additional cusp is present at the mesio-lingual part of the cingulum. A small pit is present lingually to the metacone.

Comparison: The P3 is attributed to the genus *Potamotherium*, based on the characteristic distal enlargement of the dental base. As demonstrated in Table 18, this specimen is slightly larger than the known P3 of both *Potamotherium* species. Additionally, the accessory cusps are slightly more developed in the Hammerschmiede specimen.

The absence of any M1 lingual cusps, other than the one present at the lingual cingulum is a characteristic of the Potamotheriinae and the genus *Potamotherium* in particular, which is the dominant genus of the subfamily in Europe during the Miocene. The subfamily is also represented by the genus *Semantor* Orlov, 1931 [184], which is however, far larger, and exclusively known by postcranial remains [184–186].

The genus *Potamotherium* is an aquatic or semi-aquatic carnivoran that has been described by two species: the type species *P. valletoni*, which has been found in the Late Oligocene and Early Miocene of Europe, and *P. miocenicum* from the Early and Middle Miocene of Europe [38, 134]. Additionally, it has been cited in North America as *Potamotherium* sp. in sediments from the beginning of the Hemingfordian (Early Miocene, circa 18–19 Ma) [187, 188]. [182] differentiated *P. miocenicum* from *P. valletoni*, stating (among other characteristics) that the former was larger, more robust, and it has a wider M1 with a more conical (and less crest-like) protocone. Fig 23 illustrates that there is considerable morphological variability between the members of this genus, even inside the same species. The metrical comparison at Table 18 demonstrates that indeed *P. miocenicum* is slightly larger than *P. valletoni*, but no difference

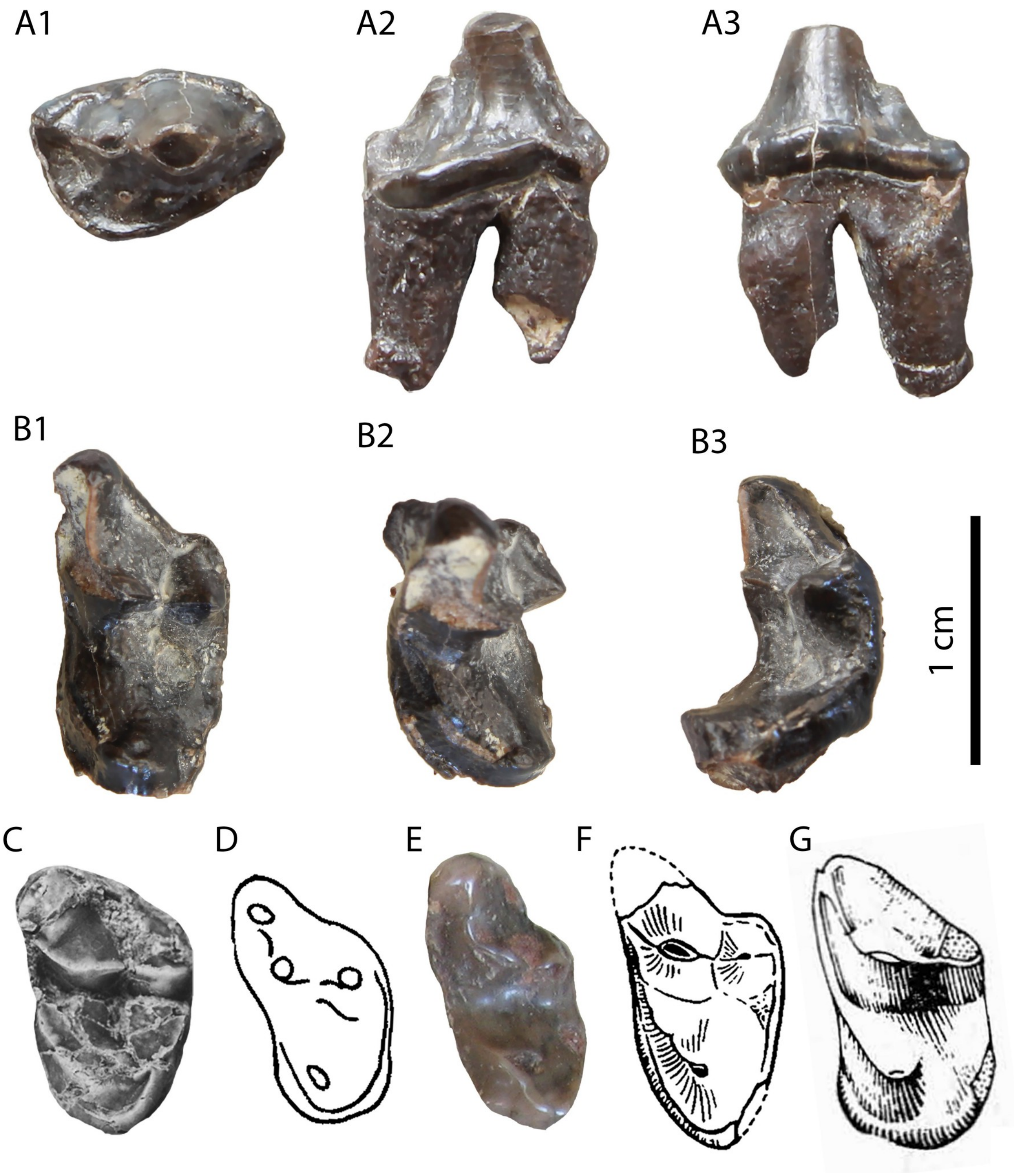

Fig 23. The material of *Potamotherium* sp. from Hammerschmiede (A, B), in comparison to specimens of Potamotherium valletoni (C–E) and Potamotherium miocenicum (F–G) from other localities: (A) right P3 from Hammerschmiede (SNSB-BSPG-2020-XCIV-3551); (B) left M1 from Hammerschmiede (GPIT/MA/10505); (C)left M1 from Enspel (Naturhistorisches Museum Mainz—5009/1a; [180]); (D) left M1 from Allier (British Museum of Natural History, London—M 7651; [125]); (E) right M1 of a skull from Allier (flipped; SNSB-BSPG-1885-I-13; [181]); (F) right M1 from Vordersdorf (flipped; Naturhistorisches Museum Wien– 126; [182]); (G) left M1 from Baigneaux-en-Beauce (Bale S.O. 5991; [183]).

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can be seen in the relative width. The specimen GPIT/MA/10505 is even larger than the known molars of *P. miocenicum* and it exhibits a higher W/L ratio. Additionally, the protocone is not present in the Hammerschmiede specimen. Even if this lingual cuspule is considered as a protocone, then it is even less developed than in *P. valletoni*. Therefore, the studied molar differs from that of both *P. valletoni* and *P. miocenicum* in its larger size, higher W/L ratio and

Table 18. Metrical comparison of the *Potamotherium* P3 and M1 from Hammerschmiede to other published specimens for the genus indicating the data source.

Species	Locality	P3L	P3W	M1L	M1W	M1W/L
Potamotherium sp. (SNSB-BSPG-2020-XCIV-3551)	Hammerschmiede	9.6	6.7			
Potamotherium sp. (GPIT/MA/10505)				(7.8)	12.8	(61%)
P. miocenicum	Voitsberg [182]	7.4	4.6	6.6	>12	<55%
	Baigneaux-en-Beauce [183]			6.4	12.2	52%
P. valletoni	Allier [125]	7.9	4.3	5.6	10.2	55%
	Wiesbaden-Amöneburg [190]	7.3	5.2	5.8	11.1	52%

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the more reduced lingual cusps. These morphological differences, together with the considerable age difference between the last appearances of *P. miocenicum* (Devinska Nova Ves Sandberg; approximately 13 Ma; MN 6; [189]) and Hammerschmiede, can be interpreted potentially as indicators of a distinct form being present in central Europe during the early Late Miocene. However, due to the scarcity of the material, additional fossils are needed to test this hypothesis about the status of this enigmatic form.

Suborder Feliformia Kretzoi, 1945 [191]

Family Viverridae Gray, 1821 [35]

Genus *Semigenetta* Helbing, 1927 [192]

Type species: *Semigenetta sansaniensis* (Lartet, 1851) [28]

Other included species: *Semigenetta elegans* Dehm, 1950 [46]; *Semigenetta cadeoti* Roman & Viret, 1934 [119]; *Semigenetta laugnacensis* (de Bonis, 1973) [193]; *Semigenetta grandis* Crusafont Pairó & Golpe Posse, 1981 [29].

Remarks: This genus was recently reviewed by [21]. It exhibits a relatively uniform morphology throughout the Miocene (MN 1/2 to MN 10) and the species differentiations are based mainly on size.

Semigenetta sansaniensis (Lartet, 1851) [28]

Lectotype: MNHN Sa 808, left hemimandible with p3–m1.

Type Locality: Sansan (France).

Referred New Specimens: HAM 1: SNSB-BSPG-1973-XIX-26, right m2. HAM 4: SNSB-BSPG-2020 XCIV-4024, right hemimandible with p3–m1 and the alveoli of p1, p2 and m2; GPIT/MA/13751, right p4; SNSB-BSPG-2020 XCIV-3614, right m1; SNSB-BSPG-2020 XCIV-5706, right m1. HAM 5: GPIT/MA/13452, right M1; GPIT/MA/12130, left p4; GPIT/MA/10298, right calcaneum.

Description: The right M1 (GPIT/MA/13452; Fig 24A) is complete with no signs of wear. It outline is sub-triangular and relatively narrow. The mesial part is relatively wider, especially at the part buccally to the paracone. The paracone is considerably higher than the metacone, but both cusps are pyramidal and pointy. There are no signs of other cusps. A faint cingulum surrounds the tooth and creats an elevation is ints lingual border that resembles a cusp.

The right hemimandible is broken at the alveolus of the canine and it preserves p3–m1 and the alveoli of p1, p2 and m2 (Fig 24D). The hemimandible is moderately robust, exhibiting a subangular lobe below m1 and m2 and two mental foramens: one below p1 and one below p2. The masseteric fossa is deep, reaching the plane of m2. The third premolar is high (higher than p4) and sharp, having a prominent distal accessory cuspid and two (one mesial and one distal) cuspids at its cingulid. The fourth premolar is relatively shorter and blunter and it has the same three accessory cuspids as the third one, but all of them are more developed. The lower carnassial exhibits faint signs of wear in its carnassial blade. The protoconid is the largest cuspid, separated from the paraconid by a deep carnassiform notch. The paraconid is slightly mesiolingually bent. The metaconid is relatively small and it is only slightly connected to the

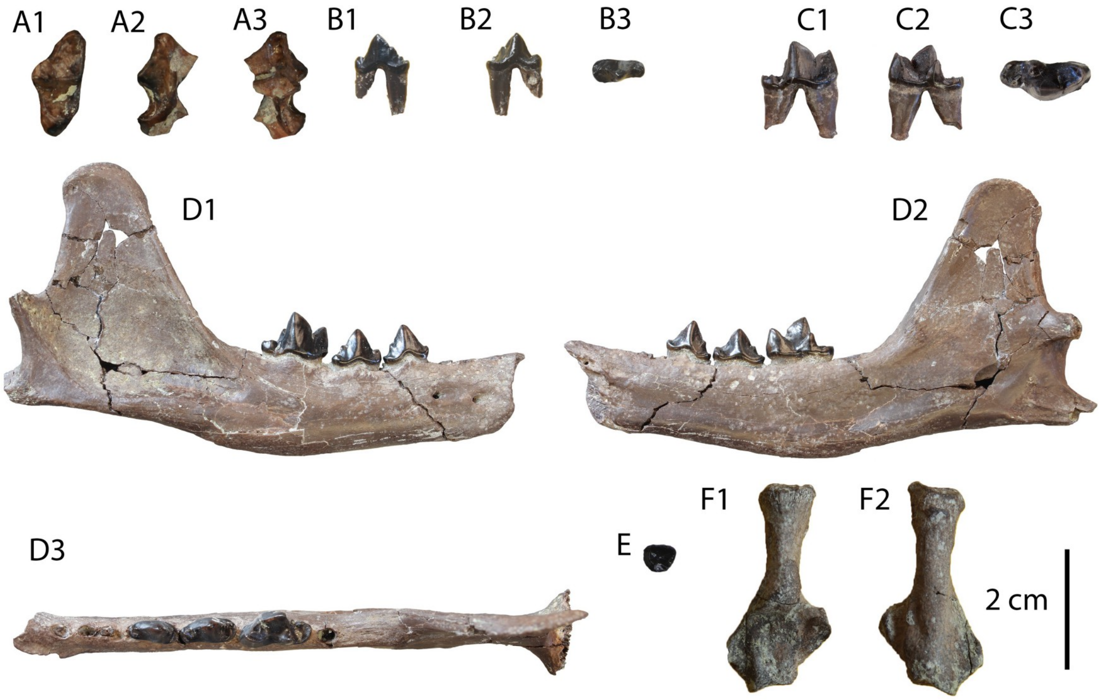

Fig 24. New material of *Semigenetta sansaniensis* from Hammerschmiede: (A) GPIT/MA/13452 right M1 in (A1) occlusal, (A2) mesial and (A3) distal view; (B) GPIT/MA/12130 left p4 in (B1) buccal, (B2) lingual and (B3) occlusal view; (C) SNSB-BSPG-2020 XCIV-5706 right m1 in buccal (C1), lingual (C2) and occlusal (C3) view; (D) SNSB-BSPG-2020 XCIV-4024 right hemimandible in occlusal (D1), buccal (D2) and lingual (D3) view; (E) SNSB-BSPG-1973-XIX-26, right m2 in occlusal view; (F) GPIT/MA/10298 right calcaneum in (F1) dorsal and (F2) ventral views. The size of the M1 (A) and m2 (E) has been doubled for the sake of visibility.

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protoconid. It is placed distally to the protoconid. The talonid is short, with a shallow basin and a low rim. Only a small hypoconid is present at its buccal side. No distinct cingulids are present in all three remaining teeth.

[4] reported an m2 from HAM 1 that they attributed to *Proputorius sansaniensis* (SNSB-BSPG-1973-XIX-26; Fig 24E). As mentioned above, this specimen is now attributed to *Semigenetta sansaniensis*. It is unworn and relatively complete, missing only its root. Its outline is semi-circular, being convex in its lingual and straight in its buccal side. The protoconid is the largest cuspid, followed by the slightly smaller hypoconid. The lingual side of the tooth hosts two small cuspulids that can be identified as reduced metaconid and entoconid.

The specimen GPIT/MA/10298 is a complete right calcaneus (Fig 24F). Its general shape is long and slender. The groove for the tendo achillis is restricted to the posterior part of the bone. The posterior talar articular surface is oval-shaped and laterally folded through the shaft. The surface between the posterior talar articular surface and the distal epiphysis is more long than wide. The sustentaculum tali is wide and long, while the middle talar articular surface is oval. The groove for the tendon of flexor hallucis longus is deep and narrow. A peroneal tubercle also exists, creating space for the attachment of muscles. Finally, the articular surface for the cuboid is semicircular laterally, until the middle of the surface, followed by a shallow groove and an additional triangular surface.

Comparison: The morphological homogeneity of the genus *Semigenetta* in the fossil record leads to the differentiations being held mainly by metrical comparisons [21]. It is demonstrated in Tables 19 and 20 that *S. sansanienis* is a forme of intermediate size between the

Table 19. Metrical comparison of the dental dimensions between the new specimens of *Semigenetta sansaniensis* from Hammerschmiede with the currently known measurements of the genus indicating the data source. Data of *Semigenetta grandis* are mentioned in Table 20.

Species	Code	p3L	p3W	p4L	p4W	m1L	m1W	M1L	M1W
S. sansaniensis	GPIT/MA/13452							4.6	8.6
	SNSB-BSPG-2020-XCIV-4024	7.1	3.2	8.0	3.7	10.5	5.0		
	SNSB-BSPG-2020-XCIV-5706					11.5	5.1		
	SNSB-BSPG-2020-XCIV-3614						6.0		
	GPIT/MA/17351				3.9				
	GPIT/MA/12130			9.0	4.0				
S. sansaniensis [22, 52, 72, 74, 78, 192, 194–198]		6.3–8.4 7.3 (20)	1.8–3.5 2.9 (19)	7.0–9.0 8.0 (20)	2.9–4.1 3.5 (19)	8.5–11.5 9.9 (44)	3.5–5.5 4.7 (44)	4.6–6.4 5.7 (7)	7.4–9.6 8.5 (7)
S. elegans [46, 119, 198–201]		5.7–6.4 6.0 (10)	2.4	6.1–7.3 6.6 (11)	2.9	7.7–8.8 8.2 (11)	4.0	4.3–5.7 4.6 (6)	6.3–7.8 6.9 (6)
S. cadeoti [119]						6.0			
S. laugnacensis [195]		4.8–5.1 5.0 (2)	1.8–1.9 1.9 (2)	5.8–6.2 6.0 (5)	2.0–2.5 2.3 (5)	7.1–7.5 7.4 (5)	3.2–3.6 3.4 (5)	6.2	3.2

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small-sized *S. elegans*, *S. cadeoti* and *S. laugnacensis* and the large-sized *S. grandis*. The herein described material fits to the values provided for *S. sansaniensis*. Though, it must be noted that the fragmentary m1 (SNSB-BSPG-2020 XCIV-3614) is slightly wider than the known specimens of this form. However, we consider this as an indicator of intraspecific variability (an aspect already discussed by [21]) and not as a character of taxonomic relevance.

The dimensions of the m2 (m2L = 2.9 mm; m2W = 2.5 mm) indicate that this tooth must belong to a small- to medium-sized feliform. The hyaenid genera *Protictitherium* Kretzoi, 1938 [202] and *Plioviverrops* Kretzoi, 1938 [202] are characterized by well-developed m2 cuspids, including a hypoconulid [103]. On the contrary, the m2 of the viverrids are more plesiomorphic. The dimensions of the known m2 of *S. sansaniensis* (2.9 x 1.9 mm from Vieux-Collonges [52]; 3.0 x 2.3 mm and 3.8 x 3.0 mm from La Grive-Saint-Alban [72]) fit very well to the size of the present specimen. This species is the only viverrid of its size during the late Middle and early Late Miocene [21], so we are inclined to tentatively attribute this molar to *S. sansaniensis*.

The described calcaneum exhibits typical feliform characteristics, such as the slenderness of the shaft (also described as mediolateral depression), the high position of the articular surface for the astragalus and the moderate development of the sustentaculum tali. However, based on the comparison of [194], the calcaneum of *Semigenetta* differs from that of the felids in the relatively lower position of the sustentaculum tali, the more developed medial tubercle and the more distodorsally oriented articular surface for the astragalus. All these characteristics seem to fit to this morphology and differentiate it from the calcaneus of *Leptofelis vallesiensis* (Salesa

Table 20. Comparison of the m1 dimensions between the known specimens of *Semigenetta grandis* indicating the data source.

Code/Locality	m1L	m1W	m1W/m1L
SNSB-BSPG-2020-XCIV-4220 HAM 4	15.3	7.4	48%
GPIT/MA/12452[21] HAM 4	15.6	7.7	49%
Castell de Barberá [29]	13.5	6.9	51%
Rudabánya [65]	12.7–14.5 13.9 (3)	5.7–6.3 6.1 (3)	43%–45% 44% (3)

https://doi.org/10.1371/journal.pone.0268968.t020

et al., 2012) [203] described in [204]. Additionally the measurements of the Hammerschmiede calcaneum (total length = 32.0 mm; maximum width = 13.5 mm) are similar to those reported by [192] for the specimen from Steinheim (total length ≈ 35.0 mm; maximum width = 15.3 mm).

Semigenetta grandis Crusafont Pairó & Golpe Posse, 1981 [29]

Holotype: IPC-IPS 94790, left hemimandible with p2–m1 and the alveolus of m2.

Type Locality: Castell de Barberá (Spain).

Referred New Specimens: HAM 4: SNSB-BSPG-2020 XCIV-4220, right m1.

Description: The specimen SNSB-BSPG-2020 XCIV-4220 (Fig 25) is a right m1 with small wear facets in its carnassial blade. It is almost identical to GPIT/MA/12452 from HAM 5 reported by [21]. It is robust, with a strong cingulid, especially in its mesiobuccal and distobuccal sides. The trigonid is long, with the protoconid being the largest cuspid. It is clearly higher than the paraconid, from which it is separated by a deep notch. The metaconid is developed, pointy and slightly distally bent. The talonid consists of a shallow basin that is oriented in a dorsobuccal-ventrolingual plane. Only a cristid-like hypoconid is present in its lingual side. The only differences between SNSB-BSPG-2020 XCIV-4220 and GPIT/MA/12452 are the slightly lower trigonid cuspids (because of the wear) and the more wrinkled enamel surface of the former.

Comparison: The large size of this specimen is enough to differentiate it from other species of viverrids that have been found in the Miocene of Europe [21]. The species *S. grandis* has been described from Castell de Barberá (type locality; [29]) and Rudabánya [65]. Both localities are considered to comprise typical MN 9 faunas [205]. No significant intraspecific differences can be traced between the specimens from these localities and Hammerschmiede. The lower carnassials from Rudabánya are slightly narrower (Table 20), and the specimens from Hammerschmiede (that represent the oldest occurrence of the species) are slightly larger. One noteworthy difference is the relatively low height of the m1 metaconid in the specimens from Rudabánya [65]. This cuspid is moderately developed in the specimen of Castell de Barberá and relatively high in the specimens from Hammerschmiede.

Viverrictis de Beaumont, 1973 [206]

Type species: *Viverrictis modica* Gaillard, 1899 [63]

Other included species: *Viverrictis vetusta* de Beaumont, 1973 [206].

Remarks: This small-sized viverrid genus includes only two species: *Viverrictis modica* from La Grive-Saint-Alban and *Viverrictis vetusta* from Vieux-Collonges and Sansan [206]

Fig 25. The new lower carnassial of *Semigenetta grandis* (SNSB-BSPG-2020 XCIV-4220) from HAM 4 in buccal (A), lingual (B) and occlusal (C) view.

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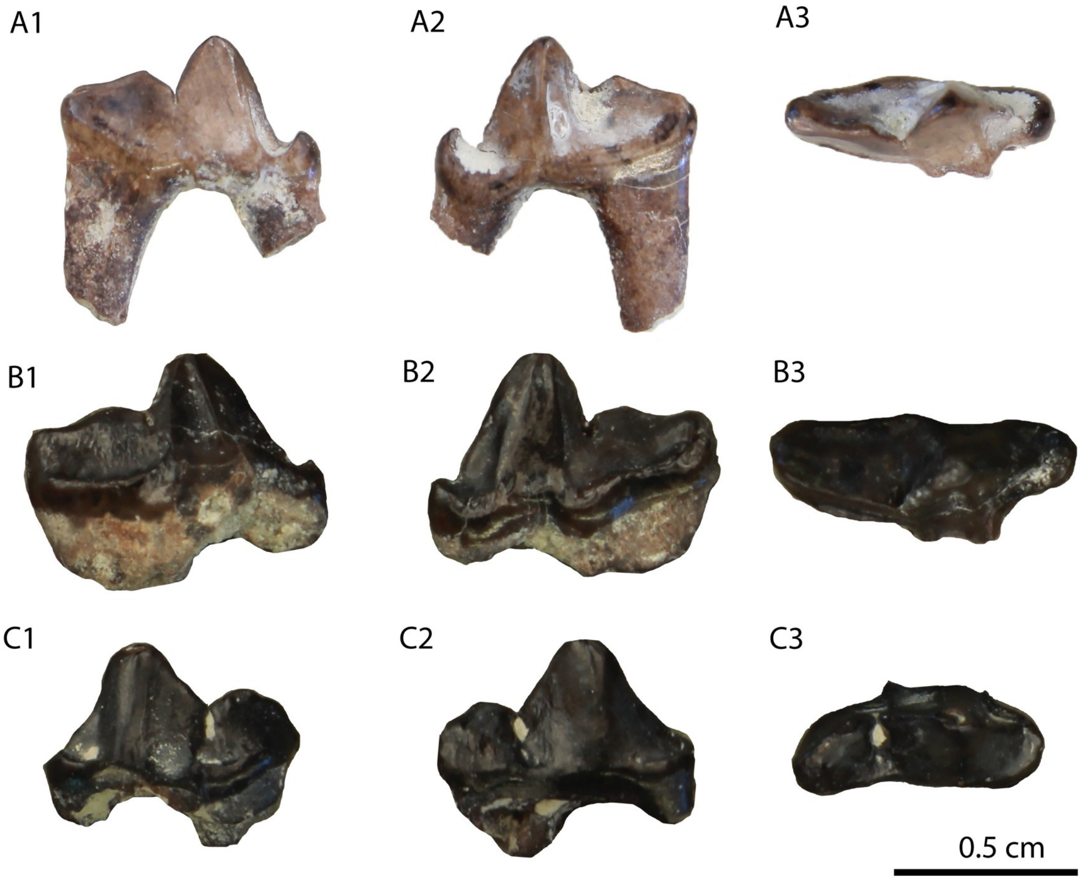

Fig 26. The P4 of *Viverrictis modica* from Hammerschmiede: (A) SNSB-BSPG-2020 XCIV-3995, right P4; (B) GPIT/MA/16659, right P4; (C) GPIT/MA/12649, left P4 in (1) lingual, (2) buccal and (3) occlusal view.

https://doi.org/10.1371/journal.pone.0268968.g026

Viverrictis modica (Gaillard, 1899) [63]

Holotype: MHNL-LGr 13710, right hemimandible with p4–m1.

Type Locality: La Grive-Saint-Alban (France).

Referred Specimens: HAM 4: GPIT/MA/16659, right P4; SNSB-BSPG-2020 XCIV-3995, right P4; GPIT/MA/12649, left P4.

Description: The upper carnassials share the same morphology (Fig 26). They are almost complete, missing only their protocone, and they have no signs of wear. The teeth are in general considerably narrow, with no signs of a cingulum. The paracone is the highest cusp. It is relatively blunt, having a crest in its buccal side and it is separated from the oblique metastyle by a deep notch. The parastyle is considerably developed and slightly hook-like, being bent distally. The protocone is missing, but its base indicates that it stemmed from the paracone plane and was oriented slightly mesially.

Comparison: This form exhibits a typical plesiomorphic viverrid morphology, having a slender upper carnassial with a slightly mesially oriented protocone and a distinct notch between the paracone and the metastyle. However, the very small size and the considerably developed parastyle are enough to differentiate it from the genus *Semigenetta* and attribute it to the genus *Viverrictis*.

This genus includes two species: *Viverrictis vetusta* from Vieux-Collonges (MN 5) and Sansan (MN 6), and *Viverrictis modica* from La Grive-Saint-Alban (MN 7/8) [206]. These two

Table 21. Metrical comparison of the P4L of SNSB-BSPG-2020 XCIV-3395 with the known datasets for *Viverrictis modica* and *Viverrictis vetusta* indicating the data source.

Species	Code	P4L
V. modica	SNSB-BSPG-2020-XCIV-3995	7.1
	GPIT/MA/12649	6.8
	GPIT/MA/16659	8.1
	LGr 1367[63]	7.0
V. vetusta	Summed [52]	6.6–7.2 7.0 (6)

https://doi.org/10.1371/journal.pone.0268968.t021

forms were differentiated by [206] based on several dental traits, despite having similar size (Table 21). One of these traits is the reduced/absent parastyle in *V. vetusta*, whereas in *V. modica* it is present [206]. Based on the considerable size of the parastyle in the Hammerschmiede specimens, it is suggested that this material belongs to *Viverrictis modica*. This report consists of the youngest record of this viverrid genus.

Discussion

Taxonomic diversity and biochronology

The small carnivoran fauna (sensu [37]) of Hammerschmiede includes 20 species belonging to 9 subfamilies: "*Martes*" *sansaniensis*, "*Martes*" cf. *munki*, "*Martes*" sp., *Circamustela hartmanni* n. sp., *Laphyctis mustelinus*, Guloninae indet., *Eomellivora moralesi*, *Vishnuonyx neptuni*, *Paralutra jaegeri*, *Lartetictis* cf. *dubia*, *Trocharion albanense*, *Palaeomeles pachecoi*, *Proputorius sansaniensis*, *Proputorius pusillus*, *Alopecocyon goeriachensis*, Simocyoninae indet., *Potamotherium* sp., *Semigenetta sansaniensis*, *Semigenetta grandis* and *Viverrictis modica*. The presence of so many species of small-sized carnivorans in a single locality is extraordinary. In particular, the channel HAM 5 includes 11 sympatric small carnivorans, while HAM 4 includes 13 sympatric forms (Table 22). Such a high diversity is resembling the extant tropical African diversities [207]. If the combined record of the three layers is taken into account (which is herein considered reasonable based on the restricted age difference between them) the fauna of Hammerschmiede includes comparable number of small carnivoran forms to some of the taxonomically richest Miocene localities, such as Sansan [72], La Grive-Saint-Alban fissures M+L7 and L3+L5 [27, 138], Rudabánya [65] and Can Llobateres 1 [87, 159, 208] (Table 23).

Many of the species are documented by very low numbers of individuals (Table 22) or even only by a single tooth. We therefore expect that the taxonomic diversity is not saturated and will even rise in the future excavation efforts. For example, the absence of the relatively common herpestid *Leptoplesictis* Forsyth Major, 1903 [137] (sensu lato; for an alternative point of view see [210]) could be covered in the future.

From a biochronological standpoint, the Hammerschmiede fauna shows several First Occurrence Dates (FOD) and Last Occurrence Dates (LOD) for small carnivorans (Fig 27). We report here the FODs of the genera *Circamustela*, *Eomellivora* and the species *Semigenetta grandis*. The documented LODs include the genera *Laphyctis*, *Lartetictis*, *Alopecocyon*, *Potamotherium* and *Viverrictis*. The dominance of LOD over FOD may reflect the biochronological position of Hammerschmiede at the end of the Astaracian mammal age, 0.3–0.5 million years before the onset of the Vallesian mammal age at 11.1 Ma [1].

Ecomorphology

Some of these species have already been studied in terms of ecomorphology, including body mass, locomotor patterns and dietary habits. In particular, [209] have discussed the attribution

Table 22. Distribution of the discussed taxa in the Hammerschmiede layers, together with their estimated body mass (BM; in kg), locomotor lifestyle (LL; GT = Generalized Terrestrial; SA = Semi-Aquatic; Sc = Scansorial; SF = Semi-Fossorial) and dietary habits (DH; I = Insectivorous; hC = Hypocarnivorous; C = Carnivorous; HC = Hypercarnivorous). Attribution to these categories is based on [209] and this study. The numbers per layer indicate the minimum number of individuals.

Species	HAM 1	HAM 5	HAM 4	BM	LL	DH
"*Martes*" *sansaniensis*		1	3	3–10	Sc	C
"*Martes*" cf. *munki*		2	1	1–3	?	C
"*Martes*" sp.	1			<1	?	C
Circamustela hartmanni n. sp.	1	1	1	1–3	Sc?	HC
Laphyctis mustelinus			1	10–30	GT	HC
Guloninae indet.		1		3–10	?	hC
Eomellivora moralesi		1		10–30	GT	HC
Vishnuonyx neptuni			3	10–30	SA	C
Paralutra jaegeri		1	2	3–10	SA	C
Lartetictis cf. *dubia*			2	3–10	SA	C
Trocharion albanense		4	1	1–3	SF	C
Palaeomeles pachecoi		2		3–10	GT/SF	hC
Proputorius sansaniensis	1			1–3	Sc	C
Proputorius pusillus	2			<1	?	C
Alopecocyon goeriachensis		1		3–10	Sc	C
Simocyoninae indet.			1	10–30	?	C
Potamotherium sp.		1	1	10–30	SA	C
Semigenetta sansaniensis	1	1	7	3–10	Sc	C
Semigenetta grandis			2	10–30	GT	HC
Viverrictis modica			1	<1	Sc	I
Number of species	5	11	13	-	-	-
Number of individuals	6	16	26	-	-	-

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to these categories of the species "*Martes*" *sansaniensis*, "*Martes*" cf. *munki*, *Laphyctis mustelinus* (as "*Ischyrictis mustelinus*"), *Paralutra jaegeri*, *Lartetictis dubia*, *Trocharion albanense*, *Proputorius sansaniensis*, *Proputorius pusillus*, *Alopecocyon goeriachensis* (as "*Alopecocyon leptorynchus*"), *Semigenetta sansaniensis* and *Viverrictis modica*. For these species we follow the attributions of [209]. The only exceptions concern the body size of *Laphyctis mustelinus* and *Lartetictis dubia*. The former species is relatively large (having an m1L approximately 15 mm; [90]). Therefore, based on the equation of [211] for the m1L of mustelids, this species is herein attributed to the 10–30 kg group. On the contrary, the latter species was attributed to the 10–30 kg group by [209], but given the small size of the Hammerschmiede specimens, the values (based on the equation of [211]) point towards the 3–10 kg category. The rest of the species are discussed in more detail here.

The very small "*Martes*" sp. has been attributed to the <1 kg body mass category, based on its very small dimensions. Additionally, given the preservation of the generalistic marten-like morphology in its upper carnassial, it was considered that this species is a carnivore, in agreement to the other members of the genus.

The genus *Circamustela* has been widely considered to be a hypercarnivorous form, judging from the reduction of the molar's grinding areas, the crest-like molar cusps, the high m1 protoconid and the low m1 hypoconid and entocristid [62]. Based on the equation of [211] for mustelids, when the m1L of *Circamustela hartmanni* n. sp. is considered, its estimated body mass is approximately 1 kg. No postcranial elements of *Circamustela* have been published up to now. Therefore, a secure attribution to a locomotor category is not possible. However, the

Table 23. Distribution of the small carnivorans (sensu [37]) among the localities of Sansan [72], La Grive-Saint-Alban fissures M+L7 and L3+L5 [27, 138], Hammerschmiede, Rudabánya [65] and Can Llobateres 1 [87, 159, 208].

		Sansan	La Grive (M, L7)	La Grive (L3, L5)	Hammerschmiede	Rudabánya	Can Llobateres 1
		MN 6	MN 7	MN 8	MN 8	MN 9	MN 9
Guloninae	"*Martes*" *sansaniensis*	x			x		
	"*Martes*" *filholi*		x	x		cf.	
	"*Martes*" *munki*		x	x	cf.		x
	"*Martes*" *delphinensis*		x	x			
	"*Martes*" *melibulla*						x
	"*Martes*" sp.				x		
	Circamustela dechaseauxi						x
	Circamustela hartmanni nov. sp.				x		
	Laphyctis mustelinus		x	x	x		
	Ischyrictis zibethoides	x					
	Plesiogulo sp.						x
	Trochictis narcisoi						x
	Trochictis sp.					cf.	
	Guloninae indet.				x		
Mellivorinae	*Eomellivora moralesi*				x		
	Eomellivora fricki						x
Lutrinae	*Paralutra jaegeri*				x	x	x
	cf. *Paralutra* sp.					x	
	Vishnuonyx neptuni				x		
	Lartetictis dubia	x			cf.		
Melinae	*Sabadellictis crusafonti*						x
	Taxodon sansaniensis	x				cf.	cf.
	Melinae indet.					x	
	Trochictis depereti		x				
Leptarctinae	*Trocharion albanense*		x	x	x		x
	Trochotherium cyamoides		x				
	Gaillardina transitoria		x				
Mephitinae	*Proputorius sansaniensis*	x			x		
	Proputorius pusillus		x		x		
	Proputorius sp.					cf.	
	Grivamephitis pusilla		x				
	Grivamephitis meini			x			
	Mesomephitis medius						x
	Promephitis pristinidens						x
	Palaeomeles pachecoi				x		
Simocyoninae	*Alopecocyon goeriachensis*	x	x	x	x		
	Simocyoninae indet.				x		
	Simocyon diaphorus					x	
	Protursus simpsoni					x	x
Potamotheriinae	*Potamotherium* sp.				x		
Viverridae	*Semigenetta sansaniensis*	x	x	x	x		x
	Semigenetta grandis				x	x	
	Viverrictis modica		x	x	x		
	Viverrictis vetusta	x					

(*Continued*)

Table 23. (Continued)

		Sansan	La Grive (M, L7)	La Grive (L3, L5)	Hammerschmiede	Rudabánya	Can Llobateres 1
		MN 6	**MN 7**	**MN 8**	**MN 8**	**MN 9**	**MN 9**
Herpestidae	*Leptoplesictis atavus*	x					
	Leptoplesictis filholi/aurelianensis		x	x			
	Jourdanictis grivensis		x				
Number of Species		9	15	10	20	10	14

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most parsimonious approach would be to suggest that it would be scansorial, as all the relatively small-sized gulonines and mustelines.

The indetermined gulonine is suggested to have a body mass of approximately 5 kg based on its m1L and the equation of [211] for the mustelids. The general morphology of this species points towards a hypocarnivorous dietary category based on the low and blunt premolars with

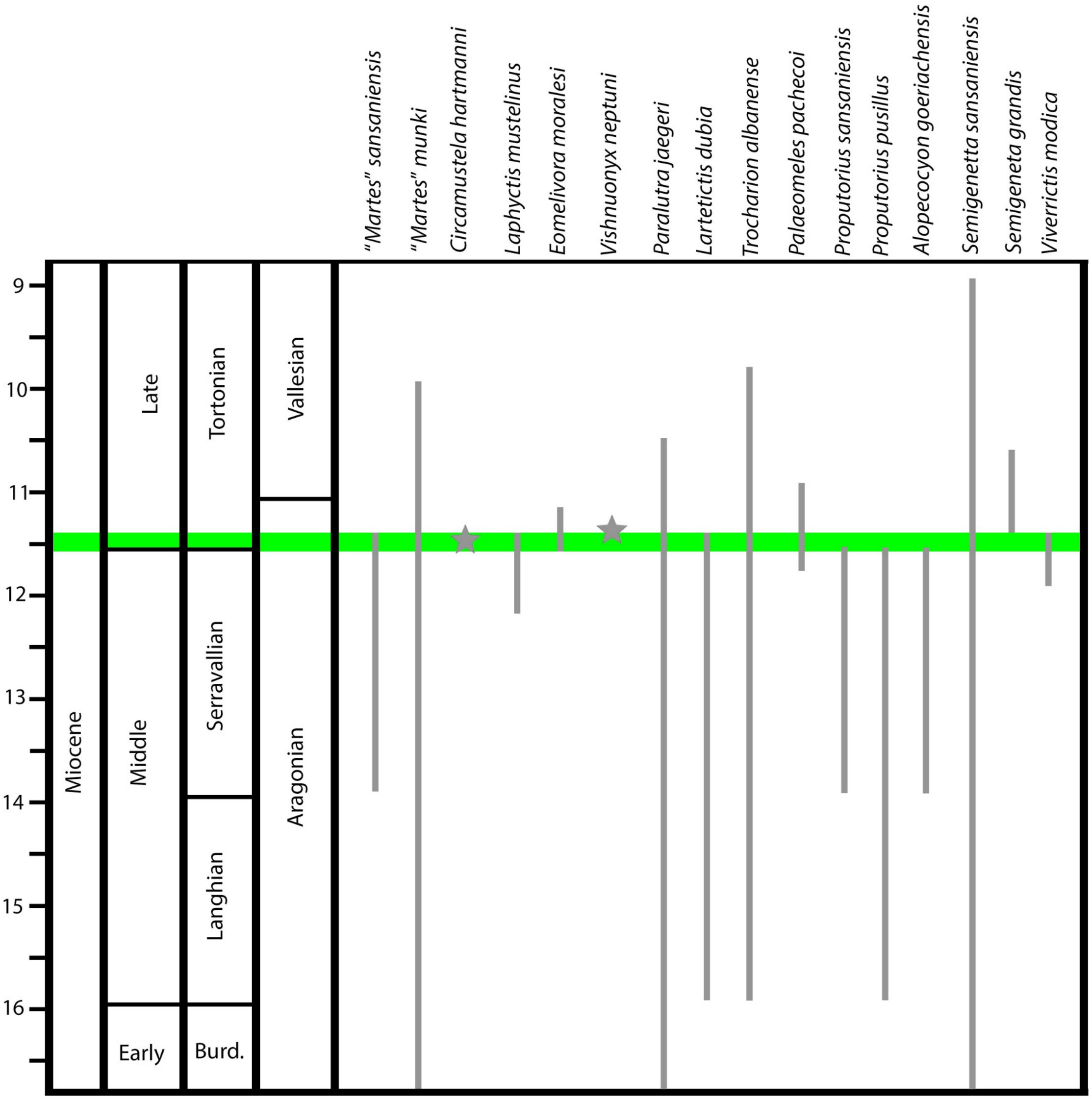

Fig 27. Stratigraphical range of the discovered carnivorans in species level.

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no developed accessory cuspids, the moderately long m1 talonid and the low m1 trigonid cuspids [212–216]. Since no postcranial can be attributed to this mandible and the exact relationships of this form are not known, then its locomotor pattern remains unclear.

The specimen GPIT/MA/09875 is the first published complete m1 *Eomellivora moralesi*. The equation of [211] for the mustelids is based mostly on small-sized animals. Therefore, it is reasonable to suggest that its prediction accuracy can be doubted in larger body masses. The m1L of *Eomellivora moralesi* is 24.7 mm (Table 9). This value is comparable and slightly larger than that for the extant wolverine, *Gulo gulo* (Linnaeus, 1758) [44] (range 19.5–22.5, average 20.8, n = 20; [217]). Therefore, it can be deduced that *Eomellivora* from Hammerschmiede had a similar or slightly larger body mass than the extant wolverine, thus 10–30 kg [218]. [100] discussed the dietary habits of *Eomellivora*, concluding that it probably was a hypercarnivorous scavenger-opportunist. [100] and [219] also provided some preliminary comments on postcranium of *Eomellivora piveteaui*, stating that they were relatively long, possibly adapted to cursoriality. However, until a more detailed study is published, we prefer to attribute *Eomellivora moralesi* to the Generalized Teresstrial group.

[22] discussed the ecomorphological traits of *Vishnuonyx neptuni*, concluding that it was a large, semiaquatic fish-eater, comparable to *Pteronura brasiliensis* (Zimmermann, 1780) [220].

Palaeomeles pachecoi is characterized by several traits that indicate hypocarnivorous adaptations, such as the wide lingual platform in M1, the low cusps of M1, the low premolars without accessory cuspids, the very long m1 talonid with small cuspules, the low m1 trigonid cuspids and the relatively large m2 [212–216]. These adaptations resemble that of the extant Eurasian badger, *Meles meles* (Linnaeus, 1758) [44]. However, the size of *Palaeomeles* (m1L ≈ 14.0 mm) is slightly smaller than that of *Meles* (range 15.4–18.5, average 16.8, n = 26; [221]). Therefore, an attribution to the 3–10 kg group seems reasonable. The postcranial anatomy of *Palaeomeles* was studied by [145]. These authors concluded that *Palaeomeles* exhibits some adaptations towards fossoriality (similar to the extant badgers), but the evolutionary stage of these characteristics was not as evident as in the extant forms. Therefore, we prefer to classify this species as Generalized Teresstrial / Semi-fossorial.

The size of Simocyoninae indet. is intermediate between that of *Alopecocyon* (3–10 kg; [209]) and *Simocyon batalleri* (≈50 kg; [222]). Therefore, the attribution to the group of 10–30 kg seems possible. Since no postcranial of *Protursus* are known and its relationships with the more evolved *Simocyon* are not clear, we prefer to retain its locomotor patterns as unknown. As [156] pointed out, the subfamily Simocyoninae is characterized by more hypercarnivorous adaptations than that of Ailurinae. These traits are less developed in the early forms, but they become more evident in *Simocyon*. However, the m2 is well-developed, with long talonid and low cuspids. Therefore, a generalistic/opportunistic diet can be suggested for this form.

The semi-aquatic lifestyle of *Potamotherium* has been discussed in detail in many studies [38, 125, 178]. In general, this genus exhibits generalized, lutrine-like adaptations that are connected with piscivory, such as the high premolars and the high m1 protoconid and metaconid; but also for durophagy, such as the broad premolars (with distinct cingula), the wide P4 protocone área and the developed m1 talonid [21, 125, 212–216]. Therefore, a mixed diet of fish and bivalves is here proposed for this form. The body mass of the Hammerschmiede *Potamotherium* is not possible to be calculated from a damaged M1. However, it has been demonstrated that it is slightly larger than *Potamotherium miocenicum*. Based on the dimensions of this species [183] the body mass of the Hammerschmiede form can be deduced to be similar to that of *Lartetictis dubia*, falling into the 10–30 kg group.

Finally, the ecomorphology of *Semigenetta grandis* was discussed in [21], concluding that it is a species slightly larger than 10 kg with hypercarnivorous adaptations and possibly terrestrial locomotor habits.

A summary of these attributions as well as the distributions of the discussed taxa in the Hammerschmiede layers are provided in Table 22.

The herein described forms can be separated into three size-groups. The large-sized (10–30 kg) *Laphyctis*, *Eomellivora*, *Vishnuonyx*, Simocyoninae indet., *Potamotherium* and *Semigenetta grandis*; the medium-sized (3–10 kg) "*Martes*" *sansaniensis*, Guloninae indet., *Paralutra*, *Lartetictis*, *Palaeomeles*, *Alopecocyon* and *Semigenetta sansaniensis* and the small-sized (<3 kg) "*Martes*" cf. *munki*, "*Martes*" sp., *Circamustela*, *Proputorius*, *Trocharion* and *Viverrictis*.

The fluvial nature of the HAM 4 and HAM 5 (and most possibly HAM 1) layers has a significant impact on the carnivoran guild of the locality as several of the taxa are characterized by semi-aquatic lifestyle. In particular, the genera *Lartetictis*, *Vishnuonyx*, *Paralutra* and *Potamotherium* have been considered as semi-aquatic carnivorans feeding mainly on fish and bivalves [22, 34, 134, 209]. All the other forms are considered to have terrestrial or, possibly, semi-arboreal lifestyle. The mutual exclusion of *Lartetictis* and *Paralutra*, pointed out by [132, 134] is not evident in Hammerschmiede, as both genera have been found in the HAM 4 layer. Both studies suggested that *Paralutra* gradually replaced *Lartetictis*. However, their coexistence in Hammerschmiede (together with their significantly overlapping stratigraphical ranges; [132]) indicate that these species were able to live together in the same ecosystem, if the available resources were sufficient. The rest of the species are mainly scansorial/terrestrial. The high frequency of possibly scansorial and arboreal species can be associated to a more closed environment.

The larger terrestrial forms (*Eomellivora*, *Laphyctis* and *Semigenetta grandis*) are relatively rare. However, a partitioning can be noted, as *Eomellivora* is found only in HAM 5, whereas *Laphyctis* is found only in HAM 4. Though, this partitioning might have been caused by sample bias. *Laphyctis* is known of being able to coexist with other similar-sized carnivorans, e. g. it is known to coexist with *Ischyrictis zibethoides* in Vieux Collonges [52] or with *E. moralesi* in Can Mata [30, 58, 91, 98]. On the other hand, *S. grandis* is found only in HAM 4.

Several forms of the small- or medium-sized groups correspond to the niche of the extant martens and weasels: "*Martes*" *sansaniensis*, "*Martes*" cf. *munki*, *Circamustela*, *Semigenetta sansaniensis* and *Viverrictis*. It can be noted that the three smaller forms ("*Martes*" cf. *munki*, *Circamustela* and *Viverrictis*) are characterized by slenderer and pointier cheek teeth. This trait has been considered as an indication of hypercarnivorous diet for *Circamustela* [62]. Therefore, it is possible that all three forms were adapted to a more flesh-based diet, whereas the larger "*Martes*" *sansaniensis* and *Semigenetta sansaniensis* had a more mixed and opportunistic diet. Simocyoninae indet. also exhibits relatively narrow m2, in agreement with the general trend of simocyonines towards an opportunistic-hypercarnivorous ecomorphology ([156]. However, given the absence of data for this form, it is not easy to deduce its dietary or locomotor habits. *Trocharion*, *Palaeomeles*, Guloninae indet., *Proputorius* and *Alopecocyon* exhibit relatively developed grinding areas (including wide upper molars and long m1 talonid) and simple, blunt premolars that point towards a more hypocarnivorous diet, based more on invertebrates and plant material.

Overall, the small-carnivoran datum of Hammerschmiede points towards a relatively closed environment that was dominated by its fluvial influence. The presence of so many carnivorans of relatively similar ecological roles in a singly locality indicates that Hammerschmiede was considerably rich in terms of niche opportunities and and prey frequencies.

Conclusions

The small carnivoran fauna of Hammerschmiede includes 20 distinct species belonging to nine different subfamilies and three size-groups, representing one of the highest taxonomic diversities reported for the Miocene of Europe. A new species of *Circamustela* is described, representing the FOD of that genus. Furthermore, the late Astaracian Hammerschmiede fauna provides the FOD for *Eomellivora* and *Semigenetta grandis*, as well as the LOD of *Laphyctis*, *Lartetictis*, *Alopecocyon*, *Potamotherium* and *Viverrictis*. Ecomorphological comparison between the discovered forms reveals a well-established niche partitioning for all forms. The coexistence of possible competitors (*Paralutra-Lartetictis*; *Viverrictis-Circamustela*; *Semigenetta sansaniensis*-"*Martes*" *sansaniensis*) can be explained by the existence of sufficient resources in the Hammerschmiede ecosystem.

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The primitive giant panda *Kretzoiarctos beatrix* (Ursidae, Carnivora) from the hominid locality of Hammerschmiede

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Abstract

The present manuscript deals with newly discovered dental material of the primitive ailuropodine *Kretzoiarctos beatrix* from the Late Miocene locality of Hammerschmiede (Germany). This is the first report of the genus *Kretzoiarctos* outside the Iberian Peninsula. Therefore, its spatial range is expanded to Central Europe, since the currently known localities (in Spain and Germany) are very similar in age. The presented material exhibits distinct features that enable its taxonomic discrimination from other Miocene ursids of Europe, such as *Agriarctos*, *Miomaci*, *Indarctos*, *Ballusia* and *Ursavus*. A thorough comparison is conducted for all these forms. The discovered specimens were used in a Dental Microwear Texture Analysis in combination to ecomorphological comparisons, in order to investigate the dietary habits of this primitive ailuropodine. The results suggested that Kretzoiarctos was not a hard-plant-eater as the extant giant panda and that it was more similar to the extant *Ursus*, having an opportunistic behaviour with occasional consumption of meat.

Keywords: Miocene, Germany, Ailuropodinae, bear, microwear

Declarations

Funding:

Conflicts of interest:

Availability of data and material:

Authors’ contributions:

Introduction

The locality of Hammerschmiede is situated at the Allgäu region, at the southwest part of Bavaria, near the small town of Pforzen. The fossiliferous sediments are found in an active clay pit, and they represent a fluvio-alluvial flood plain. Six levels have been recognized in the clay pit, with the majority of the fossils being found at the levels HAM 4 and HAM 5. These levels have been dated to 11.44 and 11.62 million years ago respectively (Kirscher et al., 2016). The locality has provided an astonishing diversity of invertebrate, fish, amphibian, reptilian and mammalian remains (Fahlbusch and Mayr, 1975; Mayr and Fahlbusch, 1975; Prieto, 2007, 2012; Prieto & Rummel, 2009a, 2009b; Prieto et al., 2011; Schneider & Prieto, 2011; Prieto & van Dam, 2012; Fuss et al., 2015; Böhme et al. 2019, 2020; Mayr et al., 2020a, 2020b, 2022; Hartung et al., 2020; Kargopoulos et al., 2021a, 2021b, 2021c, In Press). The primitive hominid *Danuvius guggenmosi* Böhme et al., 2019 stands in the spotlight of this fauna, mainly due to its adaptations that have been linked to partial bipedalism. A review of the carnivoran fauna of the locality by Kargopoulos et al. (2021a, 2021b, 2021c, In Press) has revealed the presence of the following carnivoran forms in Hammerschmiede: "*Martes*" *sansaniensis*, "*Martes*" *munki*, "*Martes*" sp., *Circamustela hartmanni*, *Laphictis mustelinus*, Gulolinae indet., *Eomellivora moralesi*, *Vishnuonyx neptuni*, *Paralutra jaegeri*, *Lartetictis* cf. *dubia*, *Trocharion albanense*, *Palaeomeles pachecoi*, *Proputorius sansaniensis*, *Proputorius pusillus*, *Alopecocyon goeriachensis*, Simocyoninae indet., *Potamotherium* sp., *Semigenetta sansaniensis*, *Semigenetta grandis*, *Viverrictis modica*, *Thalassictis montadai* and Hyaenidae indet. These 22 forms, added to the herein discussed *Kretzoiarctos beatrix*, point out that Hammerschmiede is a locality with extreme carnivoran diversity, comparable to those of La Grive Saint Alban, Sansan, Vieux-Collonges, Wintershof-West, Can Ponsic, Can Llobateres and Dorn-Dürkheim.

The family Ursidae Fischer de Waldheim, 1817 includes the extant bears and their fossil relatives. Some groups of ursids stand among the most herbivorous species in the order Carnivora Bowdich, 1821 (Stirling and Derocher, 1999; Sacco and Van Valkenburgh, 2004; Figueirido et al., 2009; Kargopoulos, 2019). The extant members of Ursidae are usually divided in three subfamilies: Ursinae Fischer de Waldheim, 1817 (extant genera *Ursus* Linnaeus, 1758, *Helarctos* Horsfield, 1825, and *Melursus* Meyer, 1793), Arctotheriinae Ameghino, 1903 (extant genus *Tremarctos* Gervais, 1855) and Ailuropodinae Grevé, 1892 (extant genus *Ailuropoda* Milne-Edwards, 1870) (Waits et al., 1999; Yu et al., 2004; Fulton and Strobeck, 2006; Abella et al., 2012). The subfamily Arctotheriinae is sometimes considered as a tribe (under the name "Tremarctini") of the Ursinae (Figueirido et al., 2009; Qiu et al., 2014). The taxonomic scheme becomes far more obscure with the addition of extinct lineages. Wagner (2010) included two more subfamilies: Agriotheriinae Kretzoi, 1929 (based on the genus *Agriotherium*) and Ursavinae Kretzoi, 1945 (based on the genus *Ursavus*). Additionally, the extinct group of hemicyonids is commonly considered as a group of ursids (Pilgrim, 1931; Astibia et al., 2000; Jiangzuo et al., 2019b), but its status as a separate family has been supported by other authors (Abella et al., 2014; Hontecillas et al., 2015; Hontecillas, 2019). Though, the exact phylogenetic relationships of the extinct groups inside the family Ursidae are far from resolved (Abella et al., 2012; Qiu et al., 2014).

The subfamily Ailuropodinae is represented today only by the giant panda *Ailuropoda melanoleuca* (David, 1869), one of the very few strictly herbivorous members of Carnivora (Chorn and Hoffmann, 1978). However, the fossil record of this lineage includes several genera with gradual adaptations towards herbivory. The oldest representative of this lineage is *Kretzoiarctos beatrix* (Abella et al., 2011). This species has been, prior to this manuscript, only described in two localities: Nombrevilla-2 and ACM/C6-Camí, both in Spain (Abella et al. 2011, 2012). The two localities share a similar age of approximately 11.6 Ma (Garcés et al. 2003; Alba et al. 2009; Moyà-Solà et al. 2009), similar to that of the HAM 5 level in Hammerschmiede (Kirscher et al. 2016). The material from Nombrevilla-2 was originally attributed to "*Ursavus depereti*" (=*Agriarctos depereti*; Fraile et al. 1997) and *Ursavus primaevus* (Álvarez-Sierra et al. 2003). It was identified as a new species of *Agriarctos* by Abella et al. (2011), while a distinct genus was created one year later, after the discovery of a nearly complete mandible (Abella et al. 2012). Its attribution to the subfamily Ailuropodinae has not been questioned up to date, but a contradiction is pending regarding its exact affinities: Abella et al. (2012) considered *Kretzoiarctos* as a member of the *Agriarctos*-*Ailurarctos*-

Ailuropoda clade, while Qiu et al. (2014) include it in the Tribe Indarctini, together with *Indarctos* and *Agriotherium*.

The genus *Agriarctos* Kretzoi, 1942 includes the species *Agriarctos gaali* Kretzoi, 1942 (Turolian of Hungary), *Agriarctos vighi* Kretzoi, 1942 (Late Miocene of Hungary) and *Agriarctos depereti* (Schlosser, 1902) (Vallesian of Europe). A new genus and species of ailuropodine, *Miomaci pannonicum* de Bonis et al., 2017, was erected recently based on material from the early Vallesian locality of Rudabánya (Hungary) and Can Ponsich (Spain). The most speciose Miocene ailuropodine genus is *Indarctos* Pilgrim, 1913. Several species have been described, but the most recent approaches identify four well-defined species in the Old World: *Indarctos vireti* Villalta Comella and Crusafont Pairó, 1943 (from the early Vallesian of Spain), *Indarctos arctoides* (Depéret, 1895) (from the late Vallesian of the Mediterranean), *Indarctos zdanskyi* Qiu and Tedford, 2003 (from the Late Miocene of China) and *Indarctos punjabensis* (Lydekker, 1884) (synonymized with *Indarctos atticus* Weithofer, 1888, *Indarctos salmontanus* Pilgrim, 1913, *Indarctos lagrelii* Zdansky, 1924, *Indarctos sinensis* Zdansky, 1924 and *Indarctos bakalovi* Kovačev, 1988) from the late Miocene of Eurasia. It must be noted that not all the synonymies mentioned above are not accepted by all scholars (Jiangzuo and Hulbert, 2021). The status of the species *Indarctos anthracitis* (Weithofer, 1889) remains doubtful (Abella et al., 2019 and references therein). A recent review of the genus can be found in Abella et al. (2019). Additionally, the species *Indarctos oregonensis* Merriam et al. (1916) and *Indarctos nevadensis* Macdonald, 1959 have been described from North America. A recent review of the North American forms can be found in Jiangzuo and Hulbert (2021). Additionally, the exact position of the genus *Agriotherium* Wagner, 1837 is still debatable.

Concerning the forms that are most closely related to the extant giant panda, the genus *Ailurarctos* Qi et al., 1989 (*Ailurarctos lufengensis* Qi et al., 1989 and *Ailurarctos yuanmouenensis* Zong, 1997) from the late Miocene of China is considered to be very closely related to the extant giant panda (Abella et al., 2012; Qiu et al., 2014). Finally, the genus *Ailuropoda* also includes some Plio-Pleistocene species from East Asia (*Ailuropoda microta* Pei, 1962 and *Ailuropoda wulingshanensis* Wang et al., 1982). Additionally, the species "*Aelureidopus" baconi* Woodward, 1915 and "*Aeluropus" fovealis* Matthew and Granger, 1923 were described, but they are now considered to be subspecies of *Ailuropoda melanoleuca* (Chorn and Hoffmann, 1978).

The present study deals with new craniodental material of *K. beatrix* from the basal Tortonian locality of Hammerschmiede. The taxonomical notes are focused on the differences of this form from other related ailuropodine genera, such as *Miomaci*, *Agriarctos* and *Indarctos*. Additionally, dental microwear texture analysis is performed in the material from Hammerschmiede to infer the dietary preferences of the species.

Material and Methods

Abbreviations

Institutional Abbreviations

AMPG: Athens Museum of Palaeontology and Geology, Athens, Greece; GPIT: Palaeontological collection of the University of Tübingen, Tübingen, Germany; IPC: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain; MHNL: Muséum d'Histoire Naturelle de Lyon, Lyon, France; MKB: Zoologisches Forschungsinstitut und Museum

Alexander Koenig, Bonn, Germany; NMNHS: National Museum of Natural History Sofia, Sofia, Bulgaria; NRM: Naturhistorika Riksmuseet, Stockholm, Sweden; SMF: Senckenberg Museum Frankfurt, Frankfurt, Germany; SMNS: Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; SNSB-BSPG: Staatlichen Naturwissenschaftlichen Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; ZMB: Zoological Collections, . Museum für Naturkunde Berlin, Berlin, Germany.

Anatomical Abbreviations

The upper teeth are symbolized with uppercase letters and the lower teeth with lowercase letters. H: maximum height of the crown of the tooth; L: maximum mesiodistal length of the tooth; Ltr: maximum mesiodistal length of the trigonid of the tooth; W: maximum buccolingual width of the tooth.

Localities' Abbreviations

ACM: Abocador de Can Mata; CL: Can Llobateres; CP: Can Ponsic; DS: Deinothere Sands; GÖR: Göriach; HAM: Hammerschmiede; LG: La Grive-Saint-Alban; LUZ: Luzinay; MEL: Melchingen; NV-2: Nombrevilla-2; OPP: Oppeln; RUD: Rudabánya; SOB: Soblay; STE: Steyregg.

Material

The specimens studied herein come from the layers HAM 4 (11.44 Ma) and HAM 5 (11.62 Ma) of the locality of Hammerschmiede (Bavaria, Germany). They were unearthed during the excavations held by the University of Tübingen between 2011 and 2021. The material is stored at the Palaeontological Collection of the University of Tübingen, Germany (GPIT).

Four extant species were used as comparative material for the MDTA: *Ursus arctos* Linnaeus, 1758 (SMF-92323, SMF-16402, NRM-20105391, NRM-20105373, NRM-A580024, NRM-A945254, MHNL-50.000520), *Ursus maritimus* Phipps, 1774 (MKB-81553, NRM-A583062, NRM-A805117, SMF-16370, SMF-16371), *Tremarctos ornatus* (Cuvier, 1825) (NRM-A580001, NRM-A580002, NRM-A580003, NRM-A580004, NRM-A583134) and *Ailuropoda melanoleuca* (SMF-5463, ZMB-17246, ZMB-17542, ZMB-37026). All individuals were living in the wild.

Methods

Measurements were taken using digital calliper and they were rounded to the first decimal point. In cases of multiple specimens per anatomical element, the descriptions concern all the available specimens. The dental nomenclature of bears is still under debate. The gradual expansion of the grinding surfaces and the consequent alternations in the shape, number and position of the cusps/cuspids and cristae/cristids conceals the true homologies between different forms (Jiangzuo et al., 2019a). In the present study we are using the nomenclature depicted in Figs. 1 and 2. This scheme is not suggested herein as the most accurate in a phylogenetic sense. Its use is restricted to the clarification of the described structures, in order to set a clear comparative frame.

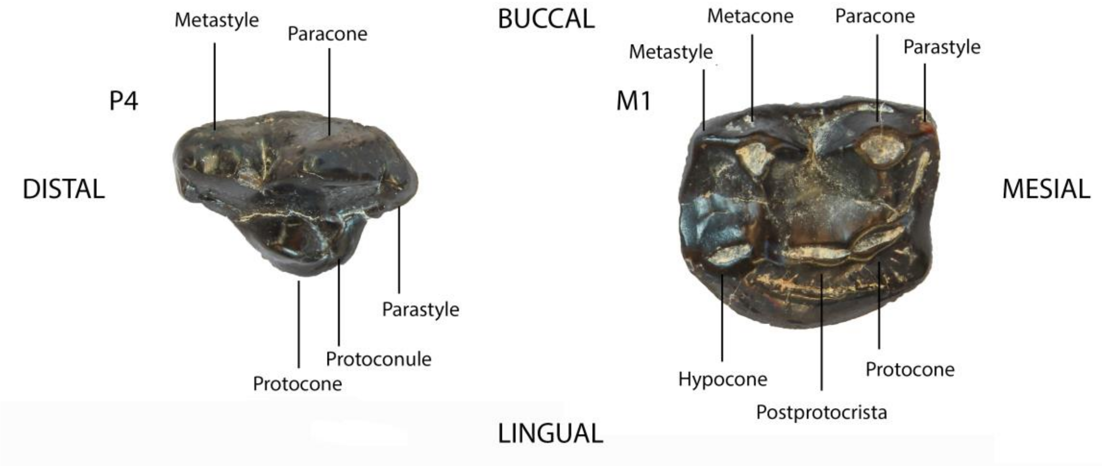

Fig. 1: Herein used dental terminology for P4 and M1 based on material of *Kretzoiarctos beatrix* from Hammerschmiede. The specimens are not in scale. Actual depictions can be found in Fig. 5.

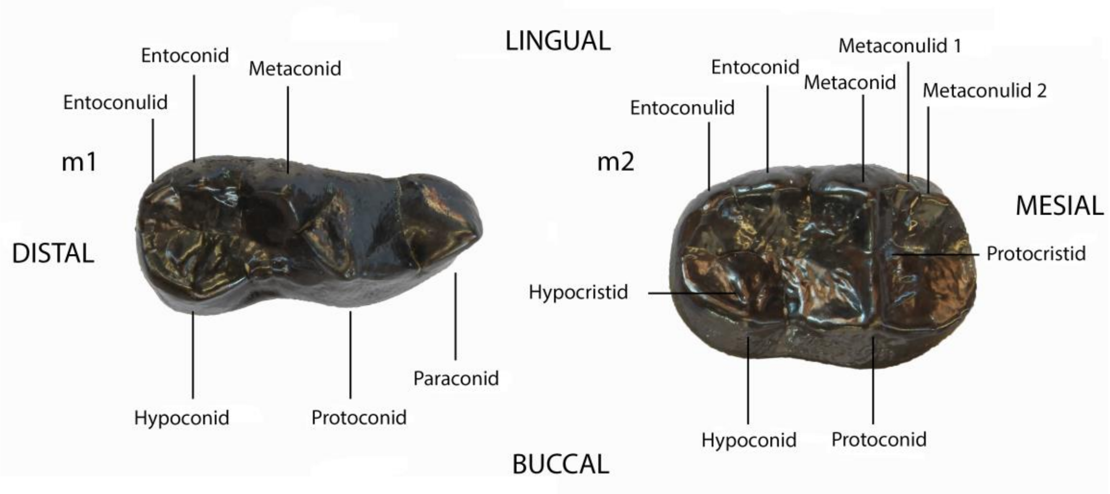

Fig. 2: Herein used dental terminology of m1 and m2 based on material of *Kretzoiarctos beatrix* from Hammerschmiede. The specimens are not in scale. Actual depictions can be found in Fig. 6.

The Dental Microwear Texture Analysis (DMTA) took place in the Biocenter Grindel and Zoological Museum, University of Hamburg. The specimens were carefully cleaned using cotton swabs that were embedded into ethanol. Silica impressions were used for every studied facet. The impressions were made using the self-mixing silicone Provil® novo light using a dispensing gun. L-shaped copper wire pieces were added to the impressions in order to define their initial orientation. The impressions were then observed using the confocal imaging profiler of a Sensofar S neox microscope. Four adjacent fields of 175.44 x 132.10 µm were analyzed for a total area of 350.88 x 264.20 µm. The recovered data were then acquired through MountainMap. The studied facets were selected in order to cover the sectorial (P4 and m1 carnassial blades) and the grinding (M1, m1 talonid, m2) surface of the dentition. These facets can be seen in Fig. 3. A detailed explanation of their positions can be found in Table 1.

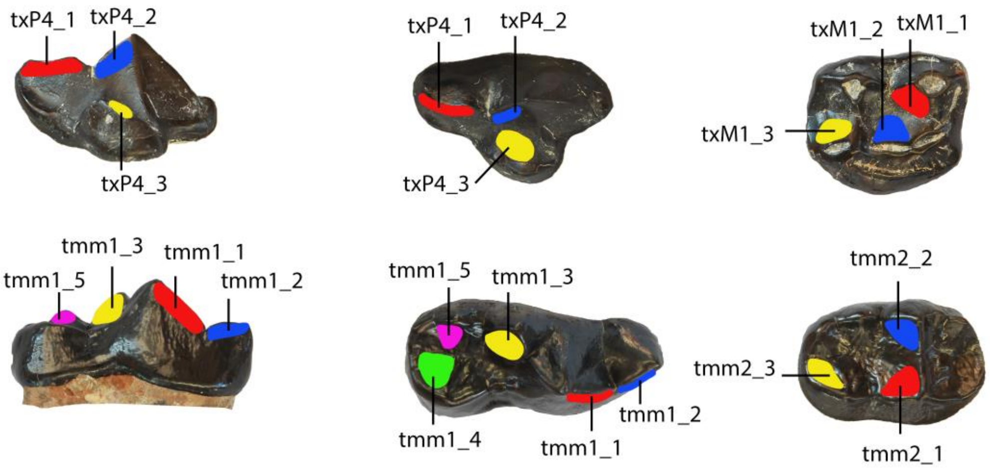

Fig. 3: The herein used facets for DMTA in P4, M1, m1 and m2.

Table 1: Detailed explanation of the position of the facets used in DMTA in the present study.

Facet	Position
txP4_1	The ventrolingual part of the metastyle of P4
txP4_2	The ventrolingual part of the paracone of P4
txP4_3	The ventromesial part of the protocone of P4
txM1_1	The distolingual part of the paracone of M1
txM1_2	The distobuccal part of the postprotocrista of M1
txM1_3	The distobuccal part of the hypocone of M1
tmm1_1	The dorsobuccal part of the protoconid of m1
tmm1_2	The dorsobuccal part of the paraconid of m1
tmm1_3	The distobuccal part of the metaconid of m1
tmm1_4	The distolingual part of the hypoconid of m1
tmm1_5	The buccal part of the entoconid of m1
tmm2_1	The distolingual part of the protoconid of m2
tmm2_2	The distobuccal part of the metaconid of m2
tmm2_3	The distolingual part of the hypoconid (distally to the hypocristid) of m2

The proxy P4SH (P4W at the level of protocone, divided by the P4L) was used for ecomorphological comparison, as proposed by Sacco and Van Valkenburgh (2004). The arcsin transformed values of this proxy were used for statistical analysis.

Systematic Palaeontology

Order **Carnivora** Bowdich, 1821
Suborder **Caniformia** Kretzoi, 1943
Family **Ursidae** Fischer de Waldheim, 1817
Subfamily **Ailuropodinae** Grevé, 1894

Genus ***Kretzoiarctos*** Abella et al., 2012

Type species. *Kretzoiarctos beatrix* (Abella et al., 2011)

Kretzoiarctos beatrix (Abella et al., 2011)

Figures 4–6.

Material. HAM 4: two P4 (SNSB-BSPG 2020 XCIV-2676, right; SNSB-BSPG 2020 XCIV-4270, right); one M1 (SNSB-BSPG 2020 XCIV-0162, right); one m2 (SNSB-BSPG 2020 XCIV-4014, left). HAM 5: two C (GPIT/MA/09631, right; GPIT/MA/09893, right); one P4 (GPIT/MA/10306, right); two M1 (GPIT/MA/09628, left; GPIT/MA/13464, left); one c (GPIT/MA/09894, left); one m1 (GPIT/MA/10304, right); two m2 (GPIT/MA/10305, right; GPIT/MA/13717, right).

Description. GPIT/MA/09631 (Fig. 4A) is a complete upper canine, while GPIT/MA/09893 (Fig. 4B) is broken just above the dentine-enamel junction. This area is more dorsally placed in the buccal side of the tooth than in the lingual one. The specimens have a robust and buccolingually compressed root with shallow fossae and grooves. The crown is relatively high and buccolingually compressed. In mesial view, the buccal surface is slightly concave, whereas the lingual one is almost completely flat. The apex is relatively blunt and it consists of the stemming point of two crests that reach the base of the dentine-enamel junction: a distal one (slightly more prominent) and a mesio-lingual one (fainter, accompanied by a parallel buccal groove). No sign of other crests or grooves is present. The overall shape of the tooth is slightly curved, with the base being more expanded distally.

Fig. 4: Upper canines of *Kretzoiarctos beatrix* from Hammerschmiede: (A) GPIT/MA/09631 right C in buccal (A1) and lingual (A2) view; (B) GPIT/MA/09893 right C in buccal (B1) and lingual (B2) view.

Three upper carnassials have been found. SNSB-BSPG 2020 XCIV-4270 (Fig. 5A) is missing only the protocone root, GPIT/MA/10306 (Fig. 5B) is missing all the roots, whereas SNSB-BSPG 2020 XCIV-2676 (Fig. 5C) retains only the protocone, the protoconule, the parastyle and the lingual base of the tooth. These premolars have three roots: one under the protocone, one under the metastyle and one under the parastyle and the mesial part of the paracone. No clear wear facets are evident in the specimens. The teeth are surrounded by a cingulum, which is stronger at its lingual part. Its distolingual part (lingually to the metastyle) hosts a small developed area that gives the impression like a small cusp, especially in SNSB-BSPG 2020 XCIV-4270. The parastyle is present (slightly individualised from the cingulum), being smaller in GPIT/MA/10306, moderate in SNSB-BSPG 2020 XCIV-2676 and larger in SNSB-BSPG 2020 XCIV-4270. The paracone is long, sharp and significantly higher than the metastyle. A faint ridge stems from the paracone apex, extending lingually towards the mesial border of the protocone complex. There is a clear notch between the paracone and the metastyle. The metastyle blade forms a faint arc connected to the mesial part of the cingulum. The protocone is well developed and is located slightly distally in relation to the paracone, reaching the plane of the carnassial notch. The valley formed between the paracone and the protocone is flatter and wider in GPIT/MA/10306 than in SNSB-BSPG 2020 XCIV-2676 and SNSB-BSPG 2020 XCIV-4270. A protoconule is present, situated at the same plane as the paracone. The protocone and the protoconule are connected with a ridge. In general the three carnassials (GPIT/MA/10306, SNSB-BSPG 2020 XCIV-2676 and SNSB-BSPG 2020 XCIV-4270) form a succession of gradually more robust teeth, in terms of total size, cusp size and cingulum development.

GPIT/MA/13464 (Fig. 5D) is a complete right M1, lacking only the distobuccal root. The wear is visible, but still restricted in the cusps and ridges of the tooth. The specimen GPIT/MA/09628 (Fig. 5E) is also relatively complete, lacking all the roots and it has no signs of wear. On the contrary, the specimen SNSB-BSPG 2020 XCIV-0162 (Fig. 5F) is broken in its mesial part and it has no signs of wear. The general outline is sub-rectangular, being slightly longer than wide. The surface of the enamel is rough, being more wrinkled at its lingual side. A broad cingulum is present in both the lingual (more developed) and the labial side (less developed) of the tooth, becoming fainter in its mesial and distal ends. The paracone and the metacone are of similar pyramidal shape and size, with the paracone being slightly larger. Two tiny cusps that correspond to the parastyle and metastyle are present in the unworn specimens, with the metastyle being slightly more developed than the parastyle. The protocone is lower and blunter than the labial cusps and it is connected with a faint hypocone through a postprotocrista. This crista converges with the lingual cingulum near the hypocone.

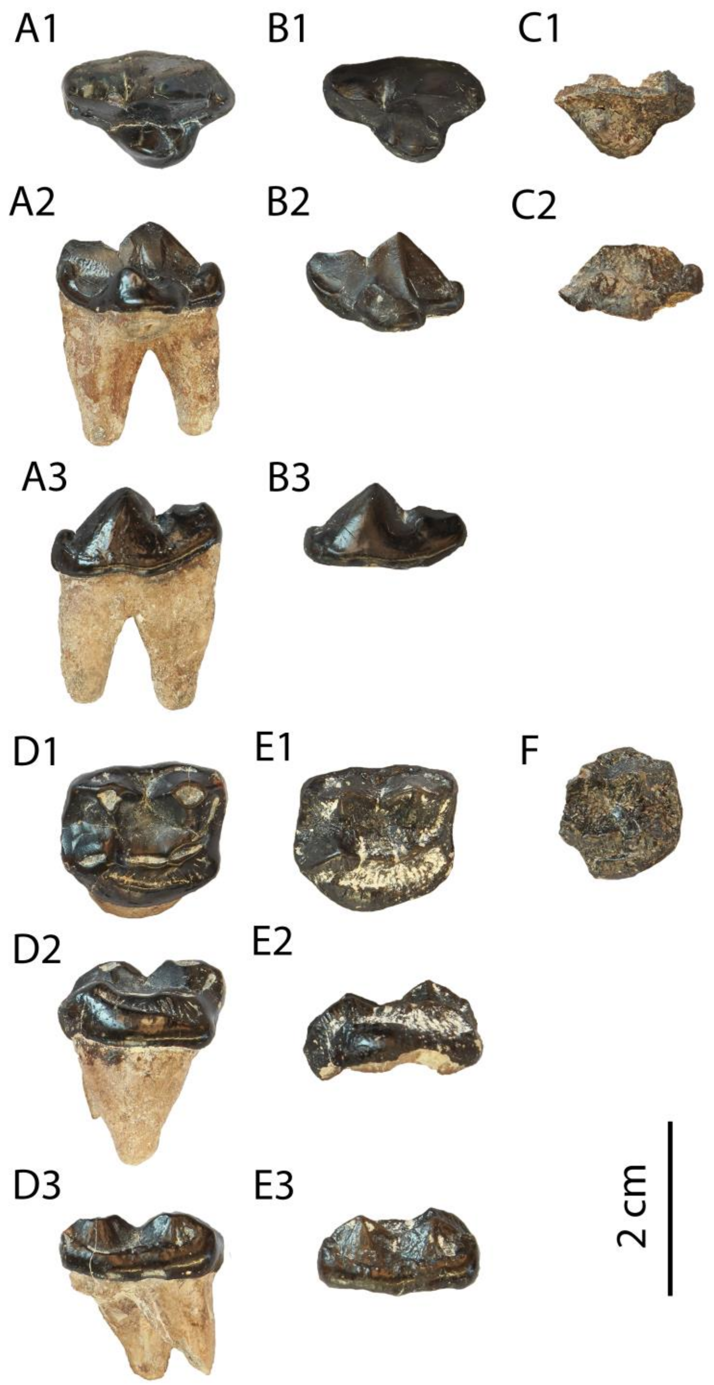

Fig. 5: Upper cheek teeth of *Kretzoiarctos beatrix* from Hammerschmiede: (A) SNSB-BSPG-2020 XCIV-4270 right P4 in occlusal (A1), lingual (A2) and buccal (A3) view; (B) GPIT/MA/10306 right P4 in occlusal (B1), lingual (B2) and buccal (B3) view; (C) SNSB-BSPG-2020 XCIV-2676 right P4 in occlusal (C1) and lingual (C2) view; (D) GPIT/MA/13464 left M1 in occlusal (D1), lingual (D2) and buccal (D3) view; (E) GPIT/MA/09628 left M1 in occlusal (E1), lingual (E2) and buccal (E3); (F) SNSB-BSPG-2020 XCIV-0162 right M1 in occlusal view.

The lower canine (GPIT/MA/09894; Fig. 6A) is broken distally, retaining however, the major part of the crown. Considerable signs of wear are exhibited in the lingual side of the tooth and in the crown’s tip. The canine is relatively short and broad, curved, with a dorsoventral ridge in its mesial side. A smooth lingual cingulum is present, while there is a faint notch in the mesial part of the tooth, labially to the aforementioned ridge.

GPIT/MA/10304 (Fig. 6B) is a complete right m1, still embedded in its alveolus, with only a faint sign of wear in the trigonid blade and in the distal surface of the metaconid. A very smooth cingulum is present in the perimeter of the tooth. The trigonid is long (occupying approximately 70% of the tooth's length) and moderately high. All the trigonid cuspids form a wide angle, and their tips are pointy, due to the absence of wear. The paraconid is the bluntest of them and it is directed mesially. It is connected to the protoconid with a developed carnassial notch. The protoconid is the largest cuspid of the lower carnassial. It is connected to the metaconid with a high protocristid. The metaconid is also broad and high, comparable in size to the protoconid, situated just above the lingual cingulum and distally in relation to the protoconid. The three talonid cuspids are high. The hypoconid is the lowest of them, seen as a small tip in the crista obliqua. An entoconulid is present in the distolingual corner of the tooth, connected to the entoconid with a small notch. The talonid basin is shallow, long and narrow.

The specimens GPIT/MA/10305 (Fig. 6C) and GPIT/MA/13717 (Fig. 6D) are two complete right second lower molars, lacking only their roots. SNSB-BSPG 2020 XCIV-4014 (Fig. 6E) preserves only part of the talonid region. As in m1, a faint cingulum encircles the tooth and there are no significant traces of wear. The largest cuspid is the metaconid, which is situated distally to two smaller cuspids that are herein interpreted as metaconulids. The metaconid is connected to the protoconid through a high protocristid. The trigonid basin is shallow and wide. The entoconid is the largest of the talonid cuspids, being situated mesially to a smaller entoconulid. The hypoconid is relatively blunt and it is the smallest cuspid of the tooth. It preserves a hypocristid in its lingual side. The talonid basin is wide and deeper than in m1, mainly due to the relative height of the protocristid.

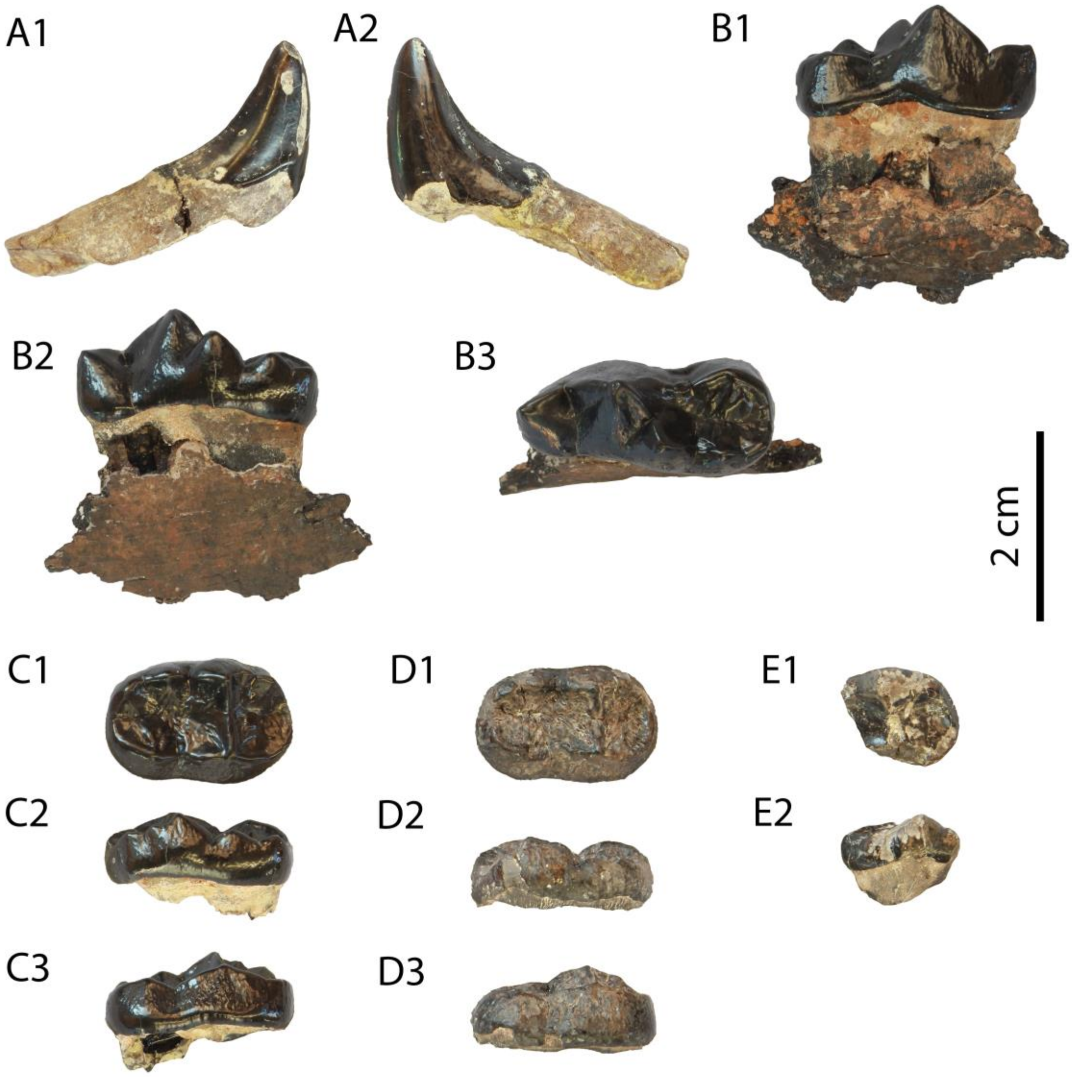

Fig. 6: Lower teeth of *Kretzoiarctos beatrix* from Hammerschmiede: (A) GPIT/mA/09884 left c in lingual (A1) and buccal (A2) view; (B) GPIT/MA/10304 right m1 in buccal (B1), lingual (B2) and occlusal (B3) view; (C) GPIT/MA/10305 right m2 in occlusal (C1), lingual (C2) and buccal (C3) view; (D) GPIT/MA/13717 right m2 in occlusal (D1), lingual (D2) and buccal (D3) view; (E) SNSB-BSPG-2020 XCIV-4014 left m2 in occlusal (E1) and lingual (E2) view.

Discussion

Comparison and taxonomic remarks

Comparison to *Ballusia*: The genus *Ballusia* Ginsburg and Morales, 1998, includes four species of primitive ursids. The exact phylogenetic position of these forms remains unclear. Based on the most recent review on this genus (Sotnikova et al., 2021), it is clear that Ballusia represents a significantly smaller form than the Hammerschmiede material. Additional morphological differences of *Ballusia* from the herein studied specimens, based on the descriptions and depictions of Dehm (1950), Qiu et al. (1985), Ginsburg and Morales (1998) and Sotnikova et al. (2021), include: a more mesially situated P4 protocone complex, a P4 paracone that is much higher than the P4 metastyle, relatively shorter M1 with more developed cingulum, higher m1 protoconid, wider m1 talonid valley, longer m2 talonid with much simpler cuspid morphology.

Comparison to *Ursavus*: The genus *Ursavus* Schlosser, 1899, includes a variety of different forms. The most recent and thorough review of this group was made by Qiu et al. (2014). Based on the measurements provided by Qiu et al. (2014, Tables 4 and 5), all the known species of this genus are significantly smaller than the Hammerschmiede material. *Kretzoiarctos* exhibits some morphological differences to all the members of this lineage: the P4 is relatively larger, less triangular and preserves a parastyle, the m1 trigonid is less developed (in terms of cuspid height and sharpness) and the m2 talonid is more developed. Since this genus includes several different forms, a more detailed comparison to the European species is herein presented. The earliest member of this group is *Ursavus isorei* Ginsburg and Morales, 1998, which has been found in variable Early Miocene localities in France. This is the smallest species of the genus and, consequently, exhibits the most extreme size difference to *Kretzoiarctos*. Additionally, its M1 exhibits a more expanded lingual part, whereas m1 has a more mesiodistally expanded talonid valley. The material of *Ursavus primaevus* Gaillard, 1899, from the type locality (La Grive-Saint-Alban) differs from the Hammerschmiede species in the slenderer P4 protocone complex, the more developed M1 metastyle, the higher m1 trigonid and the shorter m1 talonid (Gaillard, 1899; Viret, 1951). The species *Ursavus brevirhinus* Hofmann, 1887, is characterized by a more restricted P4 protocone region, a more oval-shaped M1, a higher m1 protoconid, a more developed m1 cingulum and a simpler and higher m2 (Thenius, 1949; Crusafont Pairó and Kurtén, 1976). The species *Ursavus intermedius* von Koenigswald, 1925, has been reported from the localities of Engelwies (type locality; m1 and m2) and Steinheim (P4, M1 and M2; Heizmann, 1973). The differences between the combined material from these two localities and that from Hammerschmiede include: a more triangular P4, a more globular M1 with a buccal notch between the paracone and the metacone, a higher m1 protoconid, a lower m1 metaconid and a simpler m2 talonid. Finally, the species *Ursavus ehrenbergi* Brunner, 1942 has been found only in the Turolian locality of Halmyropotamos (Greece) (Thenius, 1947). Unfortunately, it is known only from upper dentition, therefore a comparison based on lower dentition is impossible. However, based on the preserved maxilla, this species seems to be the largest European form (Qiu et al., 2014, Table 4). The upper carnassial is far smaller than that of *Kretzoiarctos*, also having more robust buccal cusps and cingulum and a larger and more developed protocone complex. Though, the dimensions of M1 are comparable to that of the present specimens. This tooth is relatively homogenous in the Miocene bears of Europe, but it can be noted that in *U. ehrenbergi* the distolingual part of M1 is less expanded than in *Kretzoiarctos*.

Comparison to *Indarctos*: The genus *Indarctos* represents a considerably larger and more derived group of ailuropodines than the one from Hammerschmiede. Based on the descriptions and depictions of Montoya et al. (2001), Baryshnikov (2002), Abella (2011), Abella et al. (2019), Jiangzuo et al. (2019b), *Indarctos* differs from the herein reported material in the following characteristics: larger size, more robust dentition, larger P4 parastyle that is separated from the P4 paracone, larger P4 protocone complex, larger P4 protoconule, lower m1 cuspids, shorter m1 metaconid, larger entoconid and entoconulid in m1 and m2 and absence of a second metaconulid in m2.

Comparison to *Agriarctos*: This form is more similar to *Kretzoiarctos* than the previous ones. That is the reason why initially the specimens from Nombrevilla were assigned to this genus. However, all the distinguishing features demonstrated in Abella et al. (2011, 2012) are evident in the Hammerschmiede material. In particular, the herein presented upper carnassial differs from those of *A. depereti* in the following characteristics: the P4 parastyle (despite being variable) is smaller, the buccal cusps of P4 are wider (only GPIT/MA/10306 is comparably slender to the Soblay specimen) and the P4 protocone complex is less developed and slightly more mesially situated. In comparison to the holotype material from Melchingen (Schlosser, 1902), the Hammerschmiede specimens exhibit: larger trigonid cuspids (especially the protoconid and paraconid), a steeper distal side of the m1 metaconid, longer m1 entoconulid with a more distinct notch with the entoconid, relatively larger m2 with higher cuspids (that create the image of deeper valleys) and well-differentiated m2 metaconulids. The relation of

P4L and M1L couldn't be tested as there is no evidence that some of the discovered specimens belong to the same individual. However, it must be noted that the larger size of *A. depereti* (proposed by Abella et al. 2012) was not verified based on the present specimens, since some teeth from Hammerschmiede (m1 and m2) are larger than those of this species (Table 2; Fig. 8).

Comparison to *Miomaci pannonicum*: All the metrical values of *M. pannonicum* are significantly lower than that of the specimens from Hammerschmiede (Table 2; Figs. 7 and 8). However, this species is known only from very few specimens and its size range cannot be estimated based on present data, especially while considering the possibility of sexual dimorphism, which has been reported in this group (Abella, 2013). The relative dimensions of each tooth are similar with the Hammerschmiede material, with the exception of the slightly relatively slenderer m1 and relatively wider m2 in *Miomaci* (Table 2). However, these deviations can be explained through intraspecific variability. The upper carnassial of *Miomaci* is almost similar to GPIT/MA/10306, but with a more developed buccal cingulum and a less developed parastyle (de Bonis et al., 2017, Fig. 3B). The M1 of *Miomaci* exhibits a very flat surface in comparison with the wrinkled enamel of the specimens from Hammerschmiede (de Bonis et al., 2017, Fig. 3B–C). However, this trait can be interpreted as individual variability or as a taphonomic effect. Additionally, the postprotocrista is isolated from the lingual cingulum in the Hammerschmiede specimens (Fig. 1F–H), whereas in *Miomaci* they merge at the level of the protocone (de Bonis et al., 2017, Fig. 3B–C). The lower carnassial of *Miomaci* exhibits relatively longer paraconid and smaller metaconid, while the lingual talonid cusps are absent (de Bonis et al., 2017, Fig. 2A & 2C). The m2 of *Miomaci* has a relatively longer trigonid (de Bonis et al., 2017, Fig. 2C).

Comparison to *Kretzoiarctos beatrix* from Spain: In general all the measurements and the relative dimensions of the specimens from Hammerschmiede are be similar to that of *K. beatrix* (Table 2; Figs. 7 and 8). The upper carnassial of *K. beatrix* (NV-2-42) is in general more robust, with a slenderer protocone neck, a more developed buccal cingulum and parastyle, the latter also being slightly more lingually placed (Abella et al., 2011, Fig. 1). The first upper molar of *K. beatrix* (NV-2-40) is very similar with that from Hammerschmiede, but its buccal cusps are more isolated, with the postmetacrista and preparacrista not reaching the mesial and distal cingulum (Abella et al., 2011, Fig. 1). The lower carnassial of *K. beatrix* (IPS46473) is too damaged to enable a detailed comparison. However, its remaining parts look rather similar to GPIT/MA/10304 (Abella et al., 2012, Fig. 1). The m2 of *K. beatrix* (IPS46473) is almost identical to the specimens from Hammerschmiede, but unfortunately the wear doesn't enable a close comparison (Abella et al., 2012, Fig. 1).

Table 2: Metrical comparison of the dental material of *K. beatrix* from Hammerschmiede (HAM 4 and HAM 5) and the species from Nombrevilla 2 (NV-2) and ACM/C6-Camí (ACM) (Abella et al., 2012), *M. pannonicum* from Rudabánya (RUD; de Bonis et al., 2017), *A. depereti* from Melchingen (MEL), Luzinay (LUZ) and Soblay (SOB) (Crusafont Pairó & Kurtén, 1976; Qiu et al., 2014); *U. brevirhinus* from Can Llobateres (CL), Steyregg (STE) and Göriach (GÖR); and *U. primaevus* from La Grive-Saint-Alban (LG), Deinothere Sands (DS) and Oppeln (OPP) (Crusafont Pairó & Kurtén, 1976).

Tooth	Species	Locality	Code	L	W	W/L	H	Ltr
C	*K. beatrix*	HAM 5	GPIT/MA/09631	18.7	11.7	0.63	31.6	-
			GPIT/MA/09893	21.8	12.6	0.58	-	-
	M. pannonicum	RUD	RUD-1948	11.5	7.9	0.69	-	-
P4	*K. beatrix*	HAM 5	GPIT/MA/10306	18.0	11.5	0.64	9.8	-
		HAM 4	SNSB-BSPG 2020 XCIV-4270	18.5	13.2	0.71	10.1	-
		NV-2	NV-2-42	18.3	13.1	0.72	-	-
	M. pannonicum	RUD	RUD-1948	13.3	8.6	0.65	-	-
	A. depereti	SOB	No Nu	19.7	13.1	0.66	-	-
			No Nu	21.3	14.5	0.68	-	-
	U. primaevus	LG & OPP	summed	13.2–16.0 14.5 (3)	9.0–11.2 9.9 (3)	0.66–0.70 0.68 (3)	-	-
M1	*K. beatrix*	HAM 5	GPIT/MA/09628	17.8	16.7	0.94	8.5	-
			GPIT/MA/13464	17.6	15.5	0.88	-	-
		HAM 4	SNSB-BSPG 2020 XCIV-0162	-	14.9	-	-	-
		NV-2	NV-2-40	17.2	15.2	0.88	-	-
	M. pannonicum	RUD	RUD-1675	14.9	13.0	0.87	-	-
			RUD-1948	13.9	13.1	0.94	-	-
	A. depereti	SOB	No Nu	18.9	16.7	0.88	-	-
			No Nu	19.9	17.2	0.86	-	-
	U. primaevus	LG & OPP	summed	13.8–15.8 14.6 (4)	11.8–13.3 12.5 (4)	0.83–0.88 0.86 (4)	-	-
c	*K. beatrix*	HAM 5	GPIT/MA/09894	(13.6)	(8.9)	0.65	20.6	-
		ACM	IPS46473	14.7	8.8	0.60	-	-
m1	*K. beatrix*	HAM 5	GPIT/MA/10304	24.5	11.6	0.47	11.7	16.9
		ACM	IPS46473	22.6	10.8	0.48	-	-
	M. pannonicum	RUD	RUD-559	19.2	8.3	0.43	-	-
				19.4	8.6	0.44	-	-
		CP	No Nu	21.2	9.5	0.45	-	-
	A. depereti	MEL	GPIT/PV/122860	23.5	12.6	0.54	12.0	17.0
	U. brevirhinus	CL & STE	summed	15.0–17.6 16.3 (3)	7.2–8.6 7.8 (3)	0.44–0.50 0.48 (3)	-	-
	U. primaevus	LG, DS & OPP	summed	19.2–20.6 19.9 (4)	10.0–10.4 10.2 (4)	0.50–0.53 0.52 (4)	-	-
m2	*K. beatrix*	HAM 5	GPIT/MA/10305	19.1	12.9	0.68	6.7	-
			GPIT/MA/13717	18.7	12.2	0.65	6.9	-
		HAM 4	SNSB-BSPG 2020 XCIV-4014	-	>11.0	-	-	-
		ACM	IPS46473	17.7	11.3	0.64	-	-
	M. pannonicum	RUD	RUD-559	14.3	10.1	0.71	-	-
		CP	No Nu	15.9	9.9	0.62	-	-
	A. depereti	MEL, LUZ	summed	17.3–17.6 17.5 (2)	10.8–11.8 11.3 (2)	0.61–0.68 0.65 (2)	-	-
	U. brevirhinus	CL, STE, GÖR	summed	11.7–13.1	7.4–9.1	0.63–0.74 0.70 (4)	-	-
	U. primaevus	LG & OPP	summed	14.2–15.1 14.6 (4)	9.2–9.6 9.5 (3)	0.61–0.68 0.65 (3)	-	-

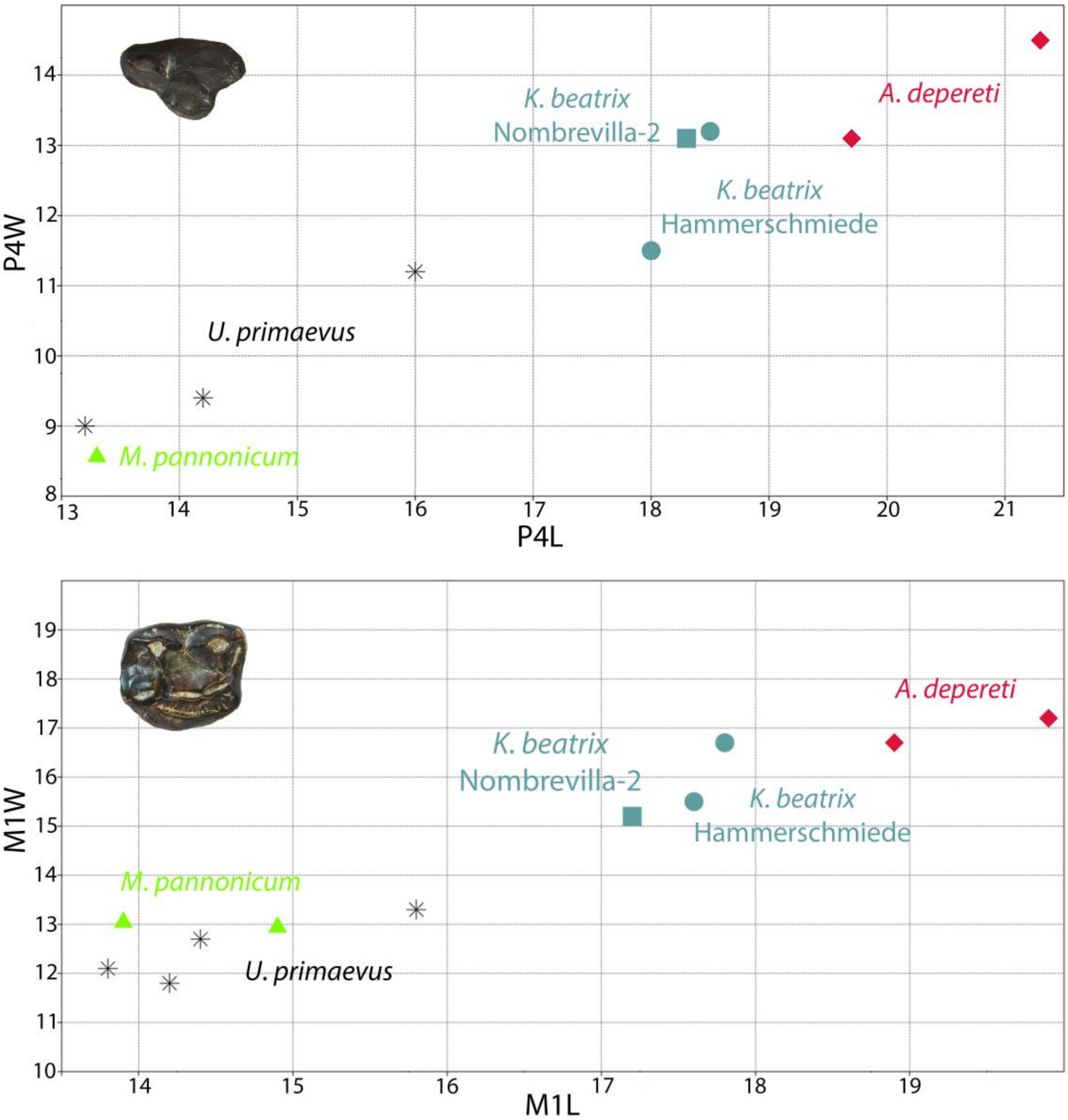

Figure 7: Comparison of the P4 and M1 dimensions of *Kretzoiarctos beatrix* (Hammerschmiede and Nombrevilla) to that of *Agriarctos depereti*, *Miomaci pannonicum* and *Ursavus primaevus*. Data sources as in Table 2.

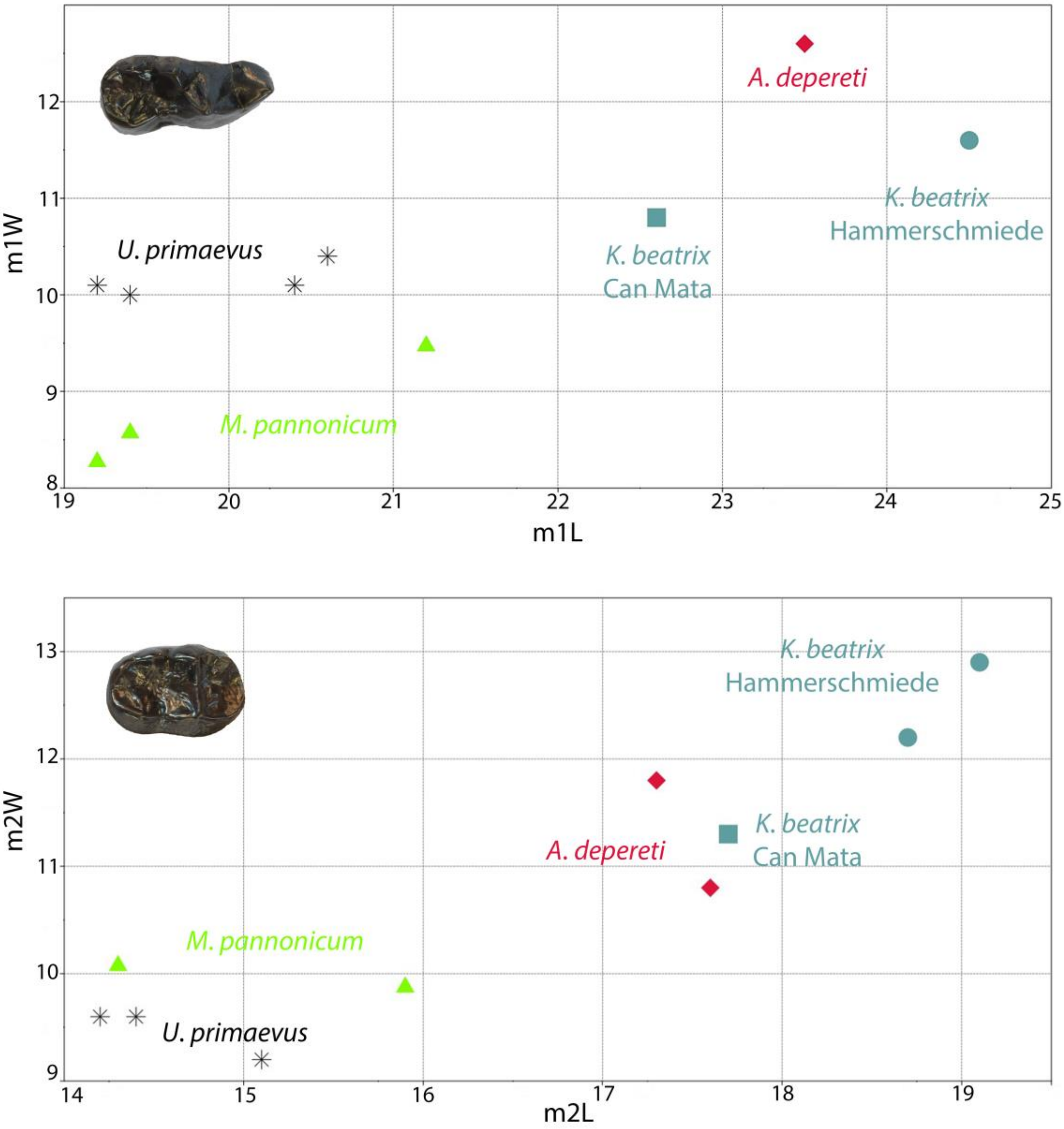

Figure 8: Comparison of the m1 and m2 dimensions of *Kretzoiarctos beatrix* (Hammerschmiede and Can Mata) to that of *Agriarctos depereti*, *Miomaci pannonicum* and *Ursavus primaevus*. Data sources as in Table 2.

Palaeoecology – Dental Microwear Texture Analysis and Ecomorphology

Four out of the eight extant bear species were used as comparative material for the microwear analysis. The giant panda (*Ailuropoda melanoleuca*) is the most herbivorous of the extant ursids with bamboo being its main source of food. All the parts (shoot, leaves and culm) of approximately 60 bamboo species are eaten by the panda (Wang et al., 2017). However, there are reports of consuming small vertebrates (including meat and bones), honey, but also other plant material, soft (irises, gentians etc.) or hard (tufted grass, fir bark etc.) (Chorn & Hoffmann, 1978). The polar bear (*Ursus maritimus*) is the most carnivorous of the extant ursids. Their diet consists mainly on seals, walruses and beluga whales, but occasionally (especially the pregnant females) also on berries and other plant material (DeMaster & Stirling, 1981; Amstrup, 2003). The remaining two studied species have a more opportunistic diet that is based on soft plant material. The brown bear (*Ursus arctos*) feeds on a seasonal variability in plants (>85%; new vegetation in spring; herbs and fruits in summer; berries and mast in autumn), but also animal material (small vertebrates or insects; large vertebrates like moose) and anthropogenic food

(Pasitschniak-Arts, 1993; Swenson et al., 2000; McLellan, 2011). It also displays three stages of food consumption: hypophagia in spring, normal activity in summer and hyperphagia in autumn (Swenson et al., 2000). Finally, the spectacled bear (*Tremarctos ornatus*) is another mainly herbivorous species, feeding on soft (and rarely hard) plant material and occasionally on invertebrates and small vertebrates as a predator or a scavenger (Peyton, 1980; Suarez, 1988; García-Rangel, 2012; Gonzales et al., 2016).

Even though the DMTA has demonstrated that the diet of *K. beatrix* was different from the one of the giant panda, no significant difference was found between the hypercarnivorous and opportunistic species. Therefore, in order to evaluate the palaeoecology of the Hammerschmiede ailuropodine, an ecomorphological comparison concerning the dental characteristics of the compared species has been conducted. The morphology of P4, M1, m1 and m2 of *Ursus maritimus*, *Ursus arctos*, *T. ornatus*, *A. melanoleuca* and *K. beatrix* is presented in Fig. 9. In general, the dentition of the polar bear is much narrower than that of the remaining species. All the grinding surfaces of the cheek teeth are decreased, including the lingual part of M1, the m1 talonid (which does not include cuspulids in its rim) and the total surface of m2 trigonid and talonid. Additionally, the protocone region of P4 and the metaconid of m1 are also rudimentary in relation to the other ursids. These characteristics create a slenderer dental form, which is better adapted to the flesh-shearing function instead of the grinding one. On the contrary, the dentition of the giant panda exhibits the exact opposite traits: the grinding surfaces of the cheek teeth (lingual part of M1, m1 talonid, m2 trigonid and talonid) are enlarged and host well-developed cusps and cuspids, while the P4 has developed protocone and hypocone and the m1 has a developed metaconid. These features create a far more robust dentition with enhanced grinding surfaces that is not so well-adapted to shear flesh. The brown bear and the spectacled bear exhibit an intermediate morphology between the two aforementioned species. The grinding surfaces are well-developed and host cuspules/cuspulids, but they are not as wide and robust as in the giant panda. Additionally, the protocone region and the m1 metaconid are well-developed, but in a considerably less degree in relation to *A. melanoleuca*. Therefore, the development degree of the grinding surfaces of the cheek teeth can be correlated to the diets of the extant ursids: the hypercarnivorous polar bear presents the most restricted surfaces, the hard-plant-eater giant panda exhibits the most robust ones, whereas the opportunistic brown and spectacled bears have an intermediate morphology. This line of thought is also followed in Sacco and Van Valkenburgh (2004). The morphology of *Kretzoiarctos* conforms better to that of the opportunistic species as the grinding surfaces, the P4 protocone region and the m1 metaconid are moderately developed. However, the P4 carnassial blade and the m1 trigonid are more developed than the opportunistic forms, while the grinding surfaces in M1, m1 talonid and m2 are less developed and don’t exhibit the complex morphology of the extant bears. In this sense, *K. beatrix* preserves a more plesiomorphic set of traits (consistent to the stratigraphical range of the species) that differentiate it from the mostly herbivorous modern ursids. These differences can be interpreted as indicators of a less plant-based diet for this form.

The results per individual (Fig. 9) and per species (Fig. 10) proved that in every case there were no outliner values that could be attributed to erroneous measurements. Therefore, the used dataset is considered to be interpretable. Figure 11 demonstrates the plotting of the different species for each of the 4 teeth used in this study. It can be seen that in almost all cases there is considerable overlap between the species. However, in every one of these graphs, the giant panda (Ailmel) is plotted to the lower-left part of the graph, the brown bear (Urarc) plots to the upper-right part of the graph and the rest of the species are plotting between them, with the spectacled bear (Trorn) having wider overlap to the giant panda. The fossil species seem to plot with the *Ursus*-group. The graphs for M1 and m2 are more indicative than those of P4 and m1. If all data are combined to one graph (Fig. 12), a similar pattern can be seen, but the overlaps are still very important.

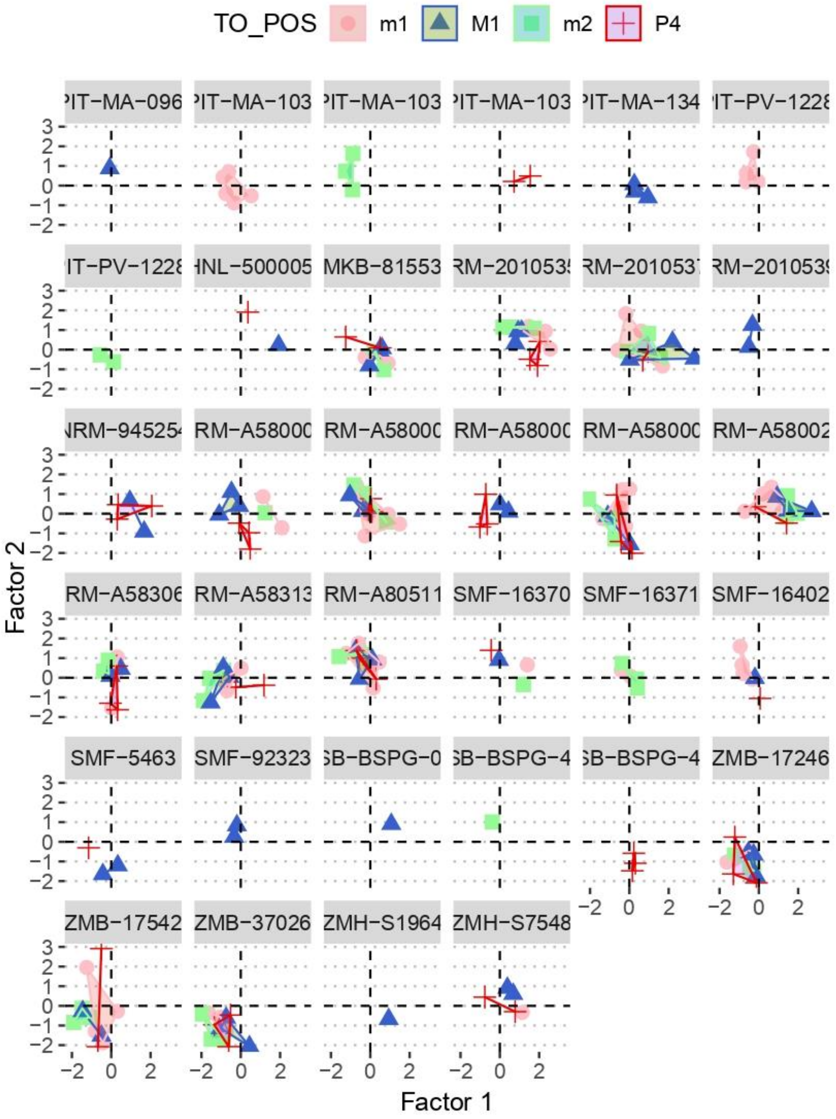

Figure 9: Plotting of all the used values per individual (for all species), in order to investigate for outliners.

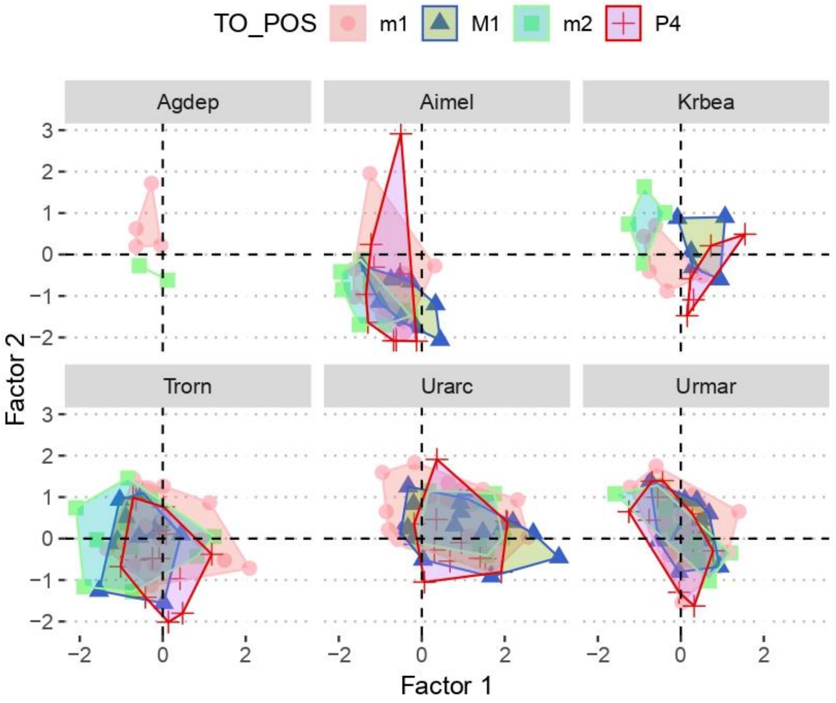

Figure 10: Plotting of all the used values per species (for all species), in order to investigate for outliners.

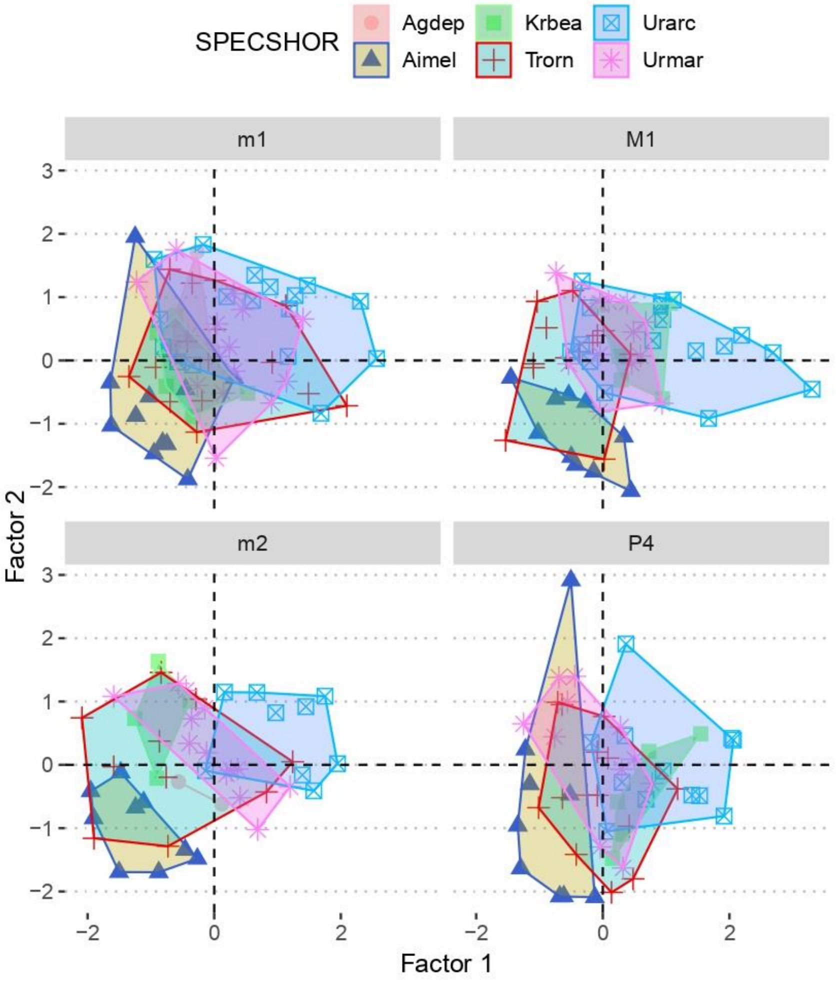

Figure 11: Plotting of the values per tooth for all species.

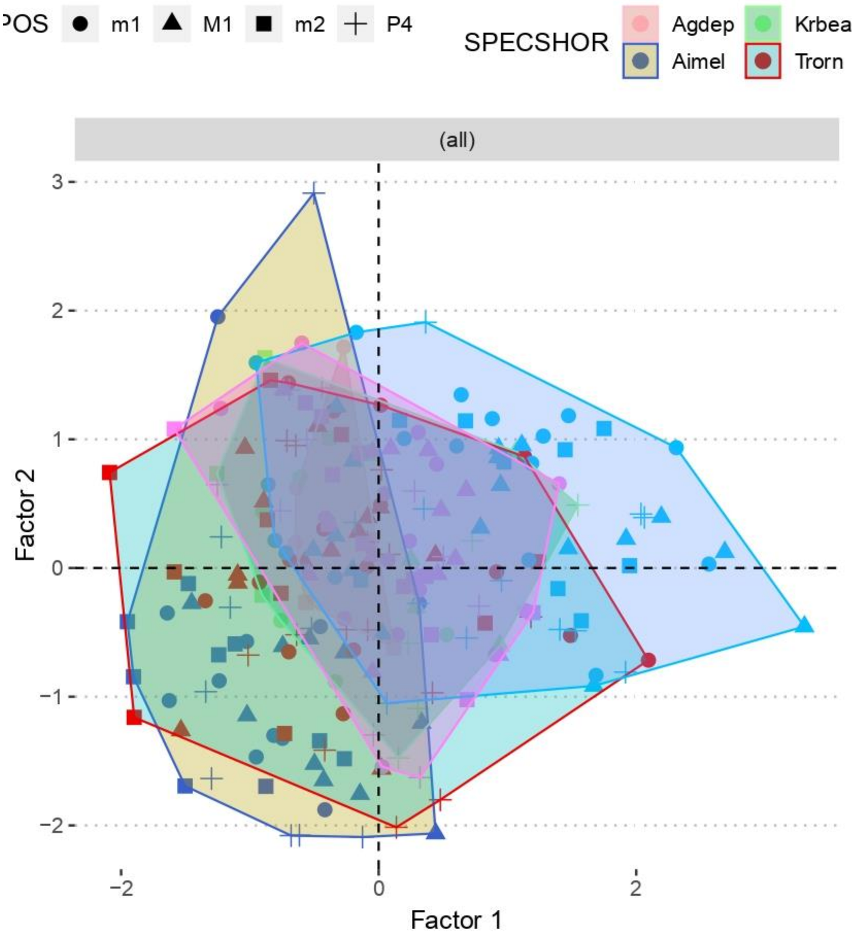

Figure 12: Combined plot of all the values for all teeth and species.

Therefore, the interpretation of these graphs would be that the fossil species were different from the giant panda, and despite being ailuropodines, they did not exhibit herbivory based on hard material. On the contrary, they plot with the extant genus *Ursus*, indicating a more opportunistic diet. However, current data failed to clearly differentiate the hypercarnivorous polar bear from the brown bear. Therefore, this method is for the moment inadequate for the interpretation of the percentage of meat in the diet of *Kretzoiarctos*. In order to investigate that, we have made a preliminary ecomorphological comparison, based on dental morphology.

Sacco and Van Valkenburgh (2004) investigated the statistical significance of several proxies to the dietary behaviour in the extant ursids. Unfortunately most of the proxies discussed by Sacco and Van Valkenburgh (2004) require the presence of complete dentitions and mandibles, so they were not applicable in the present study. However, the proxy P4SH (P4W at the level of protocone, divided by P4L) has been proved to be ecomorphologically indicative by Sacco and Van Valkenburgh (2004) and it has been used herein. As demonstrated in Fig. 10 and Table 3, the opportunistic species are characterized by higher values for this proxy, whereas the polar bear and the giant panda exhibit lower P4SH values. The low value for *A. melanoleuca* can be explained by the relatively long P4, in comparison to that of the other species (Fig. 13). The values for *K. beatrix* are plotting between the opportunistic forms and the polar bear (Fig. 14), supporting the aforementioned hypothesis.

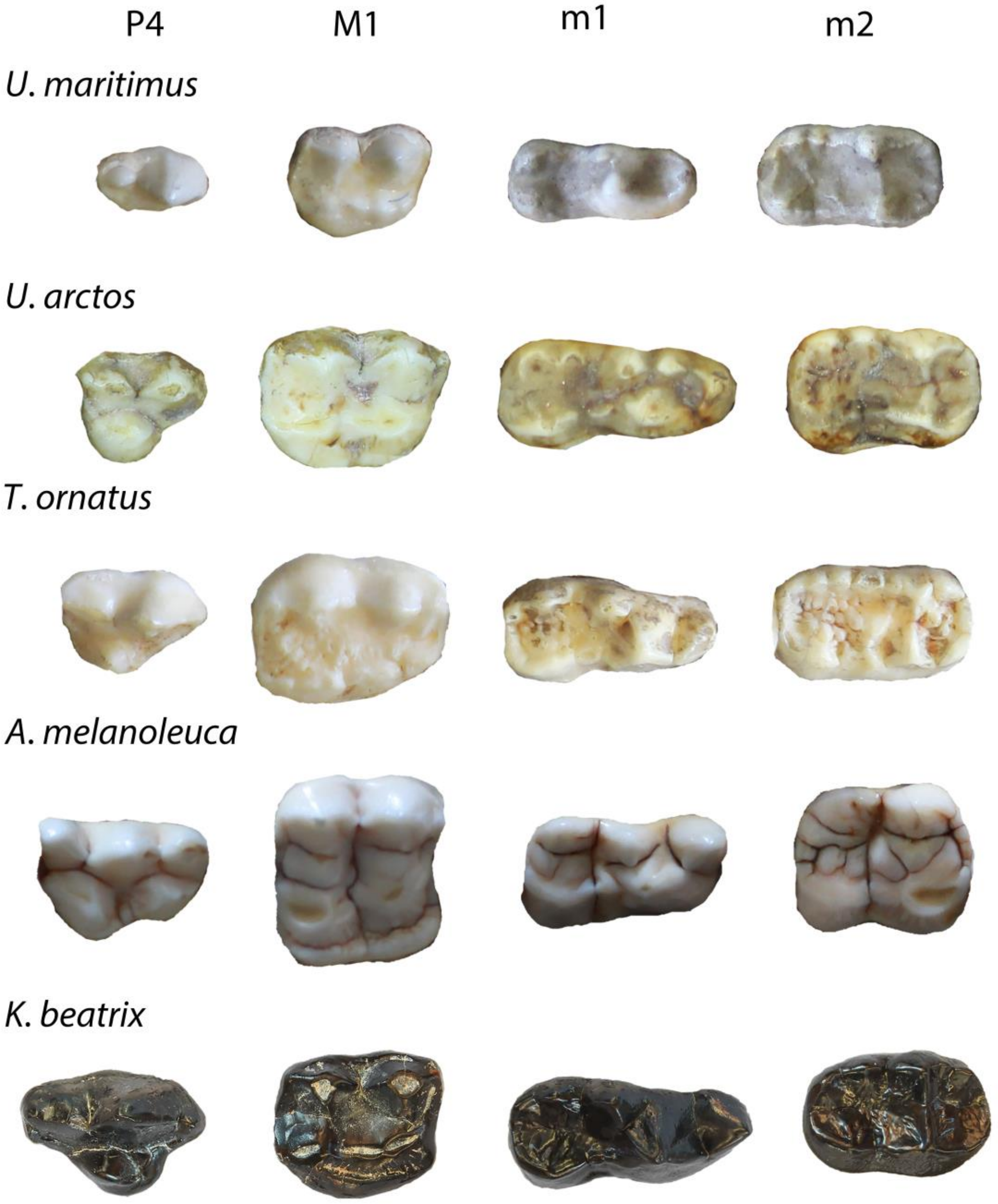

Fig. 13: Comparison of the P4, M1, m1 and m2 of *Kretzoiarctos beatrix* from Hammerschmiede to that of the extant species used in DMTA: *Ursus maritimus* (MNHN-1928-303), *Ursus arctos* (NMNHS-1020), *Tremarctos ornatus* (SMNS-573b), *Ailuropoda melanoleuca* (SMNS-2298). Not in scale.

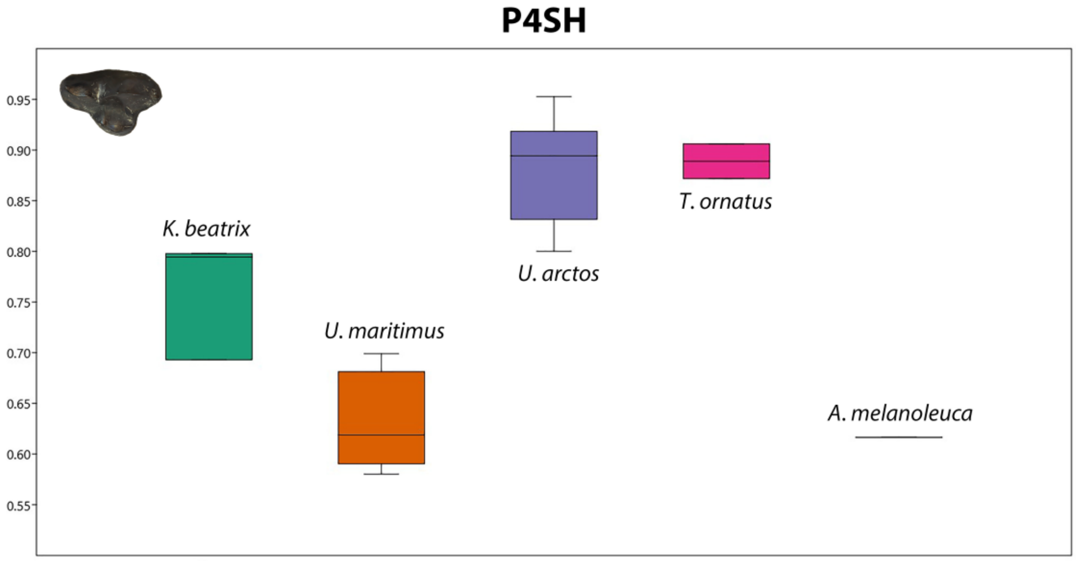

Fig. 14: Comparison of the arcsin of P4SH (P4W / P4L) of *Kretzoiarctos beatrix* to that of the extant ursids. Data in Table 3.

Table 3: P4SH values for *Kretzoiarctos beatrix* and extant ursids.

Species	Code	P4L	P4W	P4SH	arcsin(P4SH)
K. beatrix	GPIT/MA/10306	18	11.5	0.6388	0.6930
	SNSB-BSPG 2020 XCIV-4270	18.5	13.2	0.7135	0.7945
	NV-2-42	18.3	13.1	0.7158	0.7978
U. maritimus	SMNS-31849	15.94	8.74	0.5483	0.5803
	SMNS-325	15.31	8.65	0.564	0.6004
	SMNS-43704	14.33	9.22	0.6434	0.6989
	SMNS-21751	14.74	8.55	0.5800	0.6187
	NMNHS-No Nu	13.41	8.26	0.6159	0.6636
U. arctos	AMPG-EV68	15.11	10.84	0.7174	0.8000
	AMPG-EV97	15.37	12.05	0.7839	0.9010
	NMNHS-No Nu	16.48	13.43	0.8149	0.9526
	NMNHS-1024	14.91	11.99	0.8041	0.9342
	NMNHS-1023	16.07	12.53	0.7797	0.8942
	NMNHS-1463	17.47	13.42	0.7681	0.8759
	NMNHS-1032	16.5	12.95	0.7848	0.9024
	NMNHS-1017	16.12	11.78	0.7307	0.8194
	NMNHS-1020	14.48	10.82	0.7472	0.8438
T. ornatus	SMNS-26250	11.77	9.01	0.7655	0.8718
	SMNS-573b	12.35	9.72	0.7870	0.9060
A. melanoleuca	SMNS-2298	26.6	15.38	0.5781	0.6165

Conclusions

The herein presented material is identified as *Kretzoiarctos beatrix*, consisting of the first report of the genus outside the Iberian Peninsula. The discovered specimens provided the opportunity for a detailed comparison with the Miocene ursids of Europe. Microwear analysis combined with ecomorphological comparisons suggested that this species had a completely different diet than the giant panda and it was more similar to the opportunistic extant *Ursus*.

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Study of Additional Material

The five already presented papers don’t cover the study of the Hammerschmiede carnivorans completely. There is an abundance of additional material from several other taxonomic groups and some new material of the already published species that came to light after the publications were submitted. This part of the manuscript will cover these findings, offering a preliminary view on the Hammerschmiede carnivoran fauna as a whole.

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Suborder Caniformia KRETZOI, 1943

Family Amphicyonidae HAECKEL, 1866

Amphicyonidae indet.

Material: HAM 5: one right D4 (GPIT/MA/18116) and one left McIII (GPIT/MA/12132).

Description: The specimen GPIT/MA/18116 is a right D4 (Fig. 5.1.2). There are no signs of wear. The valley of the tooth hosts a deep cavity, not enabling the description of the lingual cusps and cristae. The paracone and the metacone are of similar pyramidal shape, with the paracone being slightly higher and slenderer. There are no signs of accessory cuspids. A distinct crista is starting from the metacone towards the place where the hypocone would be. A cingulum is present in the perimeter of the tooth, being more developed at its buccal side and fainter at its distal part.

Fig. 5.1.1: The right D4 (GPIT/MA/18116) of the amphicyonid of HAM 5.

GPIT/MA/12132 (Fig. 5.1.2) is a complete left McIII. It is relatively slender, in comparison with extant ursines and *Indarctos*. The proximal articular surface is trochlear-shaped, almost symmetrical, with the lateral portion being more elevated. The articular surface for the McII exhibits a semilunar proximal part, followed by a deep fossa and a strong ridge parallel to a shallow groove. A similar semilunar proximal part is present in the articular surface for the McIV, followed by a shallow tuberosity. The sagittal crest of the distal epiphysis doesn't reach the diaphysis, because the trochlea is sharply limited to the distal part of the epiphysis.

Fig. 5.1.2: The left McIII (GPIT/MA/12132) of the amphicyonid of HAM 5.

Comparison: The discovered D4 is broken in its middle part. The morphology of this area resembles that of teeth that have been decomposed by caries. However, μCT technology revealed that the remaining part of the enamel has been broken off and it currently is inside the pulp cavity. Therefore, this breakage is attributed to physical damage (possibly during the excavation) and not to caries.

The identification of this specimen as a deciduous tooth stems from the absence of any structure that can be interpreted as a protocone or another relevant cusp. This is typical for the amphicyonids, for example *Magericyon anceps* (Peigné et al., 2008, fig. 5A)

Table 5.1.1: Measurements of the D4 of the amphicyonid from HAM 5.

	L	W
GPIT/MA/18116	13.8	15.5

The discovered metacarpal is relatively short and wide, indicating that it belongs to a plantigrade caniform. Based on its large size, it could only belong to a member of the Ursidae or Amphicyonidae. The ursid *Indarctos atticus* has similarly-sized McIII (Roussiakis, 2001b). However, this species is far larger than *Kretzoiarctos beatrix*, so an attribution to the latter seems improbable. Additionally, the relatively narrower shaft, the less globular distal epiphysis and the more curved proximal epiphysis resemble more the morphology seen in amphicyonids (Ginsburg, 1961a, fig. 12.5; Argot, 2010, fig. 7). The McIII of *Amphicyon major* is 68 mm (Argot, 2010, Appendix 5), so, as also indicated by the discovered tooth, the amphicyonid from Hammerschmiede is estimate to be a really large species.

Table 5.1.2: Measurements of the McIII of the amphicyonid from HAM 5.

	L	APDpr	TDpr	APDm	TDm	APDd	TDd	APDda	TDda
GPIT/MA/12132	78.2	29.0	17.7	11.7	12.5	11.8	19.8	19.1	16.6

Family Ailuridae GRAY, 1843

Subfamily Simocyoninae DAWKINS, 1868

Genus *Alopecocyon* CAMP & VANDERHOOF, 1940

cf. *Alopecocyon goeriachensis* (TOULA, 1884)

Material: HAM 5: one left hemimandible (GPIT/MA/10300) and one right hemimandible (SNSB-BSPG-2020-XCV-0021).

Description: Two toothless hemimandibles have been found in the HAM 5 layer. The left hemimandible (GPIT/MA/10300; Fig. 5.2.1A) is broken at the ascending ramus, whereas the right hemimandible (SNSB-BSPG-2020-XCV-0021; Fig. 5.2.1B) is also broken at the middle of p3. The mandibular ramus is relatively long and narrow, while the masseteric fossa is relatively shallow. There are two mental foramina: a larger one ventrally to the mesial root of p2 and a smaller one ventrally to the center of p3. There are no remaining roots or dental crowns. However, both hemimandibles exhibit a double-rooted m2 (Fig. 5.2.1).

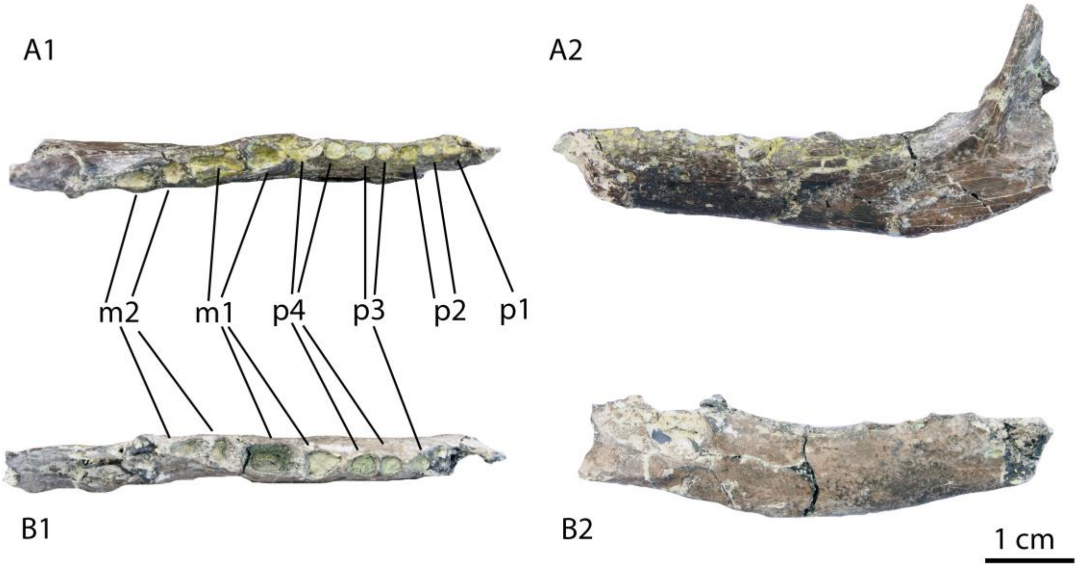


Fig. 5.2.1: The hemimandibles of cf. *Alopecocyon goeriachensis* from HAM 5.

Comparison: The presence of a developed m2 with two roots indicates that this mandibles belongs to an ailurid rather than to a mustelid. Unfortunately, there are no diagnostic characteristics for the Miocene ailurids of Europe based on the mandibular morphology. However, the size of the alveoli can be used as an indicator of the dental size of these forms. As demonstrated in Table 5.2.1, the only species that fits to this size-group is *Alopecocyon goeriachensis*, which has already been described form the HAM 5 layer (Kargopoulos et al., In Press). However, given the fragmentary nature of these specimens, it is herein preferred to refer to them as “cf. *Alopecocyon goeriachensis*”.

Table 5.2.1: Measurements of the alveoli of the discovered hemimandibles from HAM 5 in comparison to the dental dimensions of Miocene ailurids of Europe. Sources: [1]Thenius (1949), [2]Peigné (2012), [3]Ginsburg et al. (1997), [4]Werdelin (2005) and [5]Kullmer et al. (2008).

Species	Code	p1L	p1W	p2L	p2W	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W
cf. *A. goeriachensis*	GPIT/MA/10300	1.8	1.5	4.2	1.9	4.3	1.9	5.4	2.8	10.5	3.8	7.5	2.8
cf. *A. goeriachensis*	SNSB-BSPG-2020-XCV-0021							5.8	2.4	10.1	3.4	6.9	3.2
A. goeriachensis	Göriach									10.7	4.9	7.5	4.3
	La Grive									12.5	5.5	8.0	5.0
	Sansan			4.6	2.4	5.7	2.9	7.3	3.5	10.5	4.9	7.1	4.1
	Leoben					5.6	2.9	7.0	3.4	9.8	4.8	6.3	4.0
P. simpsoni	Can Llobateres												
	Rudabánya			6.3	3.6					16.5	7.4	12.4	6.8
										16.8	7.5		
M. imperialensis	Madrid											12.1	5.8
S. diaphorus	Eppelsheim			7.4	4.5	7.8	4.3	13.2	7.4	22.1	9.9	14.2	7.9
	Rudabánya	6.9		7.5	4.5	8.7	4.9	12.0	7.0	23.0	10.1		
										22.9	10.0		

Family Mephitidae BONAPARTE, 1845

Subfamily Mephitinae BONAPARTE, 1845

Genus *Proputorius* FILHOL, 1890

Proputorius sansaniensis **FILHOL, 1890**

Material: HAM 5: one left m1 (GPIT/MA/18620).

Description: One left lower carnassial has been recovered from the HAM 5 layer. It lacks its roots and the paraconid is missing (Fig. 5.3.1). There are no signs of wear. The enamel surface is faintly wrinkled. A faint cingulid is present in the buccal side of the tooth. The protoconid is the highest cuspid. Its proximal side is inclined, whereas its distal one is almost vertical. The metaconid is moderately developed, well-individualized from the protoconid and approximately half as high as the latter. The talonid is wider than the trigonid. The talonid valley is moderately wide and long. Its lingual part hosts a gradually developed pit. A hypoconid is present, followed by a tiny hypoconulid. The remaining talonid rim is marked by small notches that form minute cuspulids.

Fig. 5.3.1: The lower carnassial (GPIT/MA/18620) of *Proputorius sansaniensis* from HAM 5.

Comparison: The presence of a moderately developed protoconid, the relatively developed hypoconid, the presence of a hypoconulid, the notches in the talonid rim and the moderately developed width of the talonid indicate that this tooth belongs to a mephitid rather than a mustelid. The m1W and the discussed morphology is identical to the specimen SNSB-BSPG-1973-XIX-25 from the HAM 1 layer (Kargopoulos et al., In Press; Table 5.3.1). This consists of the first report of this species from the HAM 5 layer, furtherly supporting the resemblances between HAM 1 and HAM 5.

Table 5.3.1: Comparison of m1W for *Proputorius*. Sources: [1]Kargopoulos et al. (In Press), [2]Peigné (2012) and [3]Mein (1958).

Species	**Locality**	**Code**	**m1W**
Proputorius sansaniensis	HAM 5	GPIT/MA/18620	3.6
	HAM 1[1]	SNSB-BSPG-1973-XIX-25	3.6
	Sansan[2]	summed	3.6–4.7 4.1 (18)
Proputorius pusillus	HAM 1[1]	summed	1.6–1.7 1.7 (2)
	Vieux-Collonges[3]	summed	1.9–2.4 2.1 (15)

Family Mustelidae BATSCH, 1788

Subfamily Lutrinae BONAPARTE, 1838

Genus *Paralutra* ROMAN & VIRET, 1934

***Paralutra jaegeri* (FRAAS, 1862)**

Material: HAM 4: one right M1 (SNSB-BSPG-2020-XCIV-6821).

Description: This specimens is a right M1 that is damaged in the roots and in the paracone (Fig. 5.4.1). A faint to moderately-developed cingulum surrounds the tooth, being stronger in its distolingual part. The metacone is relatively small and pyramidal. A crista hosting a protocone and a protoconule (sensu Kargopoulos et al., 2021b) is present in the mesiolingual part of the tooth. These two cusps are higher than the metacone. The lingual platform is considerably developed, forming a clear angle just lingually to the metacone.

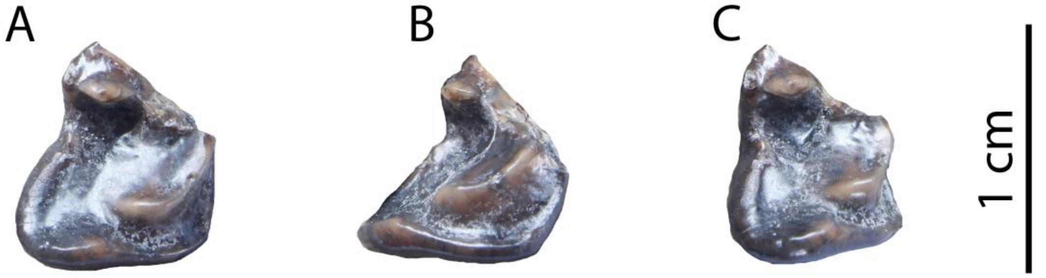


Fig. 5.4.1: The right M1 of *Paralutra jaegeri* (SNSB-BSPG-2020-XCIV-6821) in (A) occlusal, (B) medial-occlusal and (C) distal-occlusal.

Comparison: The expansion of the lingual platform indicates that this specimen belongs to a lutrine. As exhibited in Table 5.4.1, it is considerably smaller than *Lartetictis*. Additionally, the cingulum is not as developed as in this genus (Valenciano et al., 2020b). The M1L of Vishnuonyx neptuni may be similar to that of the present specimen, but the general outline of M1 for the former is far slenderer, with non-prominent lingual platform and a present paraconule (Kargopoulos et al., 2021b). Additionally, it differs from *Potamotherium* sp. in the more expanded lingual platform, the presence of protocone and protoconule, as well as in the smaller size. On the contrary, the small size, the extended lingual platform and the morphology of the mesiolingual cusps conform to the features seen in *Paralutra jaegeri* (e.g. Helbing, 1936; Heizmann, 1973; Kargopoulos et al., In Press). As already discussed in Kargopoulos et al. (In Press), this species exhibits high diversity in size and the degree of development of the lingual platform.

Table 5.4.1: Comparison of the M1L of the described specimen to that of *Paralutra* and *Lartetictis*. Sources: [1]Kargopoulos et al. (In Press), [2]Peigné (2012), [3]Heizmann & Morlo (1998), [4]Valenciano et al. (2020b) and [5]Kargopoulos et al. (2021b).

Species	**Locality**	**Code**	**M1L**
P. jaegeri	HAM 4	SNSB-BSPG-2020-XCIV-6821	7.8
P. jaegeri	Summed	Summed[1]	6.8–8.1 7.3 (8)
L. dubia	Summed	Summed[2, 3]	11.0
L. pasalarensis	Paşalar	Summed[4]	12.4–12.7 12.6 (2)
V. neptuni	HAM 4	SNSB-BSPG-2020-XCIV-1552[5]	7.6

Genus *Lartetictis* GINSBURG & MORALES, 1996

***Lartetictis* cf. *dubia* (DE BLAINVILLE, 1842)**

Material: HAM 4: one partial left hemimandible with p2 (GPIT/MA/17065); and one left m1 (SNSB-BSPG-2020-XCIV-6826).

Description: The left hemimandible is broken mesially to the canine alveolus and at the distal alveolus of p3 (Fig. 5.4.2A). The remaining mandibular ramus is relatively robust, preserving two mental foramina: one smaller below p1 and one larger below p2. There are no diastemata. The only remaining tooth is p2, which is considerably worn. However, it is clear that it is two-rooted, asymmetrical (with its distal part being longer than the mesial part) and has a moderately developed cingulid.

The presented right m1 preserves only the talonid and the metaconid (Fig. 5.4.2B). A moderately developed cingulid is present, being considerably stronger to its distobuccal part. The metaconid is slightly worn in its tip and its remaining connection to the protoconid is relatively high. The talonid is broad and partially worn/damaged in its lingual border. The lingual part of the talonid basin is lower than the buccal one. The distobuccal rim of the talonid hosts two cuspids: a small hypoconid and an even smaller hypoconulid.

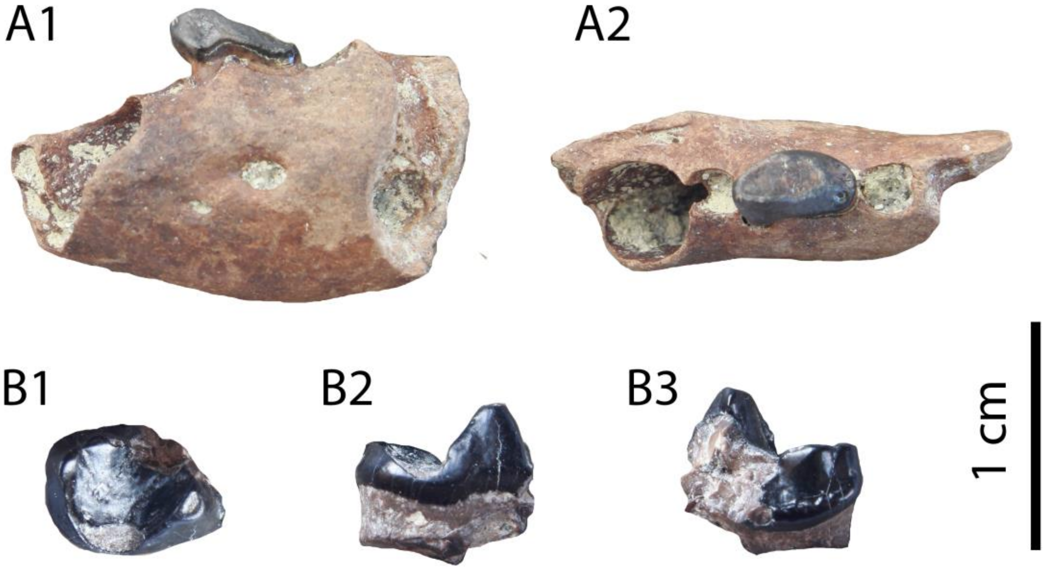


Fig. 5.4.2: Material of *Lartetictis* cf. *dubia* from HAM 4: (A) left hemimandible (GPIT/MA/17065) in (1) buccal and (2) occlusal view; right m1 (SNSB-BSPG-2020-XCIV-6826) in (1) occlusal, (2) lingual and (3) buccal view.

Comparison: Both specimens are in poor preservation and their identification is relatively problematic. However, they both exhibit characteristics that are present in the hemimandible GPIT/MA/17790, published by Kargopoulos et al. (In Press): the robust mandibular ramus, the dental size, the presence and degree of development of cingulids, the connection between the metaconid and protoconid and the morphology of the hypoconid and hypoconulid indicate that these specimens should belong to *Lartetictis* cf. *dubia*.

Table 5.4.2: Comparison of the dimensions of the *Lartetictis* material to other relevant taxa. Sources: [1]Kargopoulos et al. (In Press), [2]Peigné (2012), [3]Heizmann & Morlo (1998) and [4]Valenciano et al. (2020b).

Species	**Locality**	**Code**	**p2L**	**p2W**	**m1W**
L. cf. *dubia*	HAM 4	GPIT/MA/17065	5.3	2.9	
		SNSB-BSPG-2020-XCIV-6826			5.7
		GPIT/MA/17790[1]			6.2
		SNSB-BSPG-2020-XCIV-2683[1]			5.4
L. dubia	Summed	Summed[2, 3]	5.9	3.5	6.5–8.3 7.5 (12)
L. pasalarensis	Paşalar	Summed[4]	7.1	4.0	7.2–8.4 7.7 (7)

Family Phocidae Gray, 1821

Phocidae indet.

Material: HAM 4: GPIT/MA/16996, right premolar. HAM 5: GPIT/MA/18604, right p1; GPIT/MA/18608, left p1; GPIT/MA/09629, left premolar.

Description: The two teeth identified as p1 (GPIT/MA/18604 and GPIT/MA/18608 from HAM 5; Fig. 5.5.1A and B) are very similar, despite the fact that GPIT/MA/18604 is lacking its root and is partially damaged. Therefore, the description is mostly based on the morphology of GPIT/MA/18608. The tooth is single-rooted and the root is considerably oblique in relation to the tooth base. The surface of the tooth is asymmetrical as the distal part is far wider than the mesial one. Additionally, the lingual side of the tooth is slightly larger than the buccal one, while the cuspids' slopes are steeper in the former. A moderately developed cingulum runs through the perimeter of the tooth. The cingulum hosts several small notches that create the appearance of small cuspulids. Two of these cuspulids are situated in the mesial and distal ends of the tooth respectively. A large main cuspid is present in the mesial end of the tooth. It is followed distally by two distal accessory cuspids, the mesial of the two being larger than the most distal one. All cuspids are relatively blunt with no distinct signs of wear.

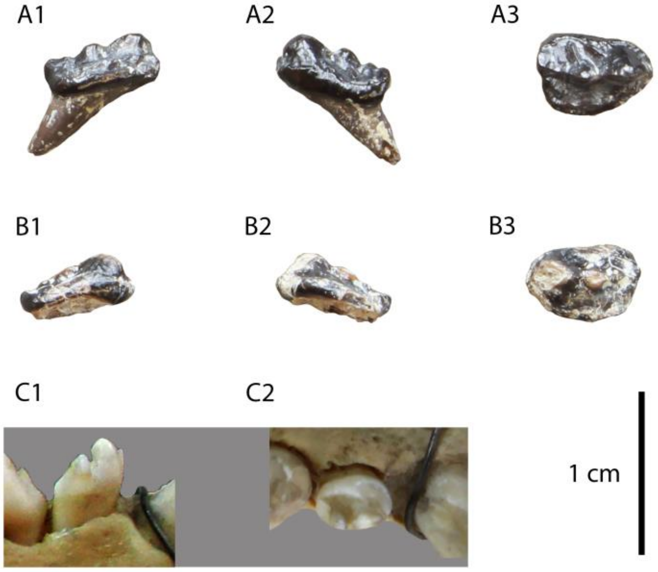


Fig. 5.5.1: The discovered p1 from HAM 5 (A: GPIT/MA/18608; B: GPIT/MA/18604) in comparison to (C) that of *Phoca vitulina* (NHMBA-2192).

The other two premolars have different morphology from these p1, but also from each other. The specimen GPIT/MA/16996 is a complete right premolar (Fig. 5.5.2A). It is double-rooted. It is asymmetrical as the distal part of the tooth is slightly wider than its mesial part and the main cuspid is slightly mesially situated. A moderately developed cingulum is present in the perimeter of the tooth. The main cuspid is relatively high and blunt. There are three accessory cuspids. One mesial accessory cuspid is present at the mesial end of the tooth being completely detached from the main cuspid. A relatively large distal accessory cuspid is stemming from the middle part of the main cuspid and another smaller distal accessory cuspid is present just mesially to the distal cingulum.

The specimen GPIT/MA/09629 at first sight looks relatively similar to GPIT/MA/16996 (Fig. 5.5.2B). However, it is considerably narrower, the cingulum is weaker, the mesial accessory cuspid is smaller and is situated in an angle to the main cuspid, the main cuspid and the first distal accessory cuspid are relatively lower and the second distal accessory cuspid is far detached from the other cuspids being located at the distal end of the tooth.

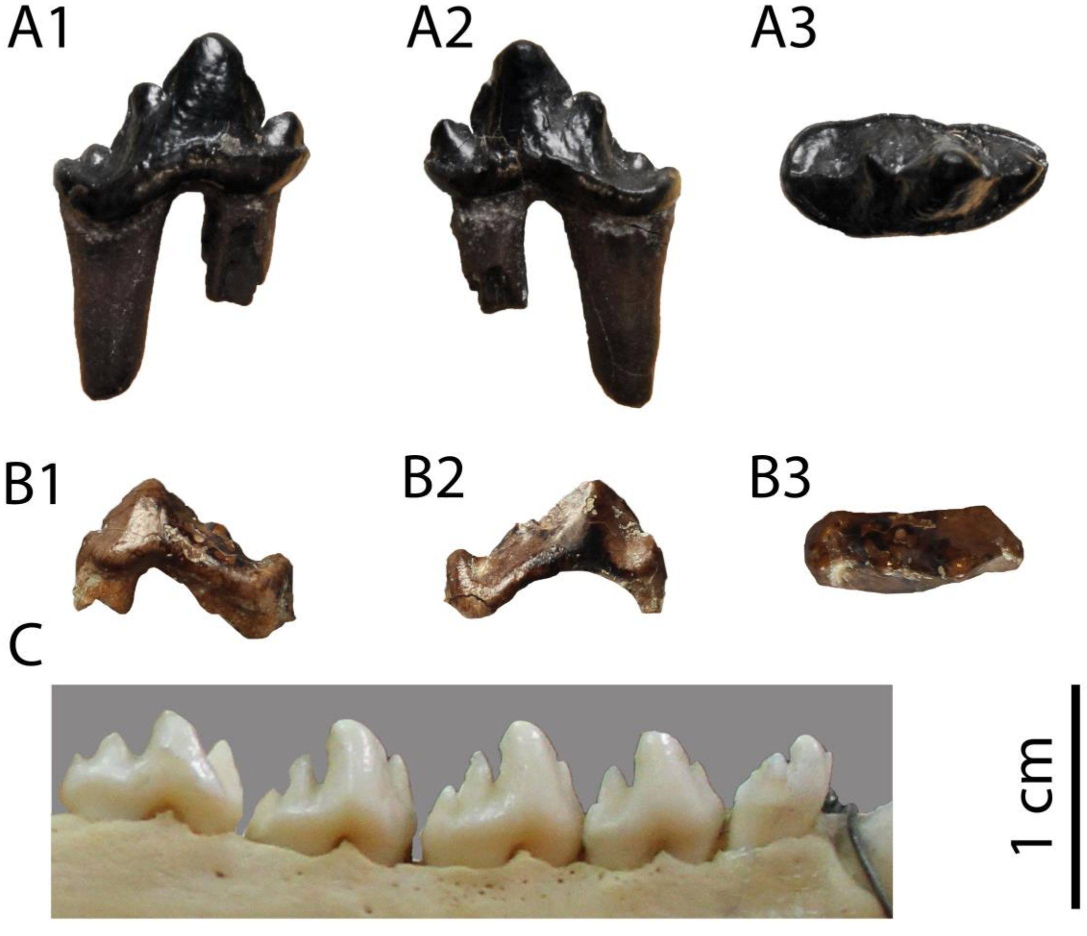


Fig. 5.5.2: the discovered premolars from HAM 4 (A: GPIT/MA/16996; B: GPIT/MA/09629) in comparison to the lower premolars of *Phoca vitulina* (C: NHMBA-2192).

Table 5.5.1: Dimensions of the discovered phocid material.

Specimen	**L**	**W**
GPIT/MA/18604	7.0	4.6
GPIT/MA/18608	7.0	4.9
GPIT/MA/09629	9.4	3.9
GPIT/MA/16996	11.4	5.3

Comparison: The presence of several accessory cuspids to these premolars was interpreted as a characteristic that was linking these specimens to the morphology seen in the phocids. As seen in Figs. 5.5.1–3, the extant species *Phoca vitulina* (Phocini) and *Lobodon carcinophaga* (Lobodontini) exhibit these well-developed accessory cuspids in the lower premolars. This trait can be seen in the tribes Phocini, Histriophocini and Lobodontini.

Fig. 5.5.3: The lower dentition of *Lobodon carcinophaga* (ZMH-1699).

One characteristic that seems to differentiate the tribes Phocini and Lobodontini is the morphology of the first distal accessory cuspid. In the former, this is detached from the relatively low main cuspid (Fig. 5.5.2), whereas in the latter it is stemming from the middle point of a higher main cuspid (Fig. 5.5.3). In this trait, the specimens from Hammerschmiede are more similar to the Lobodontini.

However, there are three problems concerning the identification of the material. Firstly, the anatomical identification of the discovered premolars is not possible, since they have been discovered as isolated teeth and not as part of a mandibular ramus. Secondly, as has been demonstrated in the Introduction, the diagnostic features between the large groups of phocids almost solely include cranial and postcranial characters and very frequently dental ones. Therefore, it is not easy to prove that these teeth belong to a member of Lobodontini. Finally, even if they are belonging to this tribe, there are no species of this group in the Miocene of Europe. Consequently, the attribution is very hard. Therefore, the material is momentarily identified as “Phocidae indet.” until more findings shed some light into its exact taxonomic position.

Suborder Feliformia Kretzoi, 1945

Family Felidae Fischer de Waldheim, 1817

Subfamily Machairodontinae Gill, 1872

Genus *Pseudaelurus* Gervais, 1850

Pseudaelurus quadridentatus (Blainville, 1843)

Material: HAM 5: One upper canine (GPIT/MA/18115) and one right p4 (GPIT/MA/13999).

Description: The specimen GPIT/MA/18115 is an upper canine (Fig. 5.6.1A) is much damaged, being broken just at the level of dentine-enamel junction and near the tip of the crown. It is a moderately curved and laterally compressed, without any signs of crenulations, grooves or cingulum.

The specimen GPIT/MA/13999 (Fig. 5.6.1B) is a right p4 with partially broken mesial accessory cuspid. There are no signs of wear. It is two-rooted with a strong buccal and distal cingulid, which is fainter in its lingual and mesial parts. The main cuspid is relatively blunt and short. Two large accessory cuspids, one distal and one mesial, are also present. The cingulid hosts a developed secondary distal cuspid.

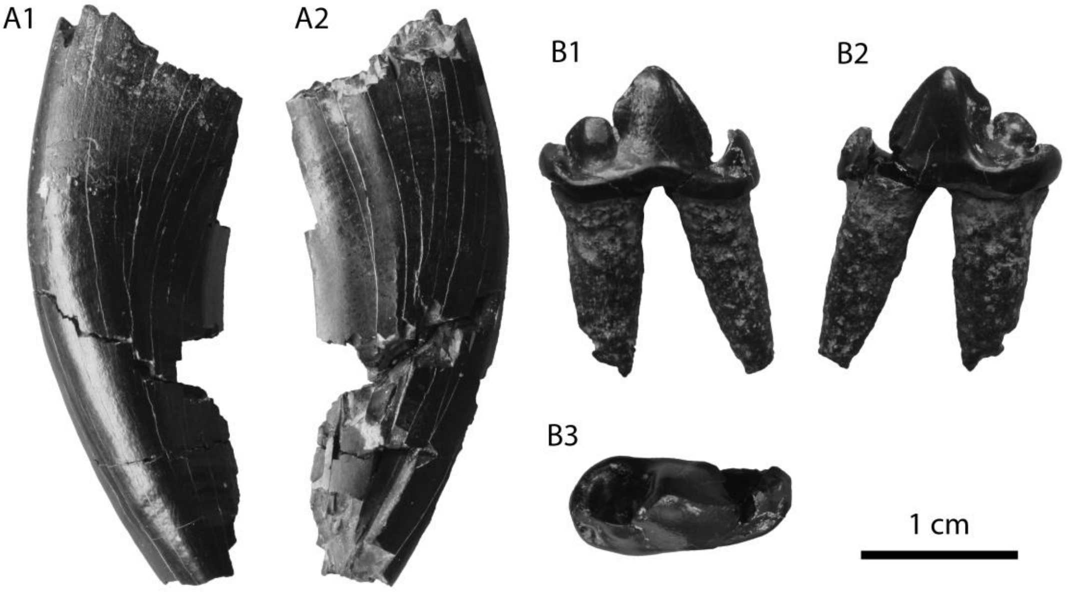


Fig. 5.6.1: *Pseudaelurus quadridentatus* from Hammerschmiede: (A) upper canine (GPIT/MA/18115) in (1) buccal and (2) lingual views; and (B) right p4 (GPIT/MA/13999) in (1) buccal, (2) lingual and (3) occlusal views.

Comparison: Concerning the upper canine, it is laterally compressed and elongated, so it must belong to a sabertooth. However, it exhibits no signs of crenulations, so it must belong to a taxon more basal than *Promegantereon* (Salesa et al., 2010). There is a size differentiation between the studied taxa, with the unnumbered species fitting better with the size of *P. quadridentatus* and *P. romieviensis* regarding the length (Table 5.6.1). Concerning the width there is a notable difference, but this can be expected given the taphonomical deformation that is evident in many specimens from Hammerschmiede. Robles et al. (2013a) state that the upper canines of *P. quadridentatus* are larger and more laterally compressed than that of *P. romieviensis*, based on material from Spain. However, based on the material from Sansan, the size distinction is not so evident. Regarding the lateral compression, Robles et al. (2013a) state that the W/L ratio is approximately 65% for *P. romieviensis* and 45% for *P. quadridentatus*. In the present specimen that ratio is 43% fitting better with *P. quadridentatus*, despite the aforementioned deformation.

Table 5.6.1: Comparison of the upper canines dimensions of Middle and Late Miocene felids. Data from: (1) Salesa et al. (2012), (2) Peigné (2012), Robles et al. (2013a), (4) Spassov & Geraads (2015), (5) Salesa et al. (2010), (6) Andersson (1998), (7) Roussiakis (2011a), (8) Crusafont Pairó & Aguirre (1972), (9) Pons-Moya (1987), (10) Geraads & Peigné (2017) and (11) Madurell-Malapeira et al. (2014).

Species	Locality	Code	L	W	H
Ps. quadridentatus	HAM 5	GPIT/MA/18115	13.5	5.8	-
Metailurini indet.	HAM 5	GPIT/MA/13719	18.3	10.0	48.7
Pri. attica[1]	Vathylakkos 3	SLQ-935	7.4	4.7	13.9
L. vallesiensis[1]	Batallones-1	’03 C4-21	6.5	4.6	-
St. lorteti[2]	Sansan & La Grive	-	8.0–10.3 9.5 (4)	5.8–7.0 8.8 (4)	19.5–20.5 20.0 (2)
Ps. quadridentatus[2, 3]	ACM/C4-C2	IPS-46474	15.2	6.1	-
	Sansan	-	11.3–15.7 12.9 (14)	7.3–9.0 8.2 (14)	30.0–35.0 32.2
Ps. romieviensis[3]	ACM	-	13.2–13.3 13.3 (2)	7.6–7.7 7.7(2)	-
Y. garevskii[4]	Karaslari Kalimantsi	-	10.4–13.2 11.8 (2)	7.1–8.9 8.0 (2)	22–25 23.5 (2)
Pro. ogygia[5]	Batallones 1	-	13.4–16.6 14.9 (28)	7.8–9.5 8.9 (21)	30.4–40.2 35.8 (26)
Me. parvulus[6]	summed	-	11.7–12.9 12.5 (3)	6.9–8.2 7.6 (3)	-
Me. major[7]	summed	-	16.7–20.6 19.0 (n=7)	10.8–12.2 11.6 (7)	-
S. teilhardi[8]	Piera	-	17.0	9.6	44.4
F. acerensis[9]	Fortuna	-	17.9	8.9	-
Mi. pamiri[10]	Kalfa	-	10.3	7.4	-
Ma. aphanistus[11]	Vallés-Penedés	-	23.1–30.2 25.7 (5)	12.2–14.7 13.7 (5)	50.0–65.6 59.2 (3)

The discovered p4 from HAM 5 fits perfectly with the measurements for *Ps. Quadridentatus* (Table 5.6.2), while its morphology seems identical with that described and depicted by Robles et al. (2013a).

Table 5.6.2: Comparison of the p4 dimensions of Middle and Late Miocene felids. Data from Roussiakis et al. (2006), Peigné (2012) and Salesa et al. (2019).

	p4L	p4W
GPIT/MA/13999	14.3	6.4
L. vallesiensis	7.4–8.5 7.7 (6)	3.2–3.9 3.5 (6)
Ps. quadridentatus	12.8–15.1 14.3 (11)	6.0–7.4 6.9 (11)
Me. major	31.0–32.0 31.5 (2)	14.0–16.0 15.0 (2)

Metailurini indet.

Material: HAM 5: One upper canine (GPIT/MA/13719).

Description: The specimen GPIT/MA/13719 (Fig. 5.6.2) is a complete right upper canine, partially damaged at the dentine-enamel junction. It is slightly curved and moderately mediolaterally compressed. A faint crest is present in its anterior and posterior borders. It doesn't exhibit any other morphological features such as serrations, grooves, cingulum etc.

Fig. 5.6.2: The upper canine (GPIT/MA/13719) of Metailurini indet. from HAM 5.

Comparison: There is a clear size difference between the two discovered canines as seen in Table 5.6.1. As aforementioned the specimen GPIT/MA/18115 fits well into the range of *Ps. quadridentatus*, but GPIT/MA/13719 is clearly larger. This could be explained through sexual dimorphism, which is frequent in felids. However, the material from Sansan, includes 14 specimens that do not display such a dimorphism (Peigné 2012, Table 42). Given the low possibility of all the 14 specimens belonging to the same sex, it is reasonable to suggest that GPIT/MA/13719 is significantly larger than any *Ps. quadridentatus* specimen found until now. The metrical comparison in Table 5.6.1 also excludes the species *Ps. romieviensis*, *S. lorteti*, *L. vallesiensis*, *Pri. attica*, *Y. garevskii* and *Me. parvulus* because they are too small, and the species *Ma. aphanistus* because it is too large.

It seems that the specimen GPIT/MA/13719 belongs to a primitive sabertooth, larger than *Pseudaelurus*, *Styriofelis*, *Miopanthera*, *Yoshi*, *Promegantereon* and *Metailurus parvulus*. However, there are no signs of crenulation in its crests, so it is not possible to belong to the genera *Paramachaerodus*, *Machairodus*, *Amphimachairodus* or any other more derived sabertooth, or even in Barbourofelidae. The genus *Dinofelis* is of similar morphology, but it is not known in the fossil record before 6 Mya.

It seems plausible that this specimen links the traits of *Pseudaelurus quadridentatus* and the genus *Metailurus*, as proposed by Viret (1951). Its morphology fits perfectly to both taxa, while its measurements fit well into the range of *Metailurus major*. However, the genus *Metailurus* is not known in Europe before MN 10, since the species *Mi. pamiri* has been attributed to the genus *Miopanthera*. Perhaps this specimen is an indicator of an earlier connection between *Pseudaelurus* and *Metailurus* in Europe. However, the distinction between the two genera is not possible based solely on the upper canine. Therefore, this form is herein referred to as Metailurini indet.

Family Barbourofelidae SCHULTZ, SCHULTZ & MARTIN, 1970

Barbourofelidae indet.

Material: HAM 5: one right humerus (GPIT/MA/09635).

Description: The humerus (Fig. 5.7.1) is broken proximally to the middle of the shaft, which is laterally compressed in a considerable degree. Therefore, a major part of this specimen in non-informative. The non-deformed part of the shaft is robust. The most proximal preserved part of the shaft is far longer than the part of the shaft just proximally to the distal epiphysis. A deltoid crest and a lateral supracondylar ridge are present. The entepicondylar foramen is slender, oval-shaped and situated right above the trochlea. The medial epicondyle and the trochlea are significantly developed, while the olecranon fossa is deep and high. The coronoid fossa is wider and deeper than the radial fossa. It must be noted that the proximal epiphysis of a radius is attached to the lateral part of the bone that may belong to the same individual.

Fig. 5.7.1: The right humerus (GPIT/MA/09635) of the barbourofelid from Hammerschmiede.

Comparison: Unfortunately, this humerus is missing its proximal part and its diaphysis is severely deformed. Therefore, the only part that can be accurately used for comparison is the distal epiphysis. Based on size only, it is clear that it belongs to a very large carnivoran, so a comparison to the already discovered families is herein attempted.

Kretzoiarctos beatrix is another large caniform that is present in the locality. The entepicondylar foramen is present in the ailuropodines: *Ailuropoda melanoleuca* (Davis, 1964), *Indarctos arctoides* (Abella, 2011), *Indarctos vireti* (Crusafont Pairó & Kurtén, 1976) and *Indarctos punjabensis* (Roussiakis, 2001b), whereas it has been lost in the ursines: *Ursavus primaevus* (Viret, 1951) and *Ursus arctos* (Erdbrink, 1953). Therefore, the attribution to the ursines can be excluded, but no to the ailuropodines.

The amphicyonids exhibit a very wide range of sizes and locomotor adaptations. The general morphology of this specimen seems similar to that of *Amphicyon* (Ginsburg, 1961a; Argot, 2010) or *Magericyon* (Siliceo et al., 2015). In general, the distal epiphysis (proximally to the trochlea) of the amphicyonids is much larger than that of the feliforms, resembling that of bears (Argot, 2010, fig. 4-II). This is more clearly seen in the development of supracondyloid ridges. Additionally, the distal epiphysis of Amphicyon is nearly flat in distal view, whereas that of the feliforms exhibits a distinct concavity between the trochlear lip and the capitulum (Argot 2010, fig. 4-III). Judging from these characteristics, the described humerus more closely resembles that of the feliforms.

Kargopoulos et al. (2021c) reported the presence of a large bone-cracking hyena in Hammerschmiede. The humeri of Hyaenidae have a very robust shaft, but most importantly they don’t have an entepicondylar foramen. On the contrary, they usually have a large circular foramen that covers part of the coronoid and radial fossae (e.g. Diedrich, 2012, fig. 7A–C).

The presence of at least one medium-sized felid species in Hammerschmiede has been presented in previous pages. The largest size of this form corresponds to that of *Metailurus major*. However, judging from the descriptions, figures and measurements given by Kovatchev (2001) for this species, the described humerus clearly belongs to a larger and more robust form, as demonstrated by the wider distal epiphysis and the more developed crests in the diaphysis. However, no other felids are known from this timespan that could match this form. The Vallesian species *Machairodus aphanistus* is considerably larger and it exhibits a more elongated diaphysis (Peigné, 2016).

Unfortunately, not many postcranial elements of barbourofelids have been published. The most extensive description of barbourofelid skeletal elements is that of Ginsburg (1961a) concerning *Sansanosmilus palmidens*. In comparison to the depiction of Ginsburg (1961a, fig. 68), the specimen from Hammerschmiede seems to have a slightly less-developed inner condyle and shallower coronoid and radial fossae. In comparison to that of *Barbourofelis*, the entepicondylar foramen is considerably larger and the supracondyloid ridge is forms a lower angle to the diaphysis (Tseng et al., 2010, fig. 3). These two genera are the most closely related to the most common species in the Aragonian and Vallesian of Europe, *Albanosmilus jourdani* (Robles et al., 2013). However, no humeri of this species have been available to comparison. The fact that the genera *Barbourofelis* and *Sansanosmilus* exhibit such a wide morphological difference, indicates that the humerus of *Albanosmilus* would not necessarily fit towards one of these two directions. Recently, postcranial material belonging to a barbourofelid has been found in new excavations in Can Mata (Spain). Based on J. Abella (pers. comm.) the morphology of this humerus is very similar to the one that was discovered.

Table 5.7.1: Measurements of the barbourofelid humerus (GPIT/MA/09635) from Hammerschmiede.

	H	APDd	TDd	Trochlear TD
GPIT/MA/09635	>222.0	39.1	66.1	49.6

Family Hyaenidae GRAY, 1821

Subfamily Ictitheriinae TROUESSART, 1897

Genus *Thalassictis* GERVAIS (1850), EX VON NORDMANN

***Thalassictis montadai* (VILLALTA COMELLA & CRUSAFONT PAIRÓ, 1943)**

Material: HAM 4: one premolar (SNSB-BSPG-2020-XCIV-5715). HAM 5: two left P4 (GPIT/MA/13720; GPIT/MA/09633).

Description: The specimen SNSB-BSPG-2020-XCIV-5715 (Fig. 5.8.1A) consists of a mesial half of a premolar. Unfortunately, since the distal part is missing and the crown tip is slightly worn, it is not possible to estimate the dimensions of the tooth, so it cannot be anatomically identified. However, it can be noted that the main cusp/cuspid is relatively high, a considerably robust cingulum/cingulid is present in the mesial border of the tooth and the enamel is thick and rough.

GPIT/MA/13720 (Fig. 5.8.1B) is an almost complete left upper carnassial, lacking only the root under the parastyle. The enamel is thick and rough. The metastyle blade exhibits signs of developed wear and a hollow is formed at the paracone. A smooth cingulum is present, which is considerably robust at the distolingual part of the tooth. The protocone is large, situated at the same level as the parastyle. The paracone is the largest cusp, separated by the metastyle and parastyle by deep notches.

GPIT/MA/09633 (Fig. 5.8.1C) is a broken left P4 that preserves only the paracone, the metastyle and the distal root. The metastyle blade exhibits signs of moderate wear. A smooth cingulum is present in the perimeter of the preserved part. The paracone is robust, higher than the metastyle, and separated by the latter with a deep notch.

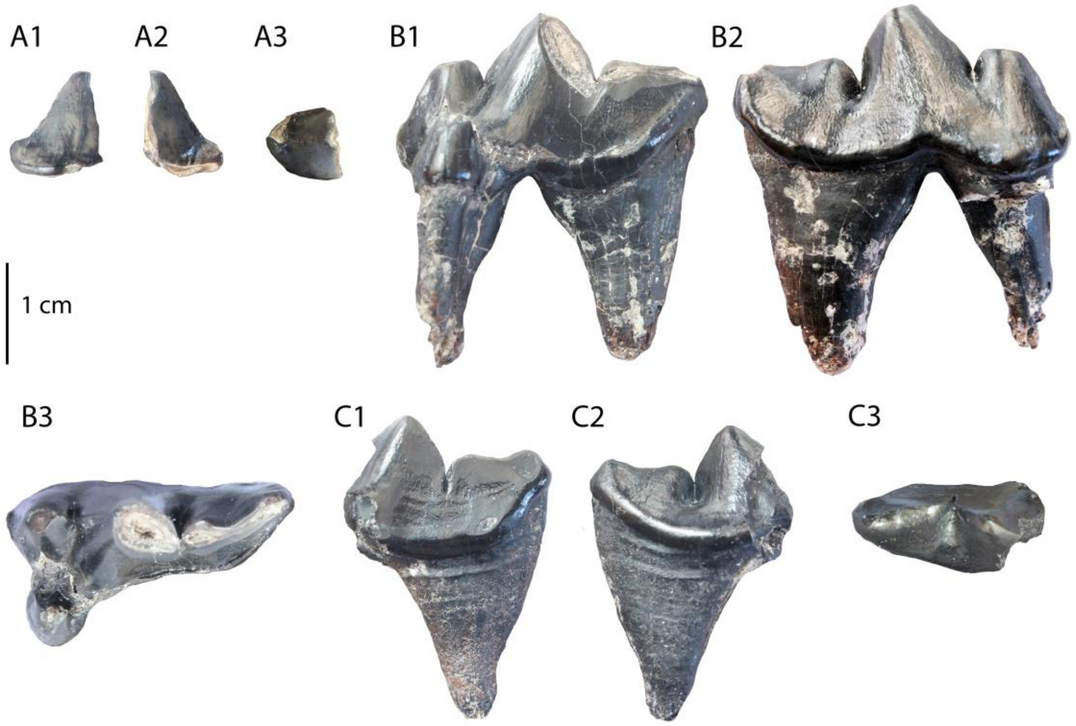


Fig. 5.8.1: The described dental material of *Thalassictis montadai* from Hammerschmiede: (A) premolar (SNSB-BSPG-2020-XCIV-5715) in (1) buccal, (2) lingual and (3) occlusal view; (B) left P4 (GPIT/MA/13720) and (C) left P4 (GPIT/MA/09633) in (1) lingual, (2) buccal and (3) occlusal view.

Comparison: Unfortunately, the discovered premolar is destroyed in a substantial degree. However, the morphology of the enamel and the general dimensions of the remaining crown indicate that this tooth must belong to a hyaenid. Since the only hyaenid form of this size in the locality is *Thalassictis montadai*, this specimen is also attributed to this species.

The two described premolars are almost similar to each other. In general, GPIT/MA/09633 is slightly slenderer with fainter cingulum than GPIT/MA/13720. The general morphology of these specimens is typical for the feliforms, with an enlarged parastyle and a carnassiform notch between the paracone and the metastyle. As discussed in previous pages, two felid taxa have been found in the locality. Table 5.8.1 shows that these carnassials are too large to be attributed to *P. quadridentatus*. However, they could belong to the unidentified Metailurini. Though, these specimens differ from the morphology seen in the metailurins in the following traits: rough and robust enamel, enlarged protocone and developed distolingual cingulum. These three characteristics point towards hyaenid affinities. The morphology and dimensions of the two carnassials conform to those published by Crusafont Pairó & Golpe Posse (1973) for *Thalassictis montadai*, which is a species that is known from the locality (Kargopoulos et al., 2021c). Therefore, they are herein attributed to this form.

Table 5.8.1: Measurements of the discovered P4 from Hammerschmiede compared to relevant taxa. Data from: (1) Crusafont Pairó & Golpe Posse (1973), (2) Peigné (2012) and (3) Roussiakis (2001a).

	P4L	P4Wm	P4Wp
GPIT/MA/13720	29.5	10.5	17.0
GPIT/MA/09633	X	≥9.4	X
Thalassictis montadai[1]	27.0 (2)	-	15.8–16.0 15.9 (2)
Pseudaelurus quadridentatus[2]	19.4–23.0 21.1 (8)	-	8.7–11.5 10.5 (9)
Metailurus major[3]	28.8–32.0 30.1 (5)	-	13.8–16.0 14.6 (6)

Coprolites

Coprolites have been used as a supplementing tool for the study of Miocene faunas for several decades. Usually, the presence of bone material (whether intact or in dissolved formed) consists of the main parameter that enabled their fossilization. Therefore, the attribution of coprolites has been focused on osteophagus species, which in the Miocene of Europe mostly corresponds to hyaenids. Coprolites can be used as tools that can uncover the dietary preferences of a predator, its way of handling the captured pray, its metabolic adaptations and elements of its ecological niche. They are also valuable, because of their mineralogical and palaeobotanical components.

An extremely high number of coprolites has been found in Hammerschmiede. However, only a small percentage of them can be associated to carnivorans. All the herein discussed specimens have been discovered in the HAM 4 layer, with the exception of GPIT/MA/10850 and GPIT/MA/16259, which have been found in HAM 5. A detailed list of this material is presented in Table 5.9.1.

Table 5.9.1: Coprolite material from Hammerschmiede attributed to carnivorans.

Code	Layer	State	Morphology	Size
SNSB-BSPG-2020-XCIV-0104	HAM 4	Complete	Oval	>5 cm
SNSB-BSPG-2020-XCIV-0774	HAM 4	Complete	Oval	>5 cm
SNSB-BSPG-2020-XCIV-1388	HAM 4	Incomplete	Oval	>5 cm
SNSB-BSPG-2020-XCIV-3299	HAM 4	Incomplete	Oval	>5 cm
SNSB-BSPG-2020-XCIV-0155	HAM 4	Incomplete	Oval	>5 cm
SNSB-BSPG-2020-XCIV-0014	HAM 4	Incomplete	Oval	>5 cm
SNSB-BSPG-2020-XCIV-3096	HAM 4	Incomplete	Oval	>5 cm
SNSB-BSPG-2020-XCIV-2248	HAM 4	Incomplete	Oval	>5 cm
SNSB-BSPG-2020-XCIV-0027	HAM 4	Incomplete	Oval	>5 cm
SNSB-BSPG-2020-XCIV-1583	HAM 4	Incomplete	Oval	>5 cm
SNSB-BSPG-2020-XCIV-0961	HAM 4	Incomplete	Oval	>5 cm
GPIT/MA/10850	HAM 5	Complete	Oval	>5 cm
SNSB-BSPG-2020-XCIV-3298	HAM 4	Complete	Oval	3–5 cm
SNSB-BSPG-2020-XCIV-6948	HAM 4	Incomplete	Oval	3–5 cm
SNSB-BSPG-2020-XCIV-0076	HAM 4	Incomplete	Oval	3–5 cm
SNSB-BSPG-2020-XCIV-0092	HAM 4	Incomplete	Oval	3–5 cm
GPIT/MA/12659	HAM 5	Incomplete	Oval	3–5 cm
SNSB-BSPG-2020-XCIV-3294	HAM 4	Complete	Oval	2–3 cm
SNSB-BSPG-2020-XCIV-3286	HAM 4	Incomplete	Oval	2–3 cm
SNSB-BSPG-2020-XCIV-3289	HAM 4	Incomplete	Oval	2–3 cm
SNSB-BSPG-2020-XCIV-6947	HAM 4	Incomplete	Oval	2–3 cm
SNSB-BSPG-2020-XCIV-3297	HAM 4	Incomplete	Oval	2–3 cm
SNSB-BSPG-2020-XCIV-6918	HAM 4	Incomplete	Flat	2–3 cm
SNSB-BSPG-2020-XCIV-6919	HAM 4	Incomplete	Flat	2–3 cm
SNSB-BSPG-2020-XCIV-6920	HAM 4	Incomplete	Flat	2–3 cm
SNSB-BSPG-2020-XCIV-6921	HAM 4	Incomplete	Flat	2–3 cm
SNSB-BSPG-2020-XCIV-6922	HAM 4	Incomplete	Flat	2–3 cm
SNSB-BSPG-2020-XCIV-6923	HAM 4	Incomplete	Flat	2–3 cm
SNSB-BSPG-2020-XCIV-6924	HAM 4	Incomplete	Flat	2–3 cm

SNSB-BSPG-2020-XCIV-6925	HAM 4	Incomplete	Flat	2–3 cm
SNSB-BSPG-2020-XCIV-6926	HAM 4	Incomplete	Flat	2–3 cm
SNSB-BSPG-2020-XCIV-6927	HAM 4	Incomplete	Flat	2–3 cm
SNSB-BSPG-2020-XCIV-6928	HAM 4	Complete	Linear	2–3 cm
SNSB-BSPG-2020-XCIV-6931	HAM 4	Complete	Linear	2–3 cm
SNSB-BSPG-2020-XCIV-6929	HAM 4	Incomplete	Linear	2–3 cm
SNSB-BSPG-2020-XCIV-6930	HAM 4	Incomplete	Linear	2–3 cm
SNSB-BSPG-2020-XCIV-6932	HAM 4	Incomplete	Linear	2–3 cm
SNSB-BSPG-2020-XCIV-6933	HAM 4	Incomplete	Linear	2–3 cm
SNSB-BSPG-2020-XCIV-6934	HAM 4	Incomplete	Linear	2–3 cm
SNSB-BSPG-2020-XCIV-6935	HAM 4	Incomplete	Linear	2–3 cm
SNSB-BSPG-2020-XCIV-6936	HAM 4	Incomplete	Linear	2–3 cm
SNSB-BSPG-2020-XCIV-6937	HAM 4	Incomplete	Linear	2–3 cm
SNSB-BSPG-2020-XCIV-6938	HAM 4	Incomplete	Linear	2–3 cm
SNSB-BSPG-2020-XCIV-6939	HAM 4	Incomplete	Linear	2–3 cm
SNSB-BSPG-2020-XCIV-6944	HAM 4	Complete	Complex	2–3 cm
SNSB-BSPG-2020-XCIV-6945	HAM 4	Complete	Complex	2–3 cm
SNSB-BSPG-2020-XCIV-6940	HAM 4	Incomplete	Complex	2–3 cm
SNSB-BSPG-2020-XCIV-6941	HAM 4	Incomplete	Complex	2–3 cm
SNSB-BSPG-2020-XCIV-6942	HAM 4	Incomplete	Complex	2–3 cm
SNSB-BSPG-2020-XCIV-6943	HAM 4	Incomplete	Complex	2–3 cm
SNSB-BSPG-2020-XCIV-6946	HAM 4	Incomplete	Complex	2–3 cm

A summary of these characteristics is presented in Table 5.9.2.

Table 5.9.2: Summary of the coprolite characteristics shown in Table 4.9.1.

	2–3 cm	**3–5 cm**	**>5 cm**	**Total**
Oval	5 (10%)	5 (10%)	12 (24%)	22 (43%)
Flat	10 (20%)	-	-	10 (20%)
Linear	12 (24%)	-	-	12 (24%)
Complex	7 (14%)	-	-	7 (14%)
Total	34 (67%)	5 (10%)	12 (24%)	51

Based on the summarized results in Tables 5.9.1 and 5.9.2, most of the coprolites are from HAM 4 (96%), Incomplete (82%), Oval (43%) and 2–3 cm (67%). Fig. 5.9.1 depicts the main morphological categories seen in this dataset.

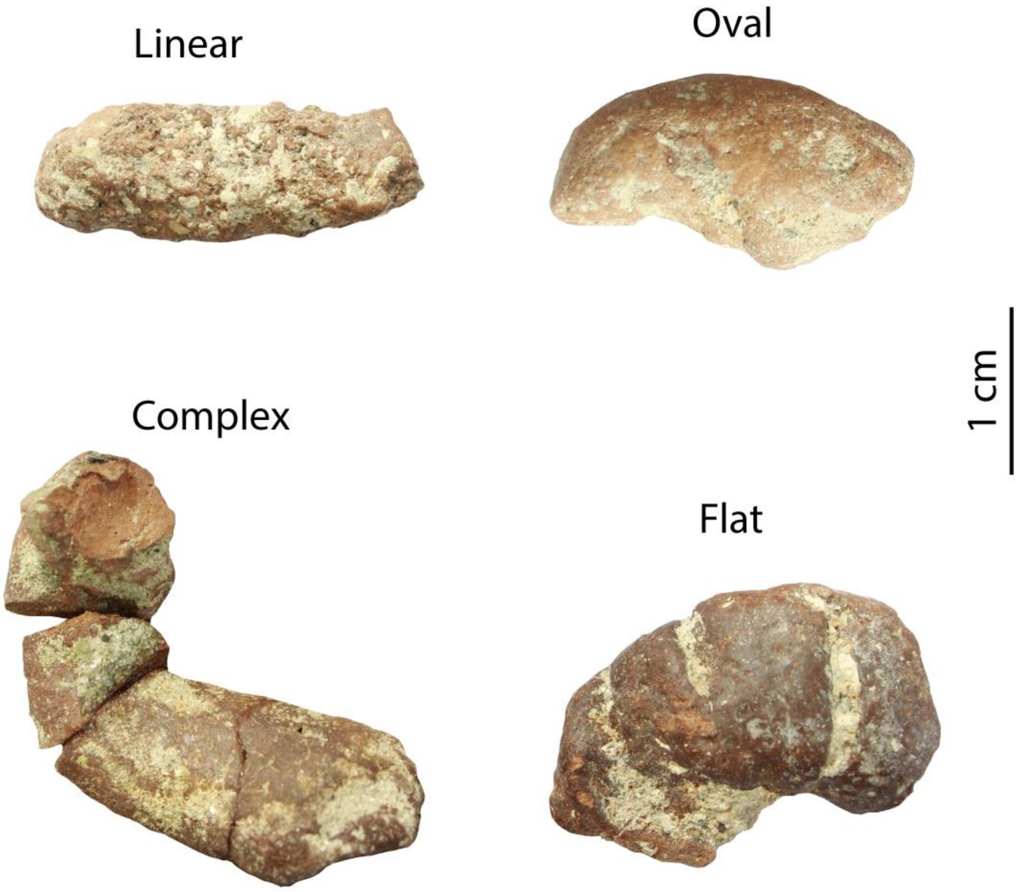


Fig. 5.9.1: The main morphological categories seen in the present dataset.

Almost all these coprolites have been scanned using the μCT of the VDR center (Center for Visualization, Digitalization and Replication) of the Eberhard Karls University of Tübingen. Most of them don’t exhibit clear bone-fragments in their interior. However, all of them have the following characteristics (Fig. 5.9.2):

- A variable degree of empty cavities inside the coprolite, which usually include pyritic formations in their walls.
- Randomly scattered sediment-filled regions.
- Small bone fragments or completely digested bone in the form of a powder.

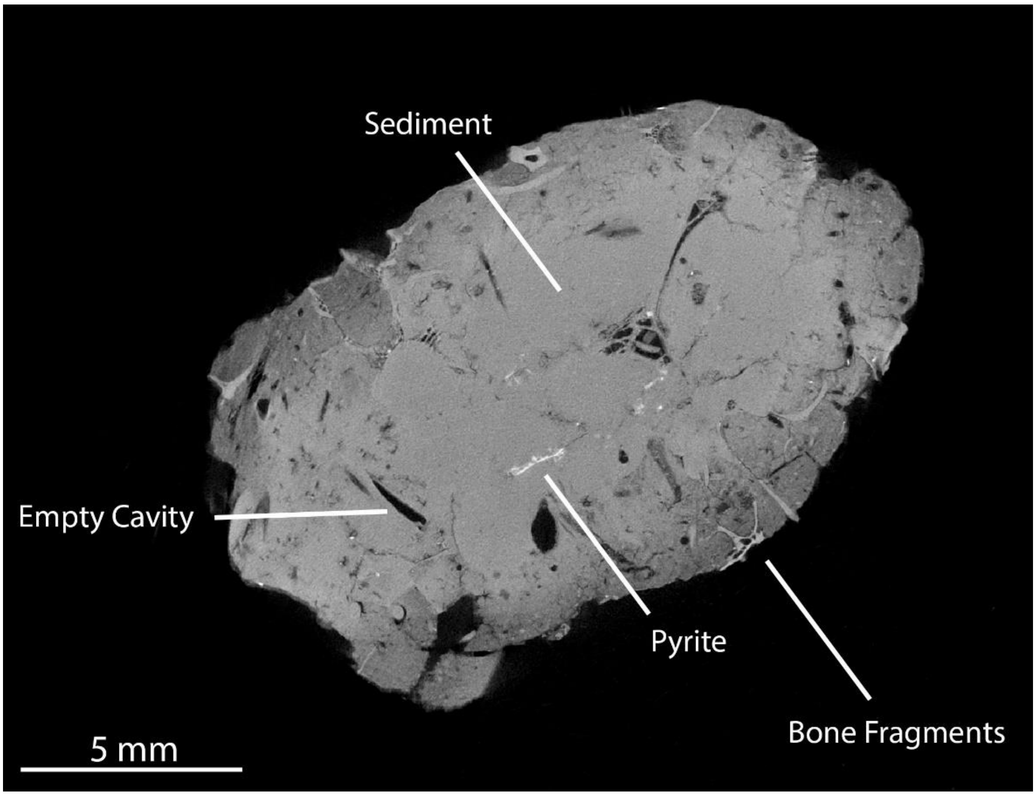


Fig. 5.9.2: CT-scan-section of SNSB-BSPG-2020-XCIV-0027 showing the presence of empty cavities, pyrite, sediment-filled regions and bone fragments.

However, some higher bone frequency has been found in a restricted number of coprolites. Some coprolites exhibit a large number of small, unidentifiable bone fragments. An example of these coprolites is SNSB-BSPG-2020-XCIV-0104, which is also complete in terms of external morphology (Fig. 5.9.3).

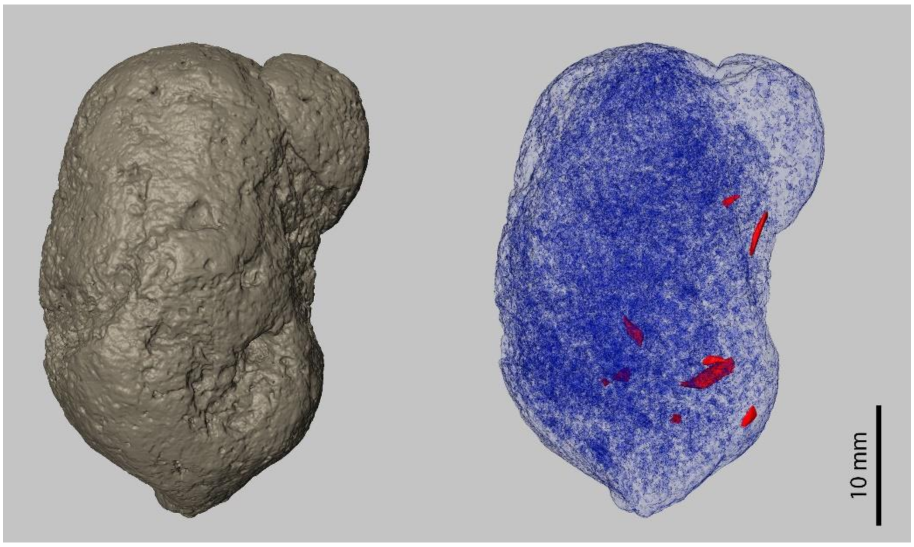


Fig. 5.9.3: External and internal morphology of SNSB-BSPG-2020-XCIV-0104 showing the discovered bone fragments.

Only one coprolite (SNSB-BSPG-2020-XCIV-0027) has been found to include distinct bones, such as fish vertebrae. The exterior and interior of this specimen can be seen in Fig. 5.9.4.

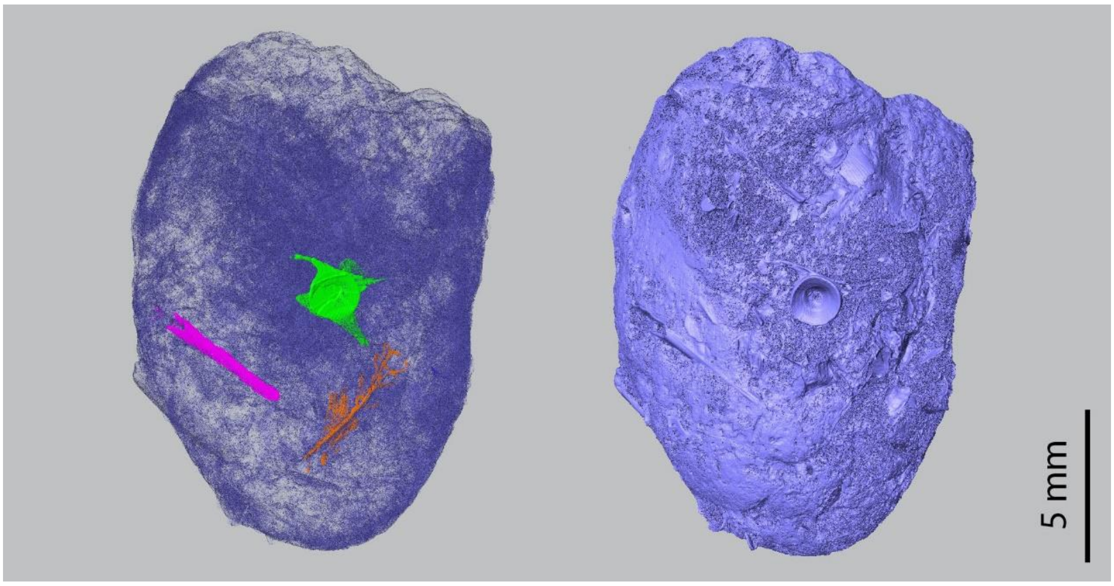


Fig. 5.9.4: External and internal morphology of SNSB-BSPG-2020-XCIV-0027 showing the discovered bone fragments. Different colors represent different structures.

Therefore, the coprolite record from Hammerschmiede is considered to be worthy of further investigation. The size presence of bones (in any form) inside the coprolites indicates that they belong to carnivores/scavengers. However, a detailed morphological comparison is needed in order to make solid suggestions about their producer.

Chapter 6

Discussion

It is clear that the locality of Hammerschmiede has yielded an astonishing variability of carnivoran remains, resulting in a total of 28 different forms. In fact, it is highly possible that this number may rise even more during the ongoing excavations. For example, the presence of *Laphyctis mustelinus*, *Alopecocyon goeriachensis*, Simocyoninae indet. and *Viverrictis modica* was recorded based on material from 2021. The detailed list of the discovered carnivorans and their distribution among the studied layers is presented in Table 6.1. Additionally, the minimum number of individuals (MNI) the estimated body mass (BM), locomotor pattern (LL) and dietary category (DH) of each form are mentioned.

Table 6.1: The carnivorans of Hammerschmiede and their distribution in different layers, including the number of individuals per layer, the estimated body mass (BM), locomotor lifestyle (LL) and dietary category (DH) for each species.

Family	**Species**	**HAM 1**	**HAM 5**	**HAM 4**	**HAM 6**	**BM**	**LL**	**DH**
Amphicyonidae	Amphicyonidae indet.		1		1	>100	?	C
Ursidae	*Kretzoiarctos beatrix*		2	2		>100	GT	hC
Phocidae	Phocidae indet.		1	1		>100	SA	PM
Mustelidae	“*Martes*” *sansaniensis*		1	3		3–10	Sc	C
	“*Martes*” *munki*		2	1		1–3	Sc (?)	C
	“*Martes*” sp.	1				<1	Sc (?)	C
	Circamustela hartmanni n. sp.	1	1	1		1–3	Sc (?)	HC
	Laphyctis mustelinus			1		10–30	GT	HC
	Gulolinae indet.		1			3–10	?	hC
	Eomellivora moralesi		1			10–30	GT	HC
	Vishnuonyx neptuni			3		10–30	SA	PM
	Paralutra jaegeri		1	2		3–10	SA	PM
	Lartetictis cf. *dubia*			3		3–10	SA	PM
	Trocharion albanense		4	1		1–3	SF	C
Mephitidae	*Palaeomeles pachecoi*		2			3–10	SF	hC
	Proputorius sansaniensis	1	1			3–10	Sc	C
	Proputorius pusillus	2				1–3	Sc (?)	C
Ailuridae	*Alopecocyon goeriachensis*		1			3–10	Sc	C
	Simocyoninae indet.			1		10–30	?	C
-	*Potamotherium* sp.		1	1		10–30	SA	PM
Felidae	*Pseudaelurus quadridentatus*		1			30–100	Sc	HC
	Metailurini indet.		1			>100	Sc	HC
Barbourofelidae	Barbourofelidae indet.		1			>100	?	HC
Viverridae	*Semigenetta sansaniensis*	1	1	7		3–10	Sc	C
	Semigenetta grandis			2		10–30	GT	HC
	Viverrictis modica		1	2		<1	Sc	I
Hyaenidae	*Thalassictis montadai*		2		1	10–30	GT	D
	Hyaenidae indet.		1			>100	?	D
Number of species		5	21	15	2	-	-	-
Number of individuals		6	28	30	2	-	-	-

The two main layers (HAM 4 and HAM 5) have yielded approximately the same number of individuals (28 and 30 respectively), but HAM 5 has provided more taxa (21 over 14 in HAM 4). This difference can be pinpointed in the 7 identified individuals of *Semigenetta sansaniensis* in HAM 4. Of the 28 carnivoran species that are included in these two layers combined, only 8 (29%) are known from both of them. This is very interesting concerning the biochronology and palaeoecology of some forms (see below). The two other layers (HAM 1 and HAM 6) have yielded 5 and 2 species respectively. However, the carnivoran datum from HAM 1 has been valuable, since it confirmed the presence of three forms that are not present in any of the other three layers: "*Martes*" sp., *Proputorius sansaniensis* and *Proputorius pusillus*.

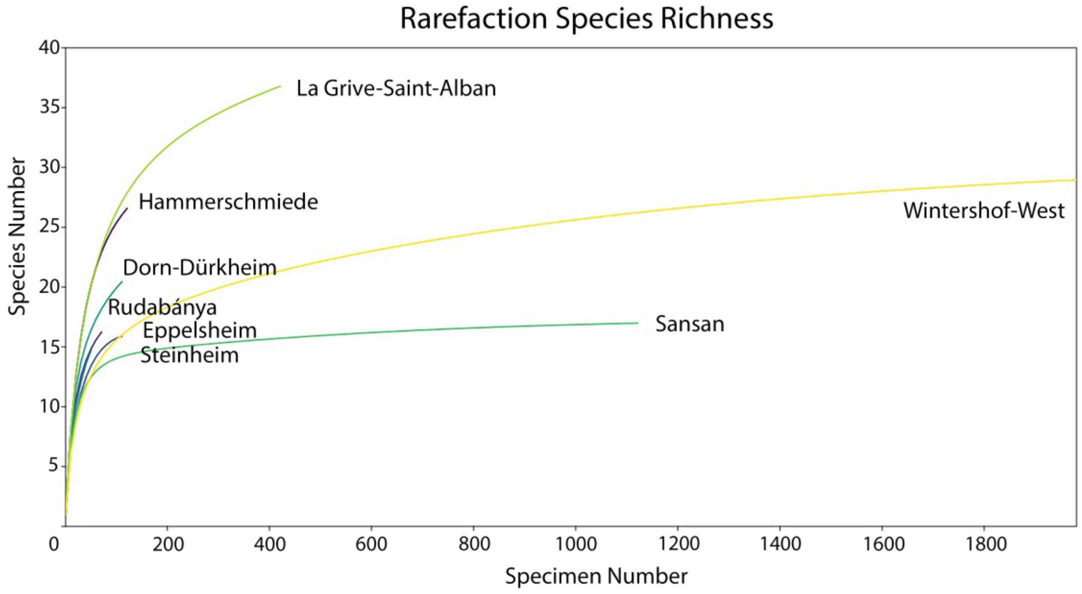
Such a high number of carnivoran species is definitely noteworthy, especially considering that at least 21 of them were sympatric in HAM 5. Table 6.2 presents the number of carnivoran species in the 53 localities discussed in the introduction. It is obvious that Hammerschmiede is the third richest locality in carnivoran species in the Miocene of Europe and Anatolia, only behind Wintershof-West (30 species) and La Grive-Saint Alban (40 species), which are both fissure fillings. This makes it the richest stratified locality in this region. Based on Mein & Ginsburg (2002), the MN 7 fissures from La Grive contain 26 carnivoran species, whereas the MN 8 fissures contain 19, so both groups are less rich than Hammerschmiede. A comparable number of carnivorans can also be seen in a handful of localities: Paşalar (27), Vieux-Collonges (25), Can Llobateres 1 (25), Dorn-Dürkheim (23), Artenay (21) and Sansan (21). The other 44 localities (83%) have yielded less than 20 carnivoran species. Of course, some localities (including Hammerschmiede) consist of several different layers (e.g., different fluvial channels in Hammerschmiede and different fissures in La Grive-Saint Alban), so such a comparison is not accurately informative about the actual biodiversity in these specific temporospatial landmarks. However, these numbers certainly reflect the influence of every locality in our knowledge of the fossil record.

Table 6.2: Number of carnivoran species per locality. Faunal data are mentioned in the Introduction. Fissure fillings are noted in italics.

Number of Species	**Localities**
41	*La Grive-Saint Alban*
30	*Wintershof-West*
28	Hammerschmiede
27	Paşalar
25	*Vieux-Collonges*, Can Llobateres 1
23	Dorn-Dürkheim
21	Artenay, Sansan
18	Eppelsheim, Pikermi
17	Pontlevoy, Rudabánya, Sahabi
16	Steinheim, Los Valles de Fuentidueña, Samos
15	Can Ponsic, Batallones
14	Paulhiac
13	Laugnac, Bézian, Csakvar, Venta del Moro
12	Çandir, Los Casiones, Castell de Barberà
11	Pellecahus, Concud
10	Göriach, Los Mansuetos
9	Sandelzhausen, Kalfa
8	Erkertshofen, Montredon, Soblay
7	Estrepouy, La Barranca, Yassiören
6	Anwil, Ravin de la Pluie, El Arquillo

5	La Romieu, Castelnau d'Arbieu, Arroyo del Val, Höwenegg, Los Aljezares, Maramena, Monticino
4	Prebreza, Yeni Eskihisar
3	Mala Miliva
2	Sibnica

A problem that occurs while comparing the species diversity of two localities is the unequal number of compared specimens. For example, the locality of Wintershof-West (that includes only two more carnivoran species from Hammerschmiede) has yielded almost 2000 carnivoran specimens identified at genus level (Dehm, 1950) in comparison to the 118 of Hammerschmiede. A methodology that has been used in order to overcome this inequality is Rarefaction analysis, as discussed in Material and Methods. Figures 6.1 to 6.3 depict the interpolated Species Richness and Shannon H index in different sets of localities.



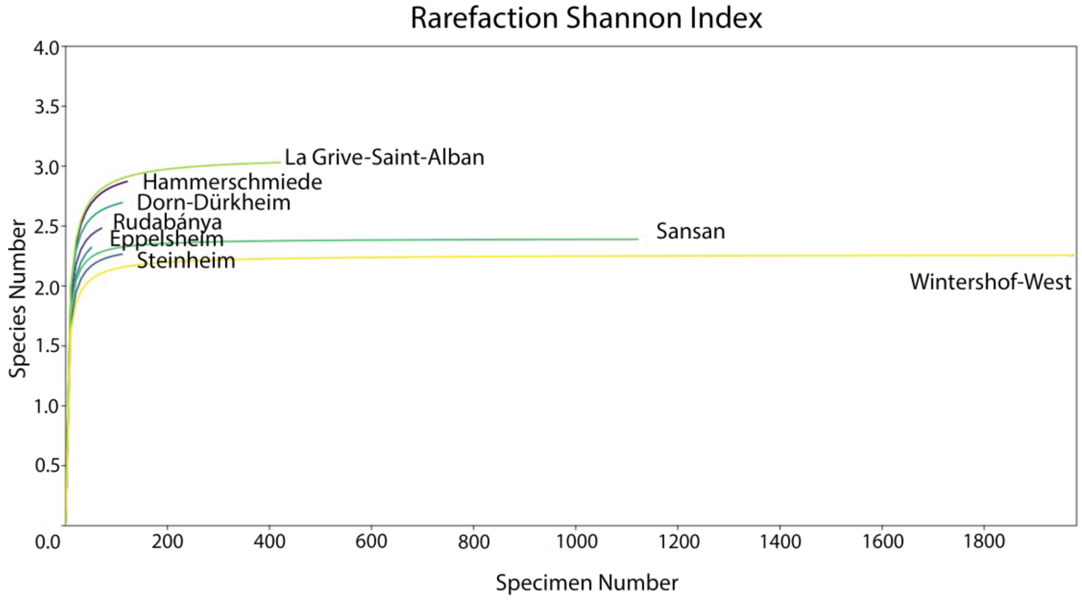
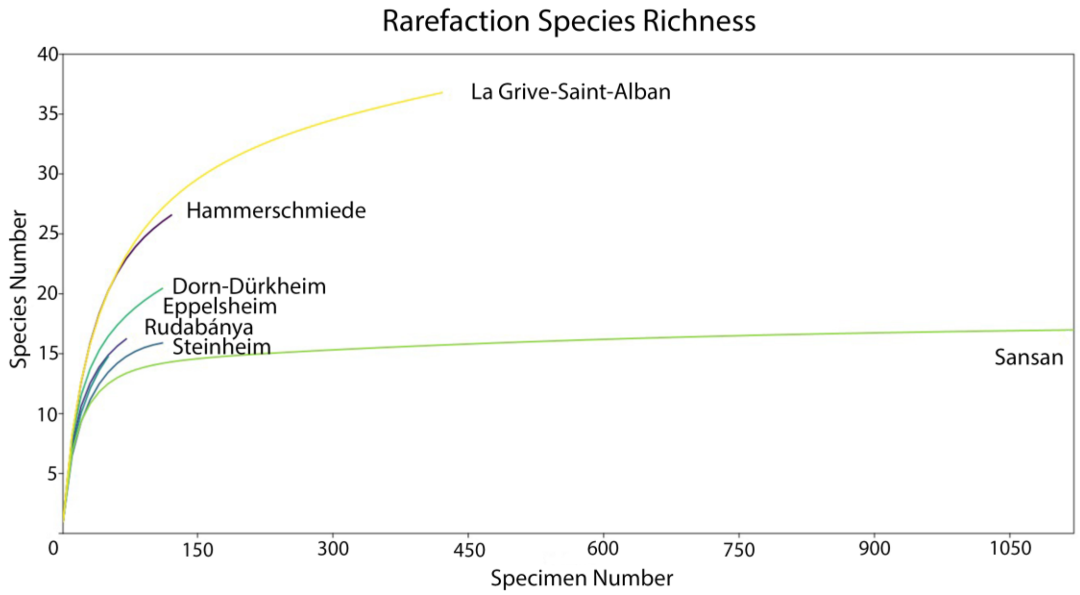


Fig. 6.1: Individual Rarefaction analyses using Species Richness and Shannon H index for Hammerschmiede, Steinheim, Eppelsheim, Dorn-Durkheim, Rudabánya, Sansan, La-Grive-Saint-Alban and Wintershof-West.



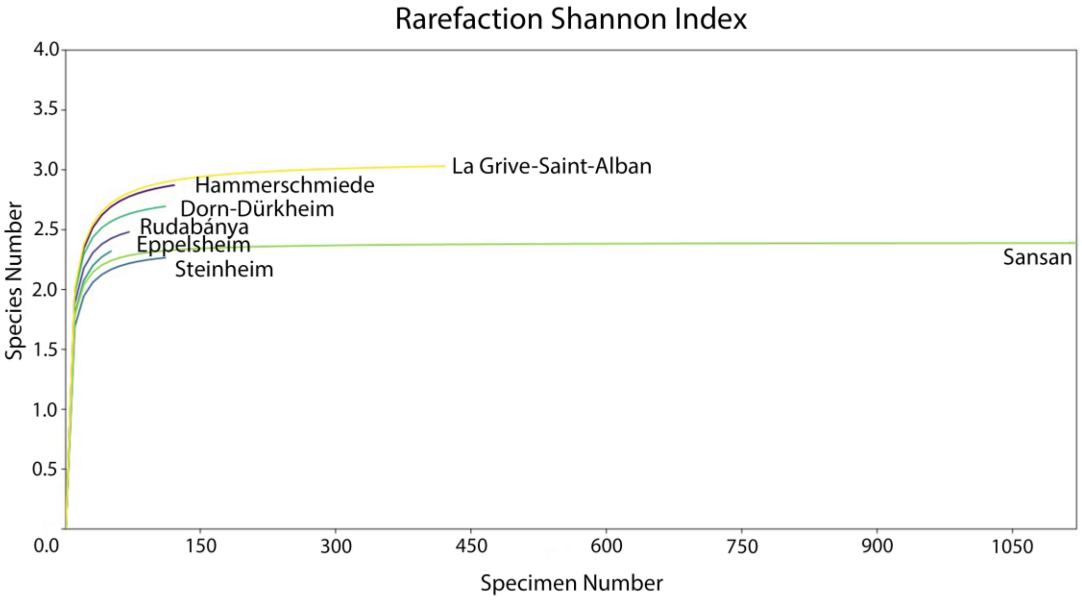


Fig. 6.2: Individual Rarefaction analyses using Species Richness and Shannon H index for Hammerschmiede, Steinheim, Eppelsheim, Dorn-Durkheim, Rudabánya, Sansan and La-Grive-Saint-Alban.

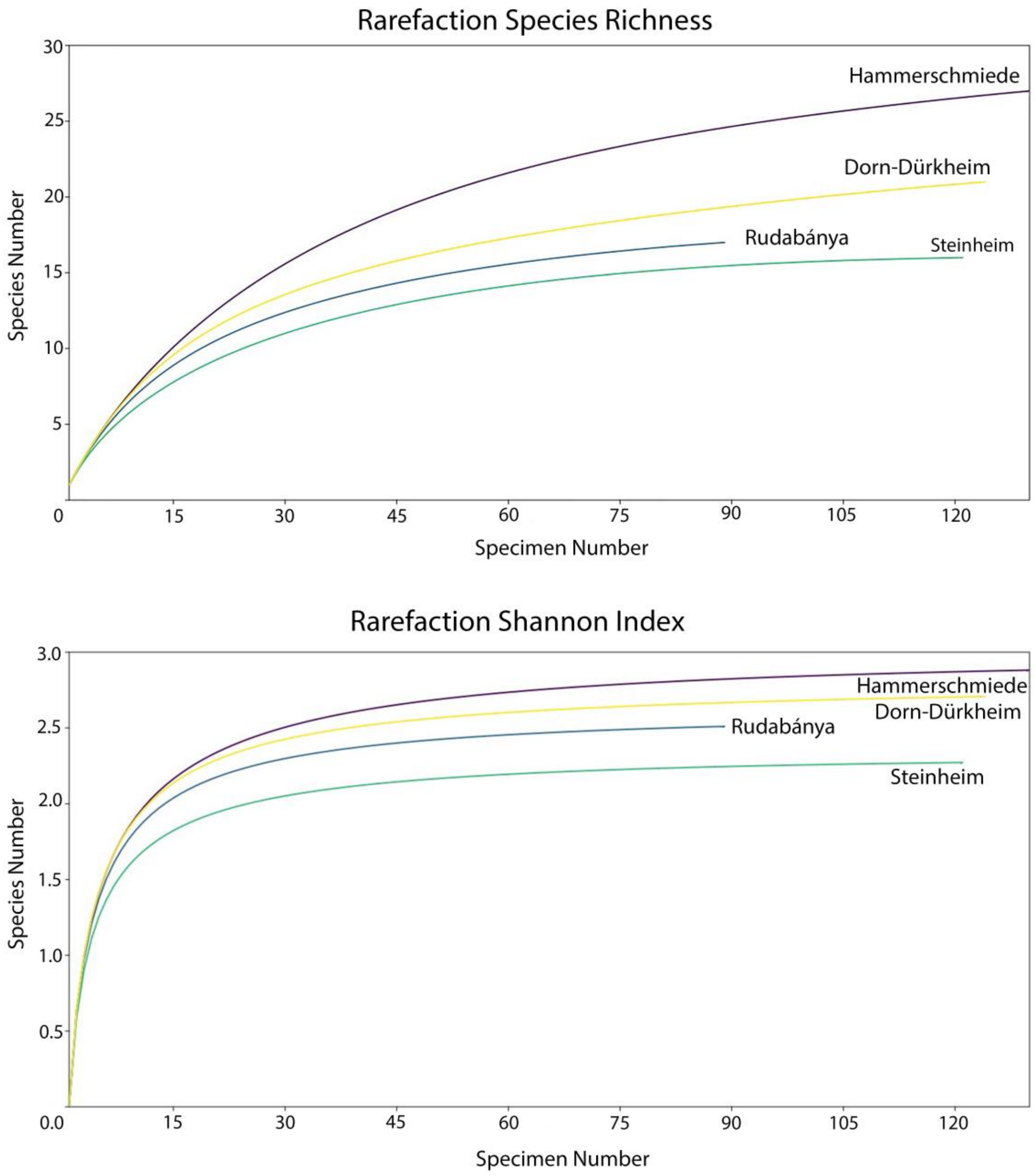


Fig. 6.3: Individual Rarefaction analyses using Species Richness and Shannon H index for Hammerschmiede, Steinheim, Dorn-Durkheim and Rudabánya.

As demonstrated in Figs. 6.1–6.3, the Species Diversity in Hammerschmiede is distinctively higher than that of Steinheim, Rudabánya, Dorn-Durkheim, Eppelsheim and Sansan. The locality of La-Grive-Saint-Alban (despite not including an exceptionally high number of specimens) has yielded many different taxa, because of its geological background. However, when the Shannon H index is estimated, the rarefaction lines of La-Grive-Saint-Alban and Hammerschmiede are very similar. Unfortunately, no data of MNI were available for every fissure, in order to make a more direct comparison. Finally, the locality of Wintershof-West, has yielded a tremendous amount of carnivoran specimens, but the total species diversity is estimated to be lower than Hammerschmiede. However, the comparison to Wintershof-West is considered to be only partly accurate, based on the considerable difference in the number of specimens. Additionally, the comparison to Eppelsheim and La-Grive-Saint-Alban is also biased by the mixed sources of specimens for these localities.

The locality of Hammerschmiede is (among other reasons) very interesting in terms of age. Its stratigraphic position (at the base of the Tortonian, linking Middle and Late Miocene) has been a vital key-point at the study of the discovered carnivorans. The current carnivoran list of the locality includes some typically Aragonian and some typically Vallesian forms (in terms of species or genera). Based on our current knowledge of these taxa, Figures 6.4 and 6.5 depict the biochronolocigal range of the discovered carnivorans in species and genus level respectively. The carnivorans that have been identified in a taxonomic rank higher than that of the genus are not included in this analysis.

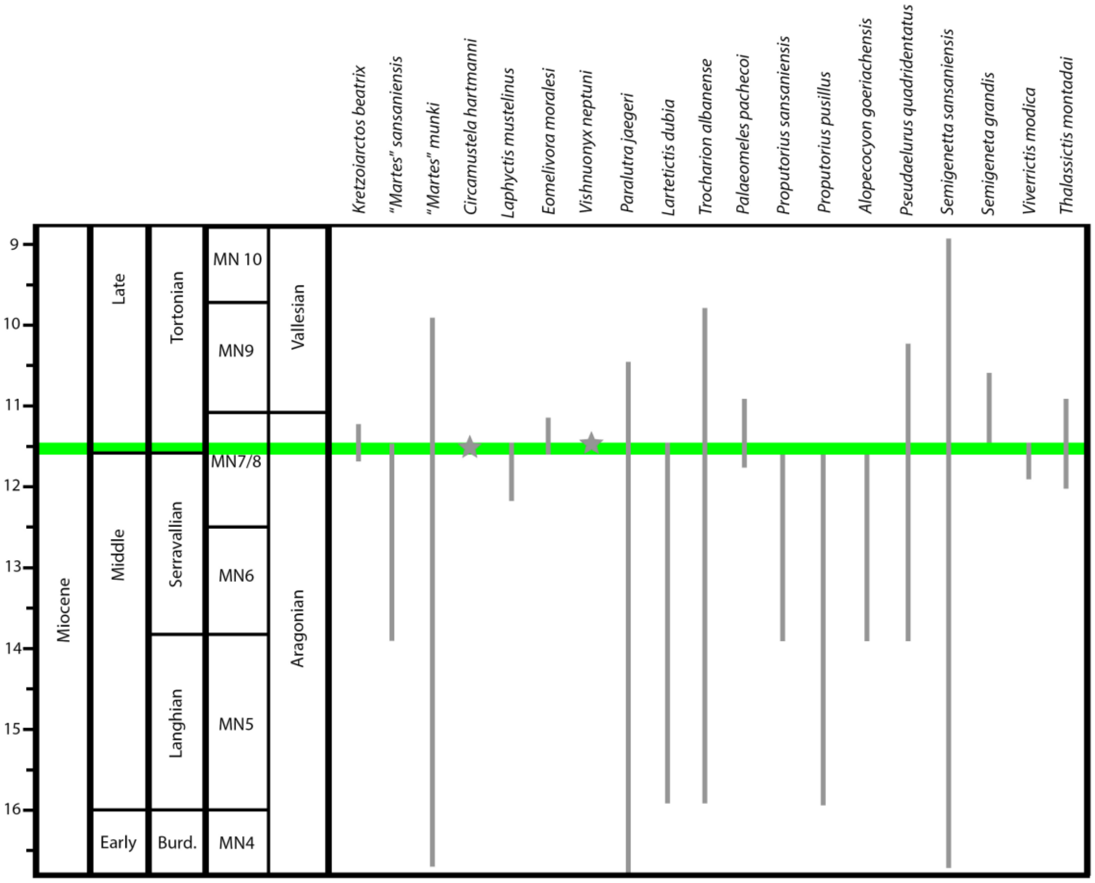


Fig. 6.4: Biostratigraphic distribution of the carnivoran species found in Hammerschmiede. The green line represents Hammerschmiede. Stars represent the two new species of Hammerschmiede that haven't been described in any other locality.

In terms of species, the locality of Hammerschmiede includes two species that haven't been found anywhere else (at least for now): *Circamustela hartmanni* and *Vishnuonyx neptuni*. The Last Occurrence Dates (LODs) of the following species are reported in the locality: "*Martes*" *sansaniensis*, *Laphyctis mustelinus*, *Lartetictis dubia*, *Proputorius sansaniensis*, *Proputorius pusillus*, *Alopecocyon goeriachensis* and *Viverrictis modica*. Additionally, the First Occurrence Dates (FODs) of *Eomellivora moralesi* and *Semigenetta grandis* are here presented.

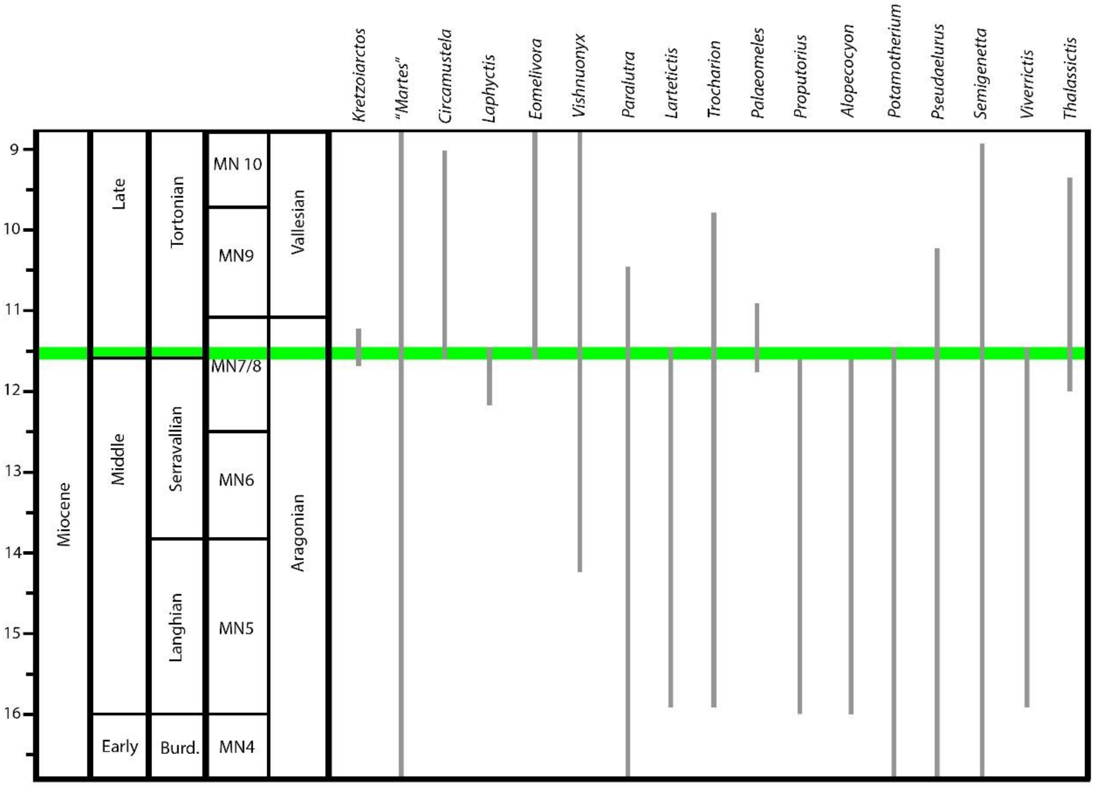


Fig. 6.5: Biostratigraphic distribution of the carnivoran genera found in Hammerschmiede. The green line represents Hammerschmiede.

Concerning the found genera, Hammerschmiede hasn't yielded any new carnivoran genera up to now. The LODs of the genera *Laphyctis*, *Lartetictis*, *Proputorius*, *Alopecocyon*, *Potamotherium* and *Viverrictis* are included in the locality's guild. The only genera FODs in Hammerschmiede are those of *Circamustela* and *Eomellivora*.

Based on the number of LODs and FODs (both in species and genus level), as well as on the stratigraphical ranges of the remaining taxa, it is clear that the carnivoran guild of Hammerschmiede includes both Aragonian and Vallesian elements. In particular, the Aragonian elements seem to dominate the fauna over the Vallesian ones. However, their coexistence in HAM 4 and HAM 5 demonstrates that the replacement of the faunal elements during the early Late Miocene happened gradually and not as a sudden event.

No unequal distribution of the Vallesian elements is recorded in the different layers: *Circamustela* is present in three layers, *Eomellivora* in HAM 5 and *Semigenetta grandis* in HAM 4. Therefore, based on the current data, the 180.000 years of age difference between HAM 4 and HAM 5 doesn't provide a key-point on the gradual dominance of the Vallesian forms.

Pie diagrams were constructed in order to depict the relative diversity of the discovered families in Hammerschmiede as a whole (Fig. 6.6), in HAM 4 (Fig. 6.7) and in HAM 5 (Fig. 6.8).

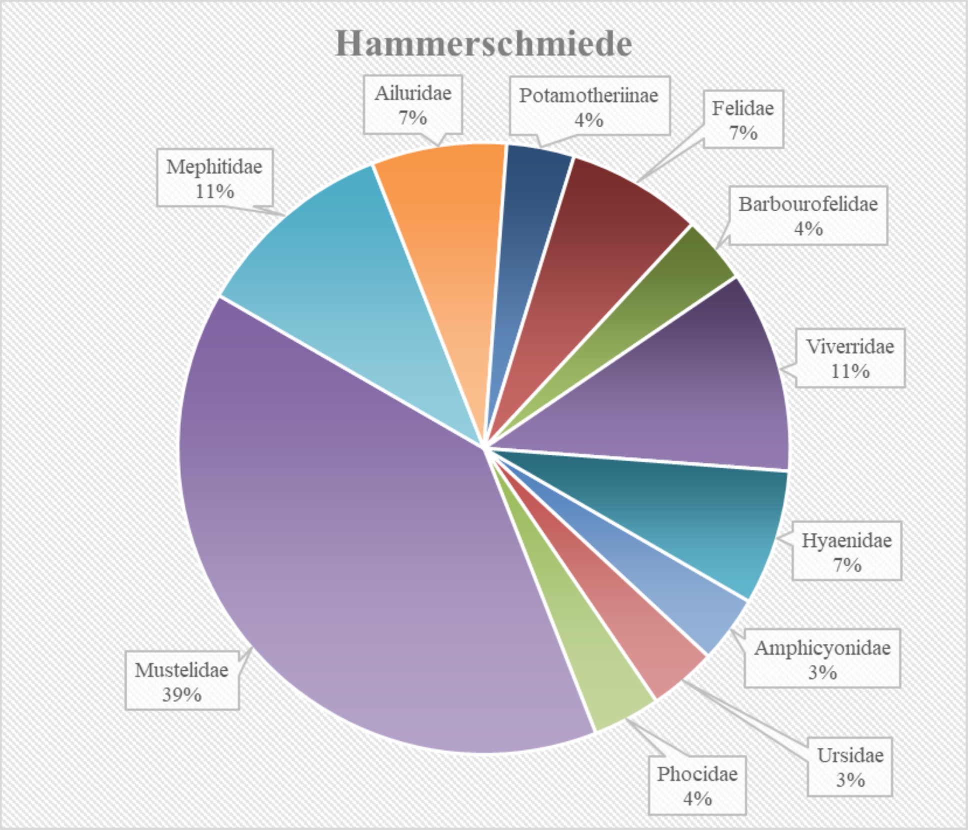


Fig. 6.6: Relative diversity (species richness) of the carnivoran families found in Hammerschmiede.

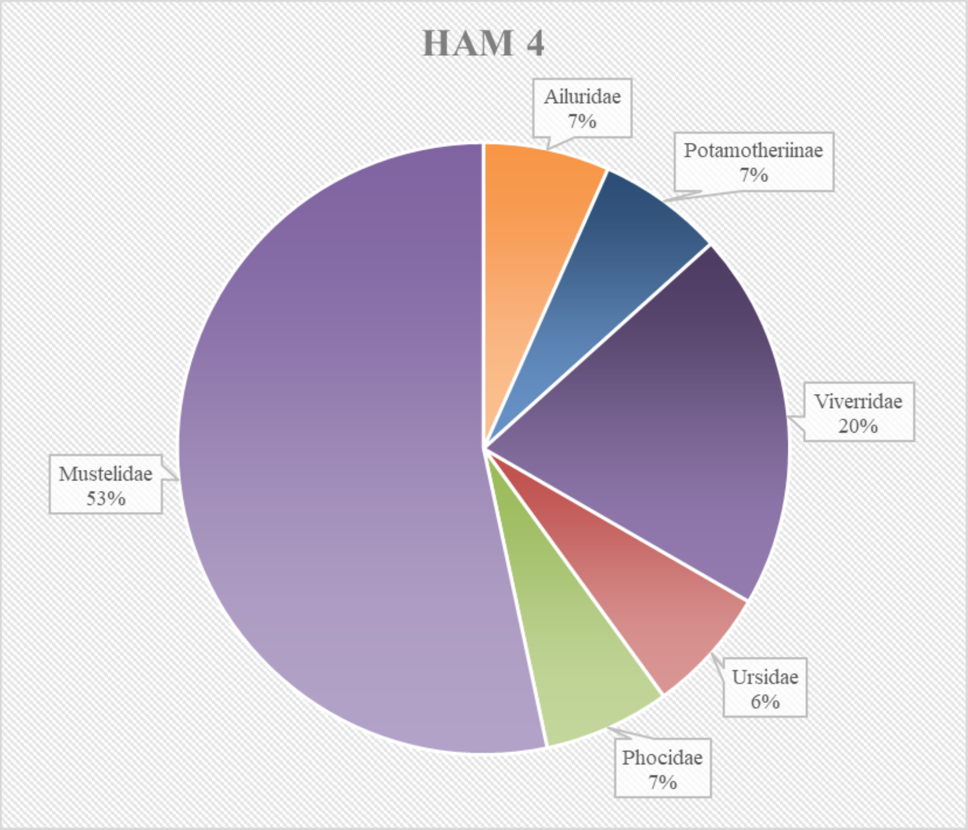


Fig. 6.7: Relative diversity (species richness) of the carnivoran families found in HAM 4.

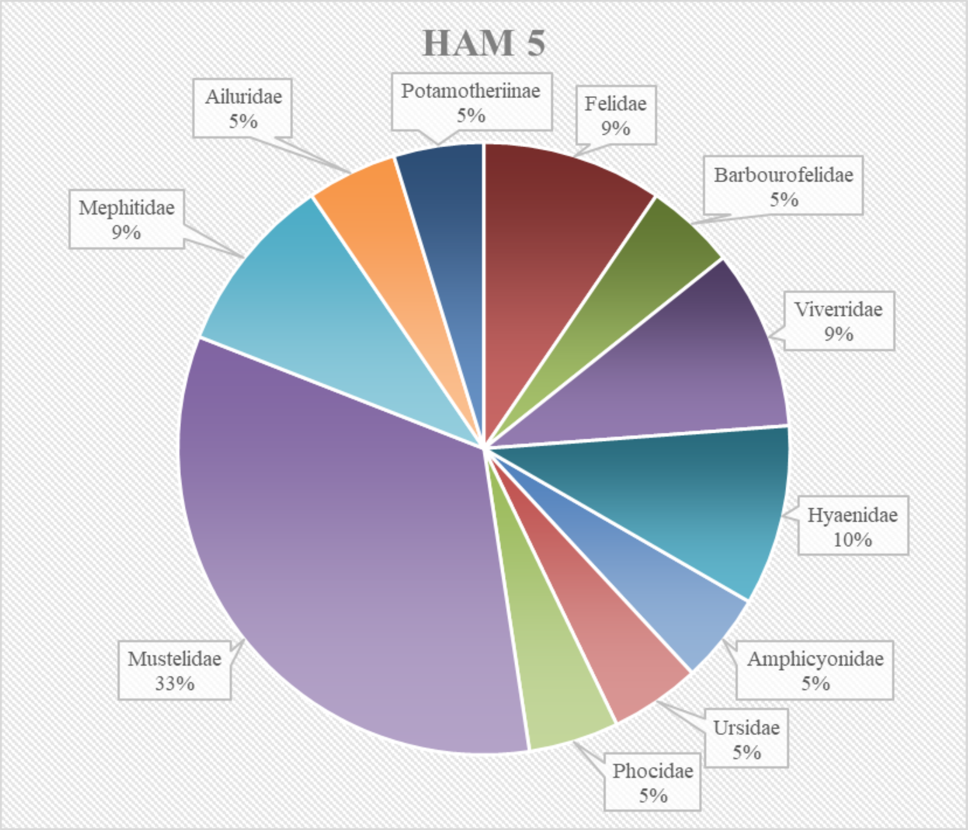


Fig. 6.8: Relative diversity (species richness) of the carnivoran families found in HAM 5.

When observing the relative diversities of the carnivoran families of Hammerschmiede, the mustelids stand out as the most diverse family with 11 different species (39%). The mephitids and the viverrids are represented by 3 species each (11%), followed by the felids, ailurids and hyaenids (2 species each; 7 %), while all the remaining families are represented only by 1 species (3%).

As also noted in Table 6.1, HAM 4 has fewer taxa than HAM 5, which is represented also in the family level. The mustelids consist most of the findings in this layer (8 species; 57%), followed by the viverrids (3 species; 22%), whereas the ursids, the phocids and the ailurids are represented only by 1 species (7%) each.

HAM 5 includes all the families found in the locality, resulting in a much more complex graph. Again the mustelids are the most variable family with 7 species (37%), followed by the hyaenids and felids (2 species each; 11%), whereas all the other families are represented only by one species.

Therefore, the common pattern between the three graphs defines that the mustelids are by far the most diverse family, whereas all the other families are represented by 1–3 species.

However, when the relative number of individuals per family is studied in a similar way, the results are considerably different in the locality as a whole (Fig. 6.9), but also in the two main layers (Fig. 6.10 for HAM 4 and Fig. 6.11 for HAM 5).

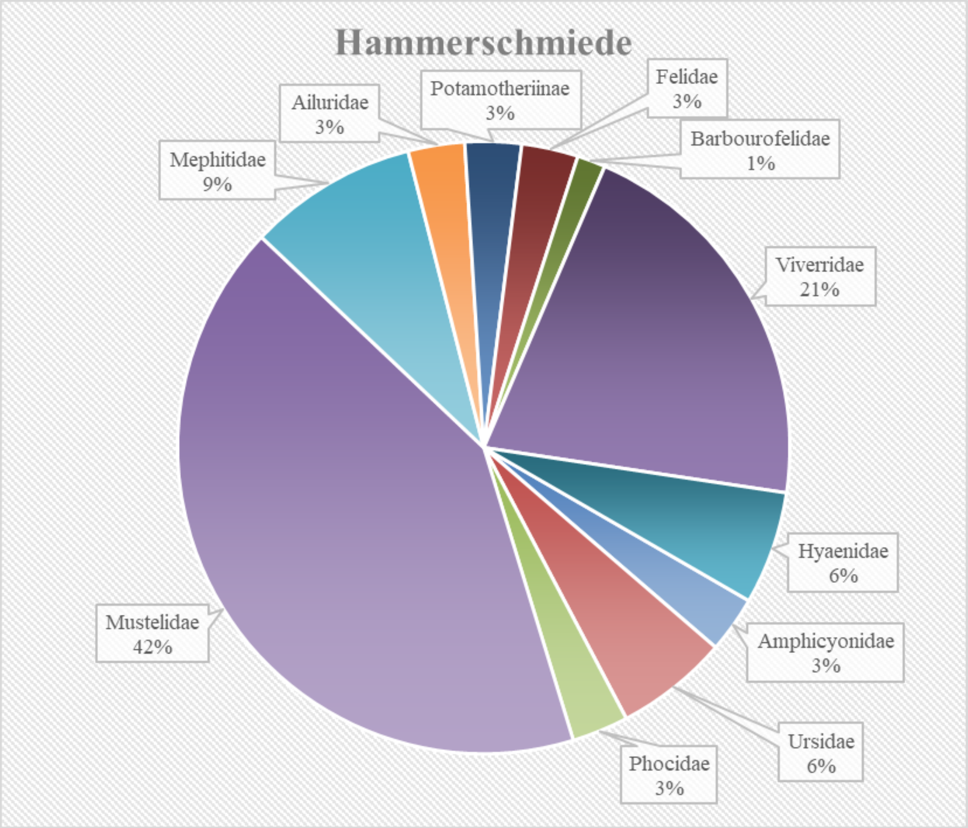


Fig. 6.9: Relative abundance (based on MNI) of the carnivoran families found in Hammerschmiede.

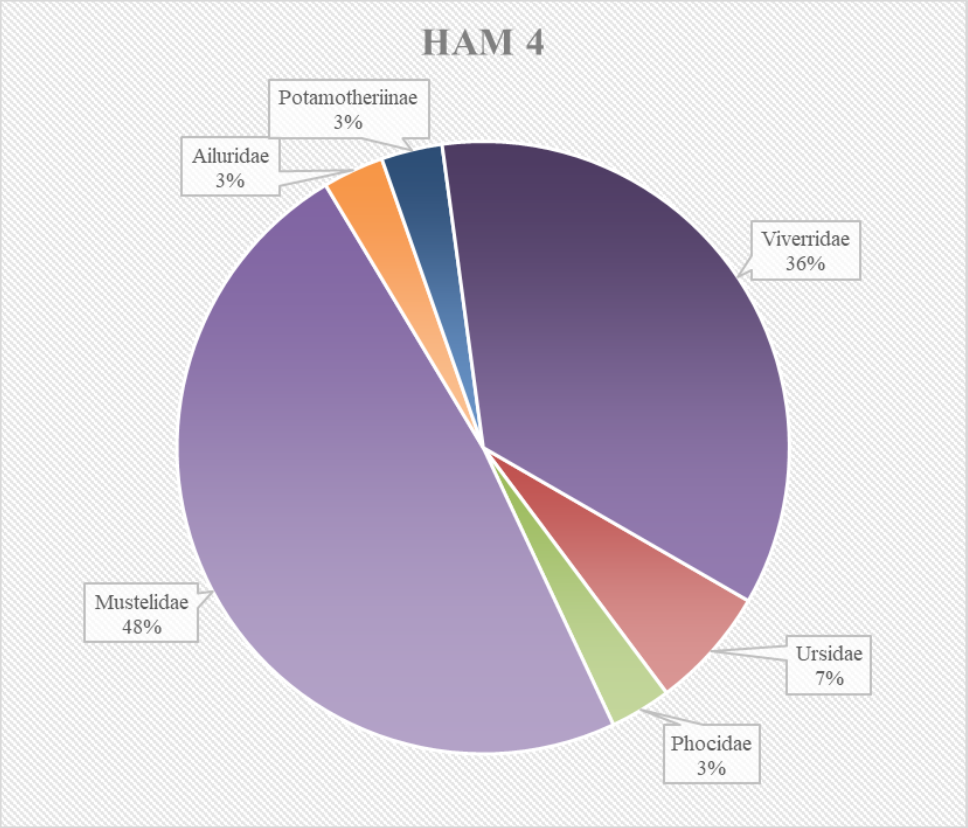


Fig. 6.10: Relative abundance (based on MNI) of the carnivoran families found in HAM 4.

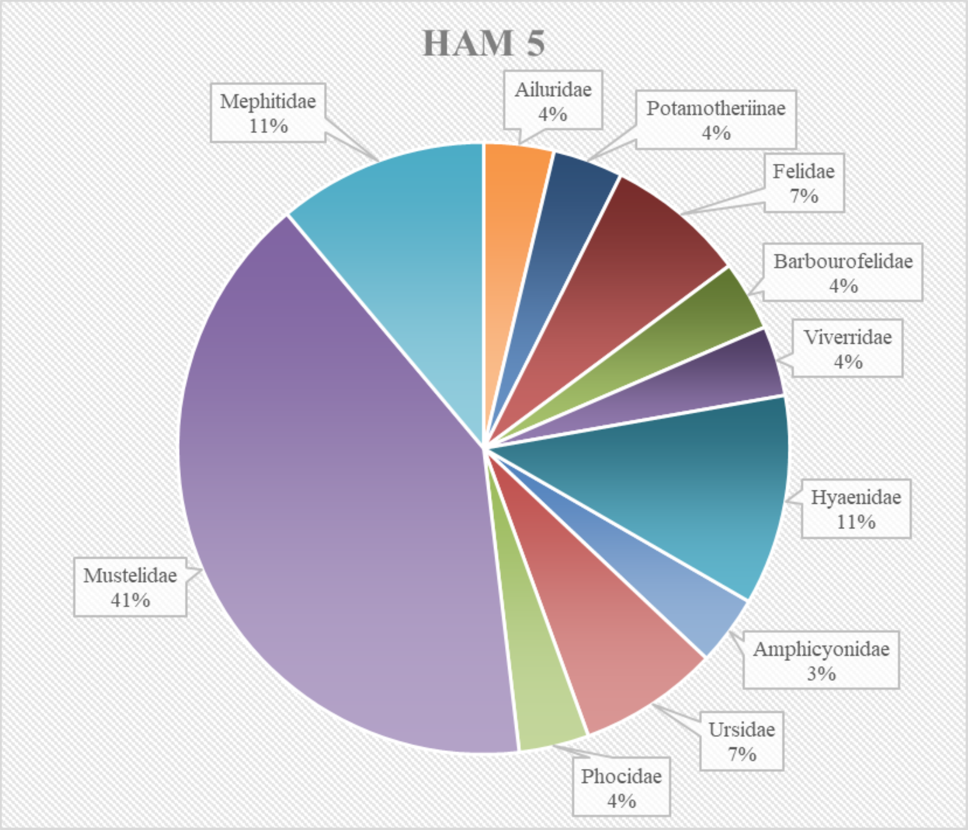


Fig. 6.11: Relative abundance (based on MNI) of the carnivoran families found in HAM 5.

Concerning the locality as a whole, not too many changes can be seen between Fig. 6.6 and Fig. 6.9. The main difference consists of the much more individuals of viverrids (12 individuals: 20%). However, the mustelids still dominate the locality with 26 individuals (43%).

This difference in the relative abundance of viverrids can be spotted in HAM 4, because of the 7 individuals of *Semigenetta sansaniensis*, as well as the existence of *Semigenetta grandis* and *Viverrictis modica*. Fig. 6.10 is the only graph, of the six already presented ones, in which a group approaches the percentages seen in the mustelids.

Fig. 6.11 closely resembles Fig. 6.8. The only noteworthy difference is in the higher percentage of mustelids, which could be interpreted by the 4 individuals of *Trocharion albanense*.

While comparing the guild of Hammerschmiede to that of other localities of similar temporospatial range, it can be seen that there are some differences in terms of relative family diversity. Fig. 6.12 depicts these relationships in some of these localities, based on the carnivoran lists given in the Introduction.

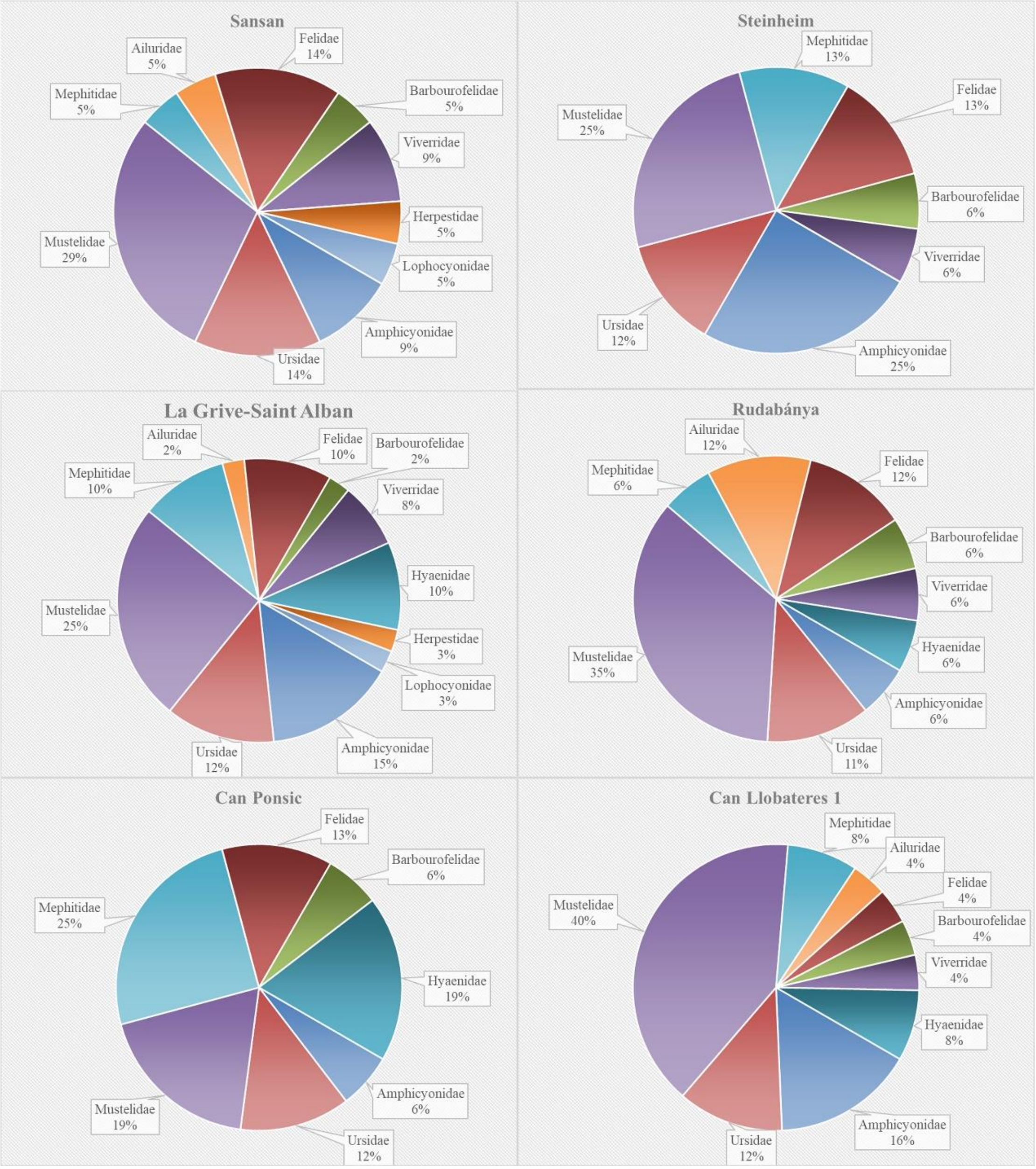


Fig. 6.12: Relative abundance of the carnivoran families found in Sansan, Steinheim, La Grive-Saint Alban, Rudabánya, Can Ponsic and Can Llobateres 1.

Comparison of these 6 guilds to that of Hammerschmiede reveals that every locality has its unique profile, exhibiting several differences than the others. Hammerschmiede includes the phocid and *Potamotherium*, which are absent in the other localities. Sansan and La Grive include herpestids that are not present as a family in Hammerschmiede. Additionally, La Grive and Sansan also include lophocyonids. The amphicyonids are always present in these localities, even reaching 25% of the guild's species in Steinheim. Additionally, amphicyonids are by far the most common carnivorans in Sansan (Ginsburg, 1961a; Peigné, 2012) and probably La Grive (Viret, 1951). On the contrary, they are pretty rare in Hammerschmiede, as they have been found only from two specimens. The locality of Can Ponsic has a surprisingly high diversity of mephitids exhibiting perhaps the most homogenous profile of the discussed localities. The barbourofelids are always present with *Albanosmilus jourdani* being the dominant species of Barbourofelidae during the Aragonian and Vallesian of Europe. However, despite their presence in Hammerschmiede, they are extremely rare (only 1 postcranial specimen) given the proven richness of the locality.

Summarizing, in comparison to these 6 Aragonian and Vallesian localities, Hammerschmiede exhibits the following unique characteristics: presence of a phocid and *Potamotherium*, very infrequent presence of amphicyonids and barbourofelids and absence of herpestids and lophocyonids, whereas the most dominant families are the mustelids and the viverrids. These characteristics will be discussed further below.

In order to compare the carnivoran guilds of different localities in a palaeoecological frame, a method for quantifying the main ecological characteristics of the included carnivorans is needed. The most commonly used parameters are body mass, locomotor habits and dietary habits. Each one of them is discussed below for every found species, based on the differentiations defined in the Material and Methods. A discussion for some forms has already been reported in Kargopoulos et al. (2021a, b, In Press, In Preparation), but the following paragraphs are approaching this subject with more detail.

- Amphicyonidae indet.
    - Body mass: It is nearly impossible to suggest a body mass based on the two available specimens. However, the preserved D4 is has a similar size to that of *Magericyon anceps* (Peigné et al. 2008). Based on Siliceo et al. (2017), the body mass for this species is estimated to be approximately 200 kg. Additionally, the McIII of the amphicyonid is larger than the one of *Amphicyon major* reported by Argot (2010). This species was also estimated to be over 100 kg (Argot, 2010). Therefore, the attribution of the Hammerschmiede amphicyonid to the >100 kg body mass category seems well-justified.
    - Locomotor habits: The only postcranium that can be attributed to an amphicyonid is the described McIII. However, it has been found in HAM 5, whereas the recovered tooth was found in HAM 6, so a clear association between them cannot be proven. The metacarpal is relatively short and broad, pointing out towards a more terrestrial form (Ginsburg, 1961b; Argot, 2010). However, it is preferred to retain an unknown status for this taxon until further material comes to light.
    - Dietary habits: Amphicyonids exhibit a very wide range of dietary adaptations. The generalized carnivore category is preferred as seen in the genus *Amphicyon* (Morlo et al., 2010). However, it is considered possible that this species might have been at least occasionally durophagous.
- *Kretzoiarctos beatrix*
    - Body mass: Based on the equation of Van Valkenburgh (1990) for the ursids, the estimated body mass for this species (based on the specimens from Spain and Hammerschmiede) would be approximately 85 kg. However, the dental measurements of *Kretzoiarctos* are similar to that of *Ursus arctos arctos* (personal data based on material from Bulgaria housed at the NMNHS). This doesn’t fit to the value mentioned above, since most adult European brown bears weight more than 100 kg

  (Pasitschniak-Arts, 1993). Nevertheless, it is clear that this species was of considerable size. Given the current absence of data on its postcranial anatomy (that would clarify the robustness of the animal) a more tentative attribution to the >100 kg body mass category is preferred.
  - Locomotor habits: Extant bears are able to exhibit a very wide range of locomotor behaviors, such as swimming, running and climbing. Given the absence of postcranial data for *Kretzoiarctos*, it is preferred to ascribe it to the Generalized Terrestrial category (as most bears are considered), pointing out that it remains possible that it could exploit many different parts of the ecosystem.
  - Dietary habits: Kargopoulos et al. (In Preparation) used DMTA to investigate the dietary preferences of this species. The results suggested that this ursid retains an opportunistic diet, similar to that of the extant *Ursus*, whereas it doesn't exhibit similarities to the extant panda.
- Phocidae indet.
  - Body mass: Unfortunately, the material of this taxon in Hammerschmiede is very restricted. Additionally, the isolation of the discovered teeth doesn't enable a secure anatomical identification. Therefore, the body mass estimation is highly speculative. However, based on dental dimensions, the specimens are slightly larger than the respective teeth of *Phoca vitulina* (Figs. 4.3.1 and 4.3.2). The adult body mass for this species is approximately 100 kg (Walker & Bowen, 1993), so the Hammerschmiede phocid is attributed to the > 100 kg body mass category.
  - Locomotor habits: Since all phocids are semi-aquatic, it is reasonable to suggest that this form also followed the same lifestyle.
  - Dietary habits: All extant phocids today are mainly feeding on fish and mollusks. The same can be expected for the Hammerschmiede seal. Additionally, since the p1 is one-rooted, there is no considerable dental wear and there is no interproximal wear (which can be interpreted as an indicator of the presence of diastemata), this form can be attributed to the Fourth Ecomorph of Phocinae (Koretsky et al., 2020), which mainly feeds on fishes rather than mollusks.
- “*Martes*” *sansaniensis*
  - Body mass: Based on the equation of Van Valkenburgh (1990) for the m1L of mustelids, the expected body mass of this species (based on the values provided by Peigné, 2012) is approximately 7 kg. A similar number is found if the equation for the skull length of the mustelids is used, based on the Hammerschmiede skull. Therefore, an attribution to the 3–10 kg category is suggested. The same category was suggested by Morlo et al. (2010).
  - Locomotor habits: This species was considered by Morlo et al. (2010) to be scansorial. Ginsburg (1961) discussed the resemblances of this species' skeleton to that of the extant martens, so the same approach is going to be followed herein.
  - Dietary habits: This species was considered by Morlo et al. (2010) as a carnivore. This is deemed reasonable based on its similarities to the

extant martens. The same morphology is also found in other species of the same genus.

- “*Martes*” *munki*
    - Body mass: The m1L equation for mustelids based on Van Valkenburgh (1990) results in a body mass of 1.3 kg. Morlo et al. (2010) attributed “*Martes*” cf. *munki* from Sandelzhausen to the <1 kg category, despite the fact that this material is slightly larger than that of the average values for the species (Nagel et al., 2009). Since the authors didn’t provide an explanation for this attribution, it is herein preferred to attribute the Hammerschmiede form to the 1–3 kg group.
    - Locomotor habits: Morlo et al. (2010) hesitated to ascribe this species to a locomotor category. However, since all the small-sized gulonines are considered to be scansorial (Morlo et al., 2010), this attribution will be tentatively followed here.
    - Dietary habits: Morlo et al. (2010) and Kargopoulos et al. (In Press) considered this species to be a carnivore, similar to “*M*”. *sansaniensis*.
- “*Martes*” sp.
    - Body mass: Unfortunately the material for this form is insufficient to estimate body mass. However, it has been noted that this species is smaller than “*Martes*” *munki*, resembling in size “*Martes*” *delphinensis*. The equation of Van Valkenburgh (1990) for the m1L of this species (based on measurements of Mein, 1958) results in 0.5 kg. Therefore, an attribution to the <1 kg group seems justified.
    - Locomotor habits: Unfortunately, no postcranial can be attributed to this form. However, since all the small-sized gulonines are considered to be scansorial (Morlo et al., 2010), this attribution will be followed here retaining a doubtful status.
    - Dietary habits: This species exhibits the same general morphology as the other species of the same genus, so it is also considered as a carnivore.
- *Circamustela hartmanni*
    - Body mass: Based on the equation of Van Valkenburgh (1990) for the m1L of mustelids, the body mass of this species is estimated to be 1.2 kg. The equation for skull length for *Circamustela peignei* (based on measurement taken in Valenciano et al. 2020a, fig. 2) results in 2.5 kg. Since *Circamustela hartmanni* is slightly smaller than *Circamustela peignei*, then it is herein attributed to the 1–3 kg group.
    - Locomotor habits: Unfortunately, no postcranial of the genus *Circamustela* have been published. Therefore the attribution remains dubious. However, since all the small-sized gulonines are considered to be scansorial (Morlo et al., 2010), this attribution will be followed here.
    - Dietary habits: The hypercarnivorous adaptations of the genus *Circamustela* have been discussed in detail by Valenciano et al. (2020a). The species *Circamustela hartmanni* also exhibits these traits seen in the other two species of the genus (Kargopoulos et al., In Press).
- *Laphyctis mustelinus*

  - Body mass: This species is known from Hammerschmiede only by one M1. However, other specimens have been found in other localities that enable us to make some estimations about its palaeoecology. Based on the m1L (value by Helbing, 1930) and skull length (value by Villalta Comella & Crusafont Pairó, 1943) resulted in 13.5 kg and 14.4 kg respectively. Therefore, this species is attributed to the 10–30 kg group
  - Locomotor habits: Morlo et al. (2010) considered this species to be generalized terrestrial. Helbing (1936) considered the extant *Gulo* and *Mellivora* to be analogues for this form, based on the material from Steinheim, so this attribution is followed also herein.
  - Dietary habits: The species *Laphyctis mustelinus* was attributed by Morlo et al. (2010) to the hypercarnivorous group. This is based in the similarities between this form and the extant wolverine (Helbing, 1936).
- Guloninae indet.
  - Body mass: Unfortunately there are not too much information about this form. However based on its m1L (Van Valkenburgh, 1990) its estimated body size is approximately 5 kg. Therefore, it is attributed to the 3–10 kg body mass group.
  - Locomotor habits: Since the exact affinities of this form are unknown and there are no postcranials from Hammerschmiede that can be attributed to it, its locomotor habits remain unknown.
  - Dietary habits: As discussed in Kargopoulos et al. (In Press), this species exhibits some hypocarnivorous adaptations, such as the low and blunt cuspids, the absence of accessory cuspids in the premolars and the moderately long m1 talonid.
- *Eomellivora moralesi*
  - Body mass: Based on the equation of Van Valkenburgh (1990) for the m1L of mustelids, the estimated body mass for this species would be approximately 65 kg. However, as also discussed in Kargopoulos et al. (In Press), this number probably is higher than it should, because the used equation is formed based on smaller animals. Kargopoulos et al. (In Press) made an analogy of *Eomellivora* to the extant wolverine, *Gulo gulo*. In fact, the m1L of *Eomellivora moralesi* is slightly higher than that of the wolverine. Therefore, the body mass of *E. moralesi* is expected to be slightly higher than that of *Gulo,* which is usually 10–20 kg and rarely up to 30 kg (Pasitschniak-Arts & Larivière, 1995). Therefore, an attribution to the 10–30 kg group is preferred, pointing out that most probably it would have been closer to 30 kg than to 10 kg.
  - Locomotor habits: Unfortunately, no postcranial material of *Eomellivora* has been described in detail. However, Valenciano et al. (2015) and Valenciano & Govender (2020) commented on the relatively long limbs of this genus that can be possibly adapted for a cursorial lifestyle. However, until this material is published, it is preferred to retain this species to the generalized terrestrial category.
  - Dietary habits: Based on the discussion of Valenciano et al. (2015) the genus *Eomellivora* can be attributed to a hypercarnivorous diet, similar

    to that of the extant wolverine, focusing on carnivory and possibly durophagy.

- *Vishnuonyx neptuni*
    - Body mass: As already discussed in Kargopoulos et al. (In Press), based on the m1L of this form (Van Valkenburgh, 1990), the estimated body mass would be approximately 10 kg. This value is problematic because it falls at the border between two categories. Since the other two lutrines clearly belong to the 3–10 kg category, it has been preferred to attribute *Vishnuonyx neptuni* to the 10–30 kg category, in order to better depict the size difference between these forms.
    - Locomotor habits: As all lutrines, despite the absence of postcranial elements, *Vishnuonyx* is believed to have had semi-aquatic lifestyle.
    - Dietary habits: The dietary habits of *Vishnuonyx neptuni* were discussed by Kargopoulos et al. (2021b), suggesting that it was a Piscivore/Mollusk-eater with possibly larger percentage of fish in its diet.
- *Paralutra jaegeri*
    - Body mass: The body mass for this species was estimated to be 3–10 kg by Morlo et al. (2010). Based on the equation of Van Valkenburgh (1990) for the m1L of mustelids, when using the m1L provided by Helbing (1936), the resulted body mass is approximately 5 kg. Therefore, this attribution seems justified.
    - Locomotor habits: The semi-aquatic adaptations of this species have been discussed in detail by Willemsen (1992).
    - Dietary habits: Similar to all the other lutrines (e.g. Willemsen, 1992) this species is considered to be a piscivore/mollusk-eater. More details can be found in Ginsburg (1968) and Willemsen (1992).
- *Lartetictis* cf. *dubia*
    - Body mass: As already discussed in Kargopoulos et al. (In Press), Morlo et al. (2010) suggested that this species should be included to the 10–30 kg category. However, based on the small size of the discovered specimens in Hammerschmiede, an attribution to the 3–10 kg category is preferred, since the estimated body mass based on the equation of Van Valkenburgh (1990) for the m1L of mustelids was approximately 5 kg.
    - Locomotor habits: This taxon is also considered to be semi-aquatic (Willemsen, 1992; Heizmann & Morlo, 1998).
    - Dietary habits: Similar to all the other lutrines (e.g. Willemsen, 1992) this species is considered to be a piscivore/mollusk-eater. More details can be found in Heizmann & Morlo (1998) and Willemsen (1992).
- *Trocharion albanense*
    - Body mass: Based on the m1L values provided by Robles et al. (2010), the estimated body mass for this species is approximately 2 kg. Therefore, the attribution to the 1–3 kg category that was preferred by Morlo et al. (2010) seems justified.
    - Locomotor habits: This species was considered by Morlo et al. (2010) to be semi-fossorial. The same approach is followed here as in Kargopoulos et al. (In Press).

  - Dietary habits: Morlo et al. (2010) attributed this species to the carnivore category. Even though some hypocarnivorous traits can be found in the dentition of *Trocharion* (robust m1 talonid, enlarged M1 surface, restricted P4), until a detailed ecomorphological study investigates these characteristics, it is preferred to retain the carnivorous status.
- *Palaeomeles pachecoi*
  - Body mass: As suggested by Kargopoulos et al. (In Press), this species is slightly smaller than the extant Eurasian badger, so it is attributed to the 3–10 kg category.
  - Locomotor habits: The postcranial material discussed by Crusafont Pairó & Golpe Posse (1982) revealed semi-fossorial adaptations for this species. Kargopoulos et al. (In Press) preferred to refer to it as "Generalized Terrestrial/Semi-Fossorial", in order to reflect that these adaptations are not as derived as in the extant badgers. However, for the sake of statistic consistency, the category SF is herein selected.
  - Dietary habits: As discussed in Kargopoulos et al. (In Press), this form exhibits some definite hypocarnivorous adaptations towards a badger-like ecomorph: wide M1 with low cusps, low premolars with no accessory cuspids, exceptionally enlarged m1 talonid with small cuspulids etc. Therefore, it is also herein considered as a hypocarnivore.
- *Proputorius sansaniensis*
  - Body mass: This form was attributed by Morlo et al. (2010) to the 3–10 kg category. However, if the equation of Van Valkenburgh (1990) for the m1L mustelids is used (based on the measurements provided by Peigné, 2012), it can be seen that the size of this species corresponds better to the 1–3 kg category.
  - Locomotor habits: The locality of Sansan has yielded some postcranial elements of this species (Ginsburg, 1961; Peigné, 2012). Ginsburg (1961) pointed out the similarities between this species skeleton and that of the extant *Martes*. Morlo et al. (2010) attributed this form to the scansorial locomotor category, which conforms to the observations of Ginsburg (1961) and is also followed herein.
  - Dietary habits: This species has a relatively plesiomorphic morphology that can be interpreted as intermediate between a carnivore and hypocarnivore ecomorph (moderately enlarged m1 talonid and M1 lingual platform; moderately developed P4). However, for the sake of parsimony, the approach of Morlo et al. (2010) considering it as a carnivore is going to be followed.
- *Proputorius pusillus*
  - Body mass: This species was attributed to the < 1 kg category by Morlo et al. (2010). Based on the m1L of the discovered specimen from HAM 1 (when the equation of Van Valkenburgh, 1990, for the mustelids is used), the corresponding body mass is indeed lower than 1 kg. Therefore, this attribution is followed herein.
  - Locomotor habits: Morlo et al. (2010) hesitated to attribute this species to a specific locomotor category. However, every other member of this

    genus was considered to be scansorial. Therefore, it is herein preferred to include this form to this category.
  - Dietary habits: This species (similarly to *P. sansaniensis*) is also considered as a carnivore, even though its small size could have been interpreted as an indicator of insectivory. However, the absence of pointy cusps is considered a deviation from this direction.
- *Alopecocyon goeriachensis*
  - Body mass: Morlo et al. (2010) placed this species to the 3–10 kg category. If the equation of Van Valkenburgh (1990) for the m1L of mustelids is used (based on the dimensions given by Peigné, 2012), the estimated body mass for this species is approximately 4 kg. Therefore, the attribution to this category is considered valid.
  - Locomotor habits: This species was considered by Morlo et al. (2010) as scansorial. This conforms to the extant tree-foraging image of a small-sized ailurid and it is followed herein.
  - Dietary habits: Morlo et al. (2010) attributed this species to the carnivore category. This seems reasonable based on the relatively plesiomorphic morphology of the cheek teeth that resemble a canid-like mustelid.
- Simocyoninae indet.
  - Body mass: As discussed in Kargopoulos et al. (In Press), this form is larger than *Alopecocyon goeriachensis*, but smaller than *Simocyon batalleri*. Therefore, it is attributed to the 10–30 kg group.
  - Locomotor habits: Since the exact affinities of this form are unknown and there are no postcranials from Hammerschmiede that can be attributed to it, its locomotor habits remain unknown.
  - Dietary habits: Since this form is considered to be closer to *Alopecocyon*, a similar diet is also proposed for it, so it is considered as a carnivore.
- *Potamotherium* sp.
  - Body mass: As noted by Kargopoulos et al. (In Press), this form is slightly larger than *Potamotherium miocenicum*, which has a m1L of approximately 13 mm (Ginsburg, 1968). This corresponds to the lower values of the range of *Lartetictis dubia* (larger than those of *L*. cf. *dubia* in Hammerschmiede). Therefore, this species is attributed to the 10–30 kg category, as discussed above. However, it is noted that it would be closer to the low range of this category.
  - Locomotor habits: The semi-aquatic adaptations of this genus have been discussed in detail by Savage (1957), Ginsburg (1968), Tedford (1976) and de Muizon (1982).
  - Dietary habits: The lutrine-like Piscivorous/Mollusk-eater adaptations of this species have been discussed in detailed by Savage (1957).
- *Pseudaelurus quadridentatus*
  - Body mass: Morlo et al. (2010) place this species to the 30–100 kg category. Based on the equation of Van Valkenburgh (1990) for the m1L of felids (and using the m1L values provided by Robles et al. 2013a), the estimated body mass of this form is approximately 50 kg. Therefore this attribution is deemed reasonable.

  - Locomotor habits: This species was considered as scansorial by Morlo et al. (2010). This attribution is further supported by the studies of Ginsburg (1961a, 1961b) and Peigné (2012).
  - Dietary habits: As in all felids, this form is considered to be a hypercarnivore.
- Metailurini indet.
  - Body mass: As demonstrated in the relevant pages, this form is similar in size to the Turolian species *Metailurus major*. Based on the equation of Van Valkenburgh (1990) for the m1L of felids, using the values provided by Zdansky (1924), the estimated body mass for this felid is approximately 100 kg. Again, this value falls in the border between two categories. Based on the skull length equation (using the values of *M. major* provided by Roussiakis, 2001a), the estimated body mass is approximately 75 kg. Therefore, the 30–100 kg category is herein preferred.
  - Locomotor habits: This form is larger than *Pseudaelurus quadridentatus*. However, it is considered to be a primitive sabertooth with no derived machairodont adaptations. This means that it is more likely that this taxon is (in terms of locomotor abilities) closer to *Pseudaelurus* than to *Machairodus*. Therefore, it is attributed to the scansorial group.
  - Dietary habits: As in all felids, this form is considered to be a hypercarnivore.
- Barbourofelidae indet.
  - Body mass: Morlo et al. (2010) suggested that *Albanosmilus jourdani* should be included to the >100 kg category, whereas *Sansanosmilus palmidens* should be in the 30–100 kg category. This can be verified based on the equation of Van Valkenburgh (1990) for the m1L of felids, using the values provided by Robles et al. (2013b) and Morlo et al. (2004) respectively. The TDd of the discovered barbourofelid humerus is 66.1 mm, whereas that of *S. palmidens* is 51.7 mm. Therefore, the Hammerschmiede form is considerably larger than the one from Sansan, so the attribution to the *A. jourdani* body mass category (> 100 kg) is preferred.
  - Locomotor habits: Not many can be said about the locomotor behavior of this form. The barbourofelids are mainly considered to be generalized terrestrial carnivorans (Morlo et al., 2010). However, until more material come to light, it is preferred to retain a doubtful attribution to this category for this taxon.
  - Dietary habits: Barbourofelids have developed hypercarnivorous adaptations, such as saber-canines and serrated teeth. Based on the derived morphology of the humerus, it can be deduced that these adaptations were present in this species, so it is considered herein as a hypercarnivore.
- *Semigenetta sansaniensis*
  - Body mass: Based on Kargopoulos et al. (2021a, In Press), this species ranges between 2 and 5 kg, so it is attributed to the 3–10 kg category.

  - Locomotor habits: The postcranial skeleton of *Semigenetta* is very close to that of the extant *Genetta* (Helbing, 1927; Heizmann, 1973; Peigné, 2012; Kargopoulos et al., 2021a). Therefore, a similar scansorial locomotion is herein suggested.
  - Dietary habits: The diet of this species was discussed in Kargopoulos et al. (2021a), concluding that it had similar dietary preferences as the extant genets, so it is considered a carnivore.
- *Semigenetta grandis*
  - Body mass: Based on Kargopoulos et al. (2021a, In Press), this species is slightly larger than 10 kg, so it is attributed to the 10–30 kg category.
  - Locomotor habits: No postcranials of this form have ever been found. Even though a similar ecomorphology to *Semigenetta sansaniensis* cannot be excluded, a more ictithere-like postcranial skeleton is also highly possible. Nevertheless, for the time being this species is also considered as having unknown locomotor habits.
  - Dietary habits: The hypercarnivorous adaptations of this form have been discussed in detail by Golpe-Posse (1981a, 1981b, 1981c).
- *Viverrictis modica*
  - Body mass: This species was attributed by Morlo et al. (2010) to the <1 kg body mass category. Since the dimensions of this species (de Beaumont, 1973a) are somewhat smaller to that of the extant *Viverricula indica* (NHMBA-13867), the same approached is followed herein. However, it is noted that a future attribution to the 1–3 kg category is considered possible.
  - Locomotor habits: This species was considered by Morlo et al. (2010) as scansorial, an approach followed also by Kargopoulos et al. (In Press). The same attribution is followed herein.
  - Dietary habits: This species was attributed to the insectivore category by Morlo et al. (2010). This is deemed reasonable based on the very small size of the animal and the very pointy cusps of its dentition that are excellent for piercing the exoskeleton of insects. This approach was followed by Kargopoulos et al. (In Press) and it is used also herein.
- *Thalassictis montadai*
  - Body mass: Based on the equation of Van Valkenburgh (1990) for the m1L of the canids (which were selected as the most closely resembling ecomorph for the ictitheres), the body mass for this species is approximately 16 kg. If the total skull length is used (based on the values provided by Crusafont Pairó & Golpe Posse, 1973), the body mass is estimated to the approximately 23 kg. Therefore, this species is attributed to the 10–30 kg category.
  - Locomotor habits: Viranta & Werdelin (2003) described some postcranial of this species from various sites in Sinap. They noted that the limb bones of this form is much stouter than those of *Hyaenictitherium wongii*, indicating that there aren’t traits of cursorial adaptations. This conforms to the general statement of Semenov (2008) that the Ictitheriinae (including *Thalassictis*) are less cursorial than the

Hyaenotheriini. Therefore, this species is herein considered as generalized terrestrial.

    - Dietary habits: This species has been considered by Turner et al. (2008) as a member of the Ecomorph Group 3 “jackal- and wolf-like meat and bone eater”, so it is herein placed to the durophagous group.

- Hyaenidae indet.
    - Body mass: This is a very large form that is similar in size (and slightly larger to) *Adcrocuta eximia* (Kargopoulos et al., 2021c). The dimensions of this species are considerably larger that of the extant *Crocuta crocuta* (Werdelin & Solounias, 1990; Beke, 2010), which ranges from 40 to 80 kg (Hayssen & Noonan, 2021). Therefore, based on the significant difference in I3 dimensions, the Hammerschmiede hyaenid is attributed to the >100 kg body mass category.
    - Locomotor habits: Since the exact affinities of this form are unknown and there are no postcranials from Hammerschmiede that can be attributed to it, its locomotor habits remain unknown.
    - Dietary habits: Even though only one incisor of this species has been discovered, it is enough to support the assumption that this species was durophagous, based on the considerable wear and the very thick enamel with distinct Hunter-Schreger bands (Kargopoulos et al., 2021c).

Several different approaches have been chosen in order to demonstrate the data discussed above. The simplest way to depict the aforementioned characteristics is by using column charts for each of the three palaeoecological proxies, in order to present the distribution of the different species per category. This method is applied for the locality as a whole, as well as in HAM 4 and HAM 5 separately.

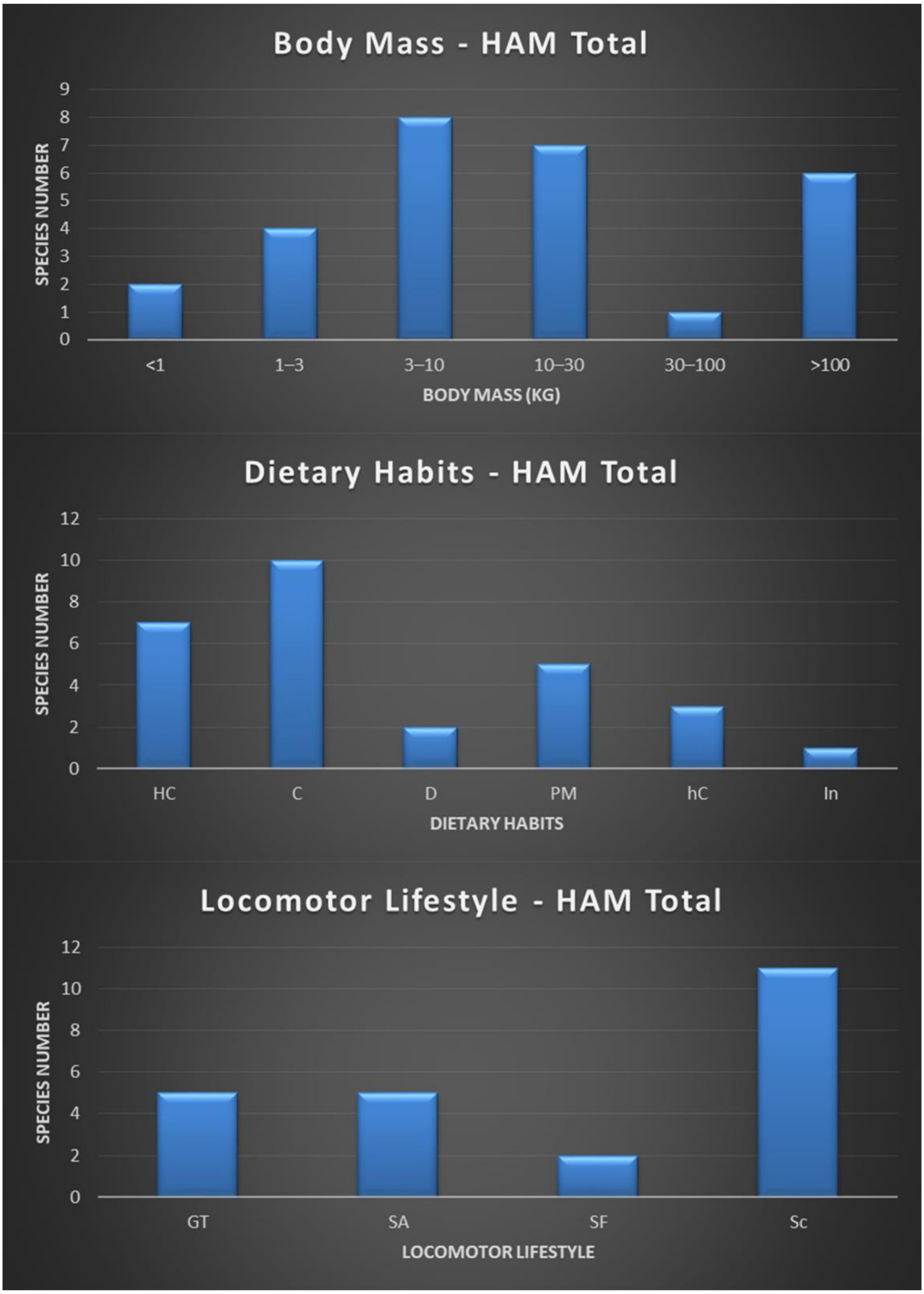


Fig. 6.13: Column charts depicting the distribution of the Hammerschmiede carnivorans in the respective categories of body mass, dietary habits and locomotor lifestyle.

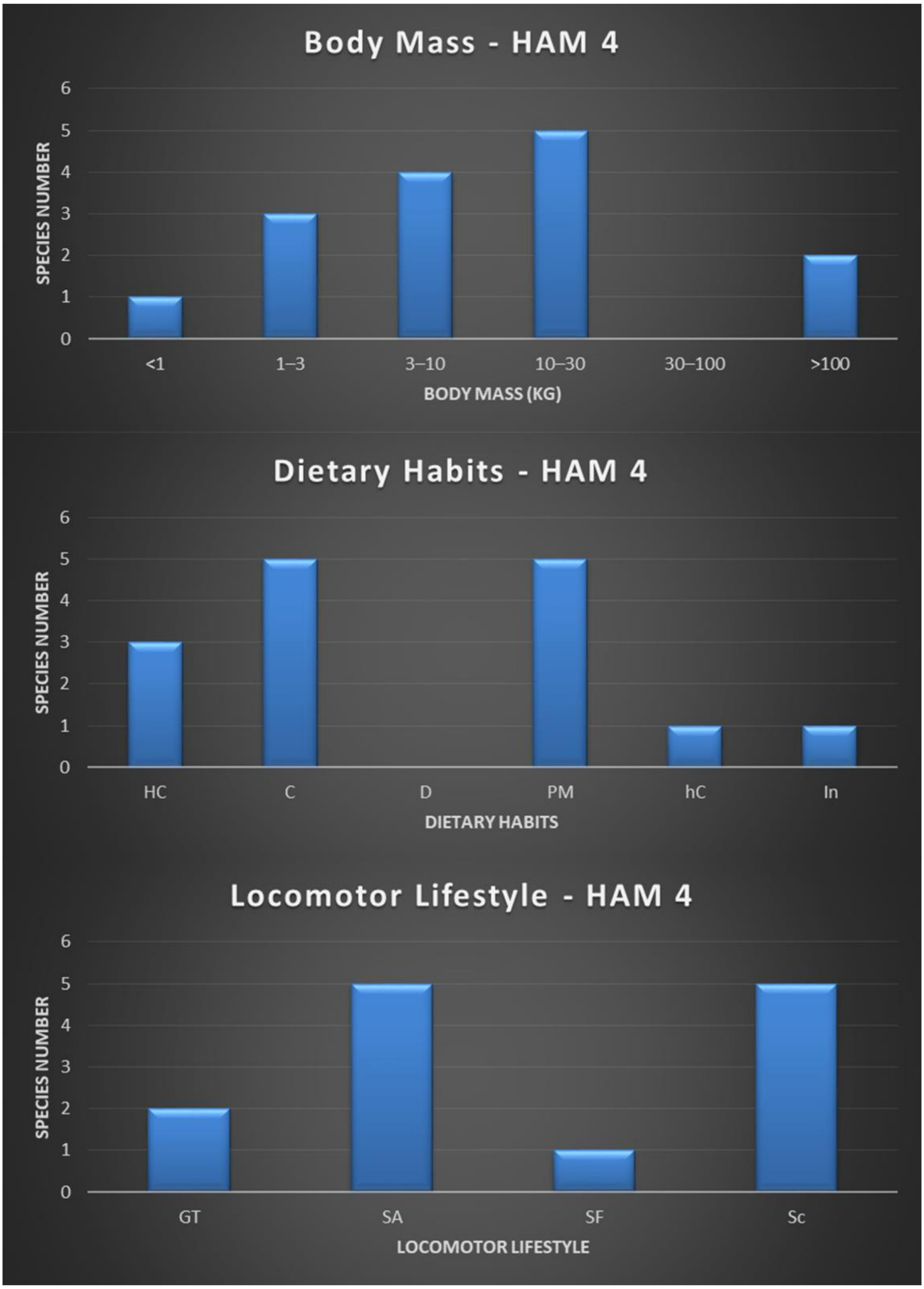


Fig. 6.14: Column charts depicting the distribution of the HAM 4 carnivorans in the respective categories of body mass, dietary habits and locomotor lifestyle.

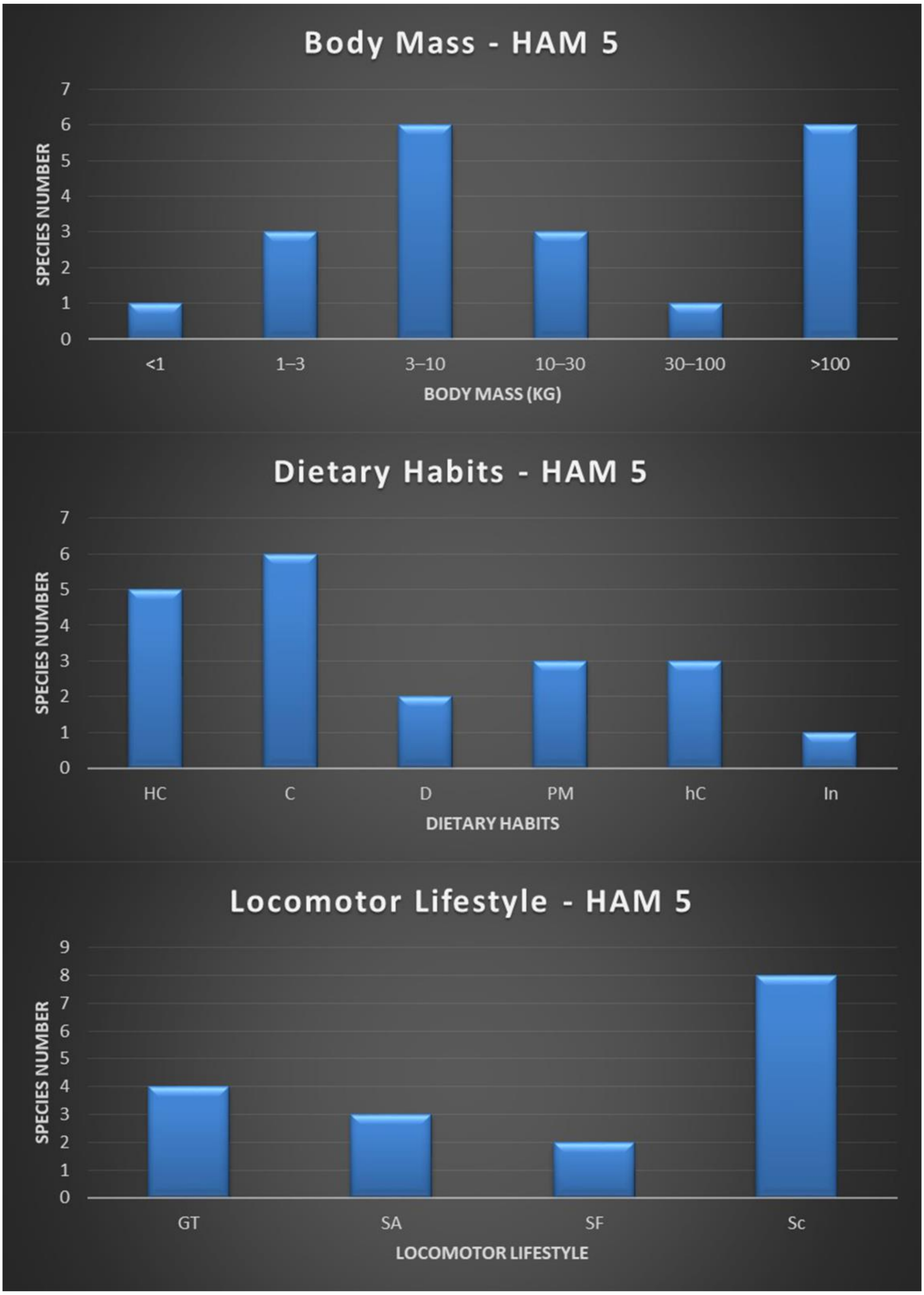


Fig. 6.15: Column charts depicting the distribution of the HAM 5 carnivorans in the respective categories of body mass, dietary habits and locomotor lifestyle.

Concerning the body mass, the distribution of the species is resembling an expected normal distribution in its lower values. This can be seen in all three Figs. 6.13–15. An interesting deviation from the normal distribution is that HAM 5 includes several large-sized carnivorans (the amphicyonid, the phocid, *Kretzoiarctos*, the barbourofelid, the felids and the hyaenid). On the contrary, the only large carnivorans in HAM 4 are *Kretzoiarctos* and the phocid. Unfortunately the large forms are known only from fragmentary remains, so their exact taxonomic position is still uncertain. However, if this distribution is not biased, then this difference in large carnivorans' distributions between the two main layers surely is a fact that needs to be investigated in further detail.

Concerning the dietary habits, reasonably most species are carnivores or hypercarnivores. The piscivores/mollusk-eaters are also abundant, indicating the plethora of river-originating dietary resources. One interesting difference between the two main layers is the absence of the durophagous carnivorans in HAM 4, as well as the lower frequency of hypercarnivores (main the felids and the barbourofelid) in the latter layer. On the contrary, HAM 4 is mainly dominated by smaller-sized more opportunistic carnivores.

Finally, concerning the locomotor lifestyles of the discovered species, the influence of the forested part of the ecosystem is evident in the presented charts as most of the species are scansorial. This category includes a wide range of different forms, from the small-sized insectivore *Viverrictis modica* to the large-sized hypercarnivore Metailurini indet. Additionally, especially in HAM 4, the semi-aquatic species are abundant, forming a large part of the guild. In HAM 4 this percentage is equal to that of the scansorial species, whereas in HAM 5 the latter are far more diverse than the former.

Summarizing, Figs. 6.13–15 point towards the following facts:

- The locality as a whole includes:
    - a relatively normal distribution of species per body mass categories
    - mostly carnivorous, hypercarnivorous and piscivorous/mollusk-eating carnivorans
    - many scansorial, but also several semi-aquatic species that indicate the considerable influence of a forested fluvial ecosystem
- The layer HAM 4 differs from HAM 5 in the:
    - much lower diversity of large-sized species
    - the absence of durophagous species and the lower diversity of the hypercarnivores
    - the higher diversity of semi-aquatic forms and the lower diversity of scansorial species

This high number of coexisting carnivorans in a single locality (and even more so in the individual layers) leads to inevitable cases of similar ecological roles between some species. This situation results in cases of interspecific competition between the different forms. The ecological similarity between the discovered carnivorans was investigated using the Paired Group (UPGMA) classic clustering (Fig. 6.16).

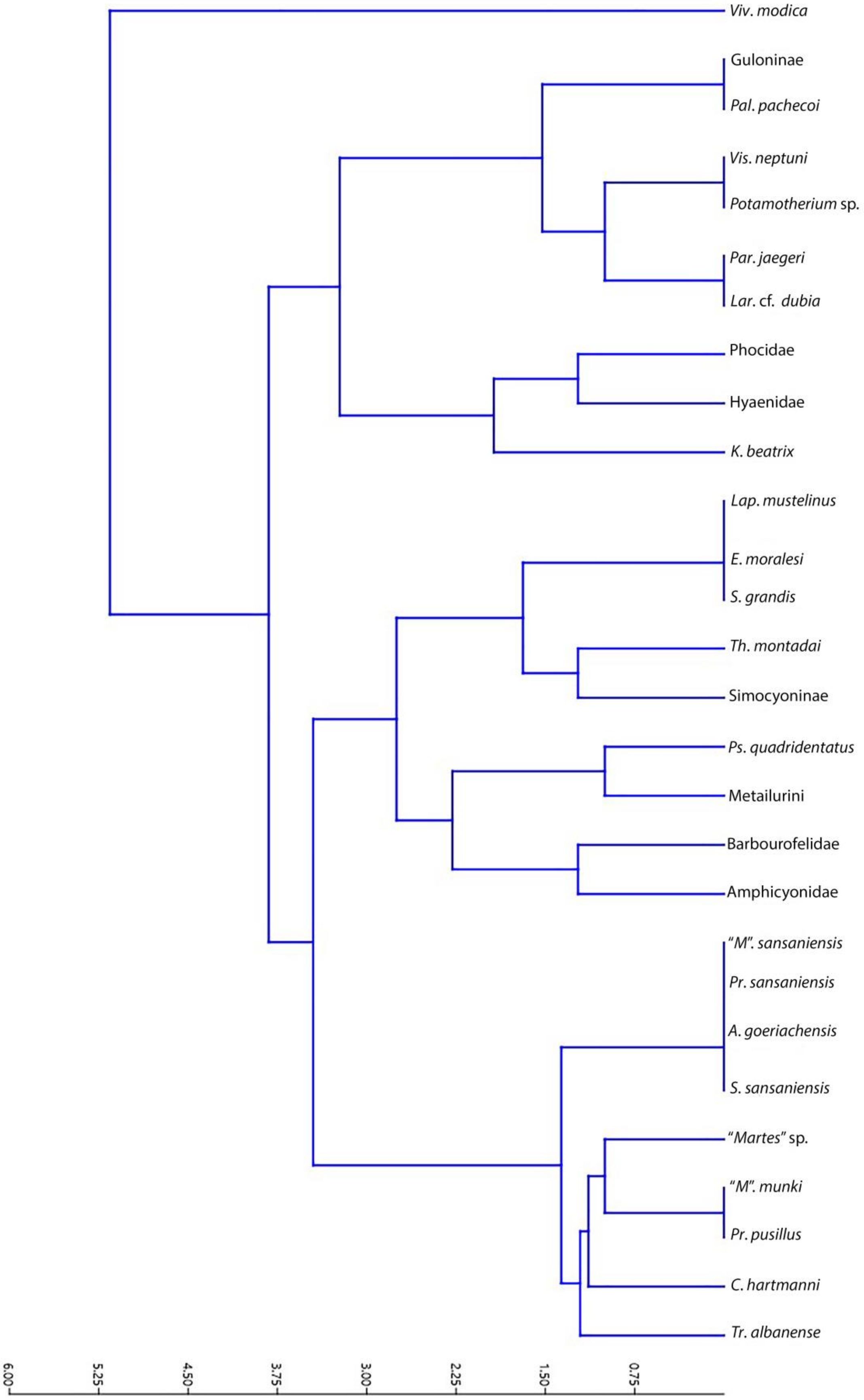


Fig. 6.16: Paired Group (UPGMA) classic clustering of the Hammerschmiede carnivorans based on their palaeoecological characteristics.

Another way to depict the same aspect is XY plots using body mass in the x-axis, dietary habits in the y-axis and presenting the different locomotor lifestyles by using different symbols. This method was preferred from the commonly used 3D graphs, because it is easier to be investigated. Again, the plot was made for Hammerschmiede, HAM 4 and HAM 5.

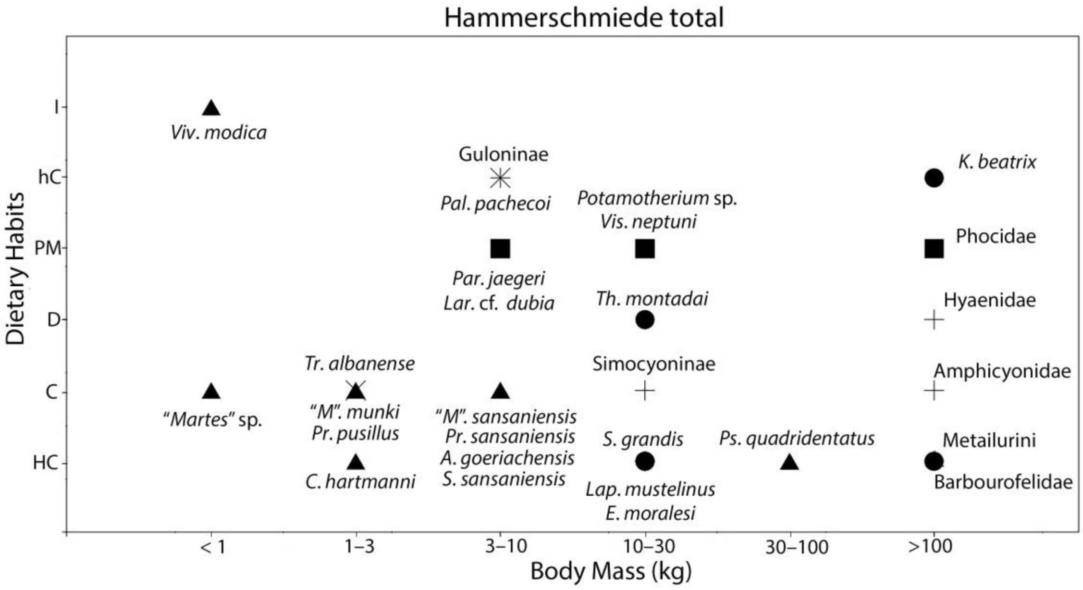


Fig. 6.17: XY plot depicting the palaeoecological comparison between the carnivorans of Hammerschmiede. Symbols: triangle – scansorial; square – semi-aquatic; circle – generalized terrestrial; X – semi-fossorial; + – unknown.

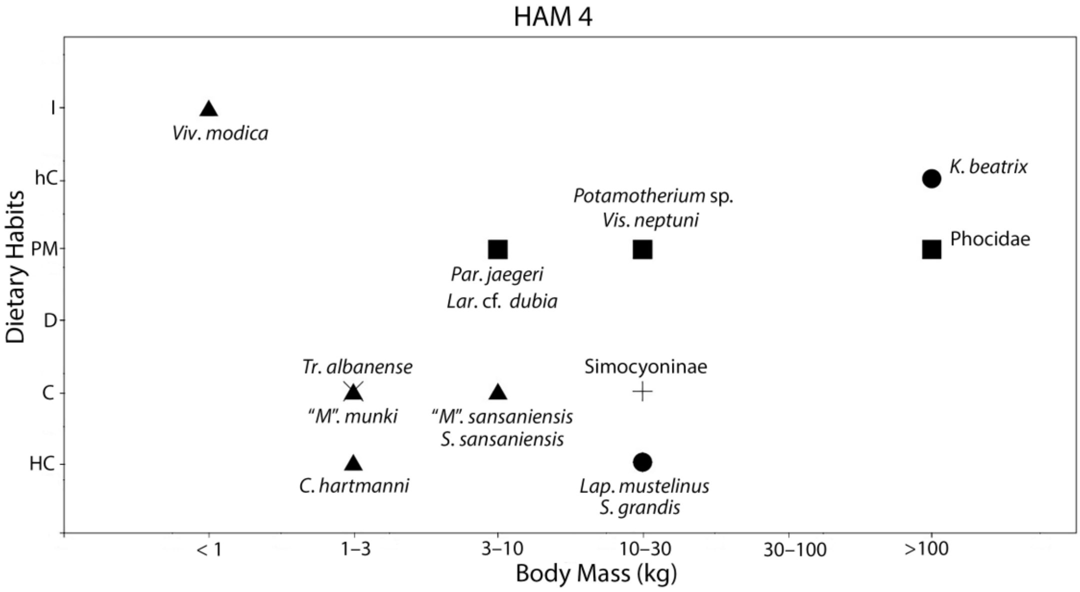


Fig. 6.18: XY plot depicting the palaeoecological comparison between the carnivorans of HAM 4. Symbols: triangle – scansorial; square – semi-aquatic; circle – generalized terrestrial; X – semi-fossorial; + – unknown.

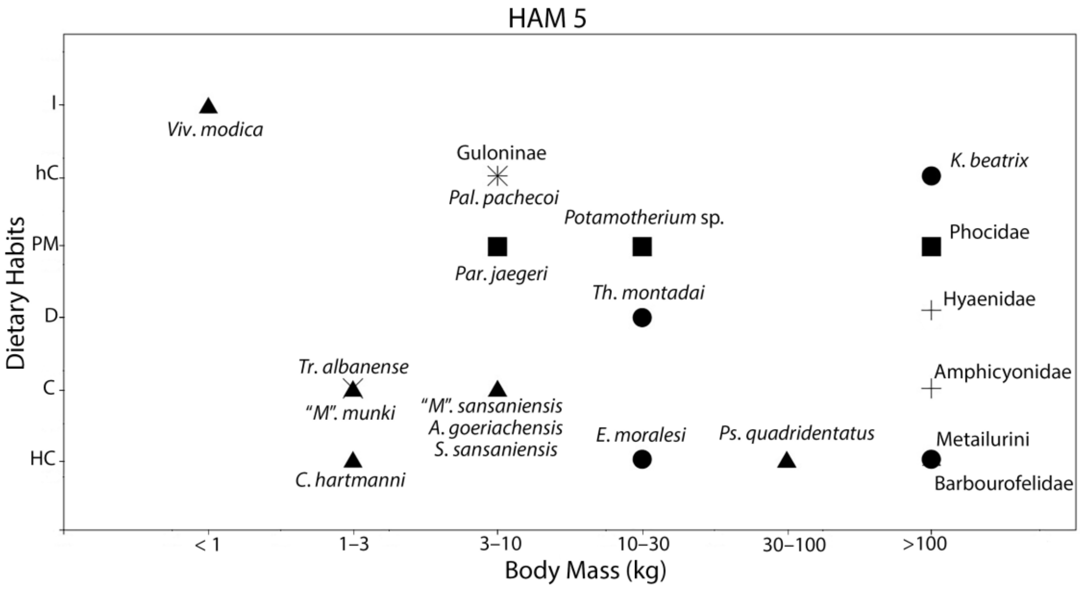


Fig. 6.19: XY plot depicting the palaeoecological comparison between the carnivorans of HAM 5. Symbols: triangle – scansorial; square – semi-aquatic; circle – generalized terrestrial; X – semi-fossorial; + – unknown.

The Figs. 6.17–6.19 depict that despite the exceptionally high number of carnivoran species in the locality, the case in which competition could have been possible are relatively rare. In other words, Hammerschmiede offers a remarkable case for niche partitioning inside the carnivoran guild. The overlapping cases that could have led to competition are discussed in detail below:

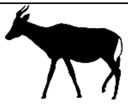
- The semi-aquatic species form two pairs of similar forms: *Paralutra-Lartetictis* and *Vishnuonyx-Potamotherium*. More interestingly, all four species are present in the HAM 4 layer. The competitive exclusion of *Paralutra* and *Lartetictis* has been considered reasonable by some authors, based on their rare coexistence (Willemsen, 1992; Heizmann & Morlo, 1998; Valenciano et al. 2020b). However, as also stated in Kargopoulos et al. (In Press), their coexistence apparently was possible, if the ecosystem resources were sufficient for them. Something similar can be deduced for the latter pair of similar otter-like species. The high number of fish species with size-ranges between 5 and 130 cm total body length (pers. comm. M. Böhme) in Hammerschmiede and the abundance of bivalves support this suggestion.
- The barbourofelid, the member of Metailurini and *Pseudaelurus* are also closely placed. The latter differs from the other two in the smaller size. The other two feliforms are differentiated in the more derived sabertooth features of the barbourofelid. This means that this form was focusing more on larger prey, without using the neighboring trees as a hunting terrain. On the contrary, the metailurine was more agile and was able to use the trees and was probably focusing on medium-sized prey. A similar coexistence case can be found in Pikermi with "*Metailurus parvulus*", *Metailurus major*, *Paramachairodus orientalis* and *Amphimachairodus giganteus*.
- *Palaeomeles* and the undetermined gulonine are also similar and they coexist in HAM 5. However, the opportunistic foraging of the hypocarnivorous species creates more feeding choices and, consequently, reduces the risk of

competition for the same resources. Therefore, even though these species most probably covered a similar niche, they didn't compete, because the ecosystem can easily support two small-/medium-sized carnivoran species. Something similar can be seen today with *Meles* and *Nyctereutes*. Nevertheless, both species are relatively rare in the locality.

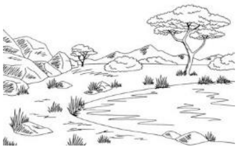
- Another case of rare overlapping species is that of *Laphyctis* and *Semigenetta grandis* in HAM 5. It is possible that these two species didn't act only as hypercarnivorous predators, but also as scavengers, similar to the extant *Gulo* and *Canis* respectively. In this sense, these forms can be seen as the replacements of the durophagous species seen in HAM 5. The high diversity of the Hammerschmiede ecosystem would inevitably result to a considerable amount of available carcasses, so the presence of scavengers is expected.
- Perhaps the clearest case of competition in the locality is that of "*M*". *sansaniensis* and *S. sansaniensis*, which is enhanced by *A. goeriachensis* in HAM 5. These species cover the niche of scansorial opportunistic carnivores of 3–10 kg. Based on the details of their dentition there is a gradient that slightly differentiates them: (a) *Alopecocyon* has an elongated m2 and M2 present, (b) "*Martes*" exhibits a typical gulonine morphology and (c) *S. sansaniensis* presents less-developed m1 talonid, m2 and M1. Therefore, *Alopecocyon* can be seen as the most hypocarnivorous of these three species, *Semigenetta* as the most hypercarnivorous and "*Martes*" covering an intermediate position. This differentiation perhaps could have been chaperoned by different activity patterns. For example, the extant martens and genets are nocturnal, while the red panda is diurnal.

Consequently, even though there are some cases of possible competition between the discovered carnivorans, nearly all of them can be explained by taking a closer look to their specific characteristics. Otherwise, it is highly possible that the abundance and variability of the resources of the locality must have been a critical factor that enabled the coexistence of so many species.

All the information that have been discovered for each species are demonstrated in the following species profiles:

Species **Amphicyonidae indet.**	*Family* Amphicyonidae	*Suborder* Caniformia
Range: Unknown	Hammerschmiede: HAM 1 & HAM 6	
Body Mass >100 kg	*Body Plan* 	*Locomotion* Unknown
Diet:	     	
Possible Competitors: Hyaenidae indet., Barbourofelidae indet.		

<table>
<tr><td colspan="2">Species
Kretzoiarctos beatrix</td><td>Family
Ursidae</td><td>Suborder
Caniformia</td></tr>
<tr><td colspan="2">Range: MN7/8 of Europe</td><td colspan="2">Hammerschmiede: HAM 4 & HAM 5</td></tr>
<tr><td>Body Mass
>100 kg</td><td>Body Plan

(Possibly)</td><td colspan="2">Locomotion

Generalized Terrestrial</td></tr>
<tr><td colspan="4">Diet: </td></tr>
<tr><td colspan="4">Possible Competitors: Amphicyonidae indet. (?)</td></tr>
</table>

<table>
<tr><td colspan="2">Species
Phocidae indet.</td><td>Family
Phocidae</td><td>Suborder
Caniformia</td></tr>
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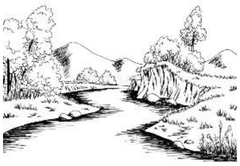
Semi-aquatic</td></tr>
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“Martes” sansaniensis</td><td>Family
Mustelidae</td><td>Suborder
Caniformia</td></tr>
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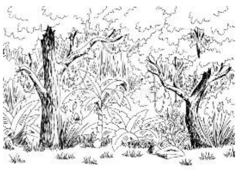
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“*Martes*” cf. *munki*</td><td>*Family*
Mustelidae</td><td>*Suborder*
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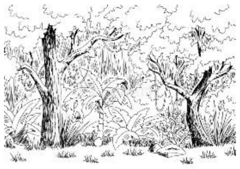
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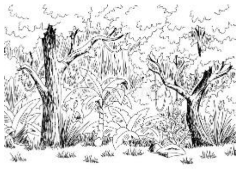
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Mustelidae</td><td>*Suborder*
Caniformia</td></tr>
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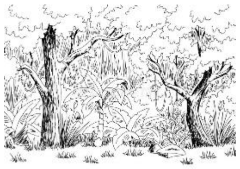
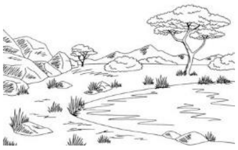
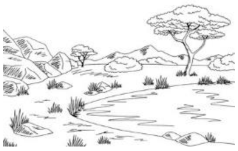
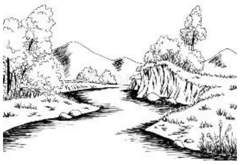
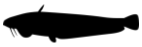
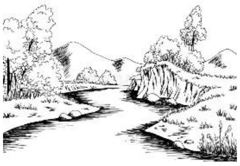
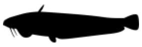
<tr><td>*Body Mass*
1–3 kg</td><td colspan="2">*Body Plan*
</td><td>*Locomotion*

Scansorial (?)</td></tr>
<tr><td>Diet:</td><td colspan="3"></td></tr>
<tr><td colspan="4">Possible Competitors: *Semigenetta sansaniensis* (?)</td></tr>
</table>

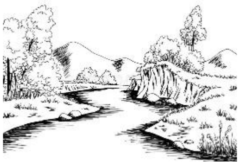
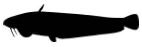
Species **Laphyctis mustelinus**	*Family* Mustelidae	*Suborder* Caniformia
Range: MN 7/8 of Europe	Hammerschmiede: HAM 4	
Body Mass 10–30 kg	*Body Plan* 	*Locomotion*  Generalized Terrestrial
Diet:		
Possible Competitors: *Semigenetta grandis*		

Species **Guloninae indet.**	*Family* Mustelidae	*Suborder* Caniformia
Range: Unknown	Hammerschmiede: HAM 5	
Body Mass 3–10 kg	*Body Plan* Unknown	*Locomotion* Unknown
Diet:		
Possible Competitors: *Palaeomeles pachecoi*		

Species ***Eomellivora moralesi***	*Family* Mustelidae	*Suborder* Caniformia
Range: MN 7/8 of Europe	Hammerschmiede: HAM 5	
Body Mass 10–30 kg	*Body Plan* 	*Locomotion*  Generalized Terrestrial
Diet:		
Possible Competitors: *Thalassictis montadai* (?)		

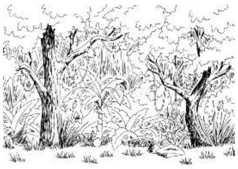
Species ***Vishnuonyx neptuni***	*Family* Mustelidae	*Suborder* Caniformia
Range: MN 7/8 of Europe	Hammerschmiede: HAM 4	
Body Mass	*Body Plan*	*Locomotion*
10–30 kg		 Semi-aquatic
Diet:	  	
Possible Competitors: *Potamotherium* sp., Phocidae indet.		

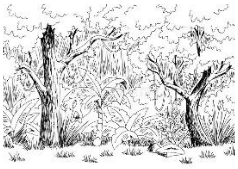
Species ***Paralutra jaegeri***	*Family* Mustelidae	*Suborder* Caniformia
Range: MN 4 to MN 9 of Europe	Hammerschmiede: HAM 4 & HAM 5	
Body Mass	*Body Plan*	*Locomotion*
3–10 kg		 Semi-aquatic
Diet:	  	
Possible Competitors: *Lartetictis* cf. *dubia*		

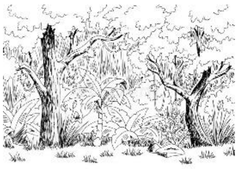
Species ***Lartetictis* cf. *dubia***	*Family* Mustelidae	*Suborder* Caniformia
Range: MN 5 to MN 7/8 of Europe	Hammerschmiede: HAM 4	
Body Mass	*Body Plan*	*Locomotion*
3–10 kg		 Semi-aquatic
Diet:	  	
Possible Competitors: *Paralutra jaegeri*		

Species ***Trocharion albanense***	*Family* Mustelidae	*Suborder* Caniformia
Range: MN 5 to MN 9 of Europe	Hammerschmiede: HAM 4 & HAM 5	
Body Mass 1–3 kg	*Body Plan* Unknown	*Locomotion*  Semi-fossorial
Diet:		
Possible Competitors: *Palaeomeles pachecoi* (?), Guloninae indet. (?)		

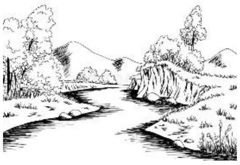
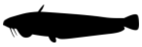
Species ***Palaeomeles pachecoi***	*Family* Mephitidae	*Suborder* Caniformia
Range: MN 7/8 to MN 9 of Europe	Hammerschmiede: HAM 5	
Body Mass 3–10 kg	*Body Plan* 	*Locomotion*  Semi-fossorial
Diet:		
Possible Competitors: Guloninae indet., *Trocharion albanense* (?)		

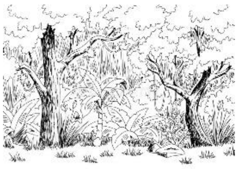
Species ***Proputorius sansaniensis***	*Family* Mephitidae	*Suborder* Caniformia
Range: MN 5 to MN 7/8 of Europe	Hammerschmiede: HAM 1 & HAM 5	
Body Mass 3–10 kg	*Body Plan* 	*Locomotion*  Scansorial
Diet:		
Possible Competitors: *Semigenetta sansaniensis*, *Alopecocyon goeriachensis*, "*Martes*" *sansaniensis*		

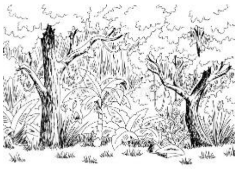
Species ***Proputorius pusillus***	*Family* Mephitidae	*Suborder* Caniformia
Range: MN 5 to MN 7/8 of Europe	Hammerschmiede: HAM 1	
Body Mass 1–3 kg	*Body Plan* 	*Locomotion*  Scansorial
Diet:		
Possible Competitors: “*Martes*” cf. *munki*		

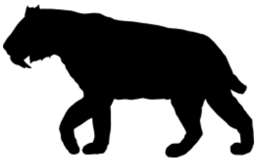
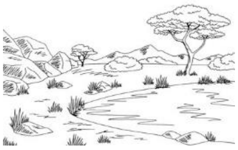
Species ***Alopecocyon goeriachensis***	*Family* Ailuridae	*Suborder* Caniformia
Range: MN 5 to MN 7/8 of Europe	Hammerschmiede: HAM 5	
Body Mass 3–10 kg	*Body Plan* 	*Locomotion*  Scansorial
Diet:		
Possible Competitors: *Semigenetta sansaniensis*, *Alopecocyon goeriachensis*, “*Martes*” *sansaniensis*		

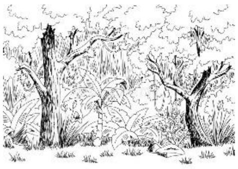
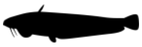
Species **Simocyoninae indet.**	*Family* Ailuridae	*Suborder* Caniformia
Range: Unknown	Hammerschmiede: HAM 4	
Body Mass 10–30 kg	*Body Plan* Unknown	*Locomotion* Unknown
Diet:		
Possible Competitors: “*Martes*” cf. *munki*		

Species ***Potamotherium* sp.**	*Family* indet.	*Suborder* Caniformia
Range: MP 28 to MN 7/8 of Europe	Hammerschmiede: HAM 4 & HAM 5	
Body Mass 10–30 kg	*Body Plan* 	*Locomotion*  Semi-aquatic
Diet:	  	
Possible Competitors: *Vishnuonyx neptuni*, Phocidae indet.		

Species ***Pseudaelurus quadridentatus***	*Family* Felidae	*Suborder* Feliformia
Range: MN 6 to MN 9 of Eurasia	Hammerschmiede: HAM 5	
Body Mass 30–100 kg	*Body Plan* 	*Locomotion*  Scansorial
Diet:	   	
Possible Competitors: Metailurini indet.		

Species **Metailurini indet.**	*Family* Felidae	*Suborder* Feliformia
Range: Unknown	Hammerschmiede: HAM 5	
Body Mass 30–100 kg	*Body Plan* 	*Locomotion*  Scansorial
Diet:	   	
Possible Competitors: *Pseudaelurus quadridentatus*		

Species **Barbourofelidae indet.**	*Family* Barbourofelidae	*Suborder* Feliformia
Range: Unknown	Hammerschmiede: HAM 5	
Body Mass 30–100 kg	*Body Plan* 	*Locomotion*  Generalized Terrestrial (?)
Diet:	  	
Possible Competitors: Metailurini indet., Amphicyonidae indet.		

Species ***Semigenetta sansaniensis***	*Family* Viverridae	*Suborder* Feliformia
Range: MN 4 to MN 10 of Europe	Hammerschmiede: HAM 1, HAM 4 & HAM 5	
Body Mass 3–10 kg	*Body Plan* 	*Locomotion*  Scansorial
Diet:	    	
Possible Competitors: *Semigenetta sansaniensis*, *Alopecocyon goeriachensis*, “*Martes*” *sansaniensis*		

Species ***Semigenetta grandis***	*Family* Viverridae	*Suborder* Feliformia
Range: MN 7/8 to MN 9 of Europe	Hammerschmiede: HAM 4	
Body Mass 10–30 kg	*Body Plan* Unknown	*Locomotion* Unknown
Diet:	  	
Possible Competitors: *Laphyctis mustelinus* (?)		

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Viverrictis modica</td><td>Family
Viverridae</td><td>Suborder
Feliformia</td></tr>
<tr><td colspan="2">Range: MN 7/8 of Europe</td><td colspan="2">Hammerschmiede: HAM 4 & HAM 5</td></tr>
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10–30 kg</td><td>Body Plan
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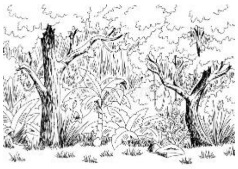
Scansorial</td></tr>
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Thalassictis montadai</td><td>Family
Hyaenidae</td><td>Suborder
Feliformia</td></tr>
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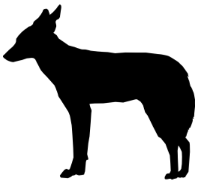
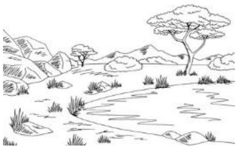
<tr><td>Body Mass
10–30 kg</td><td>Body Plan
</td><td colspan="2">Locomotion

Generalized Terrestrial (?)</td></tr>
<tr><td>Diet:</td><td colspan="3"></td></tr>
<tr><td colspan="4">Possible Competitors: Eomellivora moralesi (?)</td></tr>
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<table>
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Hyaenidae indet.</td><td>Family
Hyaenidae</td><td>Suborder
Feliformia</td></tr>
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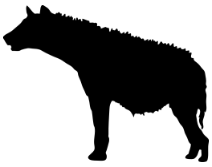</td><td colspan="2">Locomotion
Unknown</td></tr>
<tr><td>Diet:</td><td colspan="3"></td></tr>
<tr><td colspan="4">Possible Competitors: Amphicyonidae indet., Barbourofelidae indet.</td></tr>
</table>

Conclusions

The carnivoran guild of Hammerschmiede has been found to include an exceptional diversity of different forms. The discovered 28 species are: Amphicyonidae indet. (at least 1 species), *Kretzoiarctos beatrix*, Phocidae indet. (at least 1 species), “*Martes*” *sansaniensis*, “*Martes*” cf. *munki*, “*Martes*” sp., *Circamustela hartmanni* (new species), *Laphyctis mustelinus*, Guloninae indet. (1 species), *Eomellivora moralesi*, *Vishnuonyx neptuni* (new species), *Paralutra jaegeri*, *Lartetictis* cf. *dubia*, *Trocharion albanense*, *Palaeomeles pachecoi*, *Proputorius sansaniensis*, *Proputorius pusillus*, *Alopecocyon goeriachensis*, Simocyoninae indet. (1 species), *Potamotherium* sp., *Semigenetta sansaniensis*, *Semigenetta grandis*, *Viverrictis modica*, *Pseudaelurus quadridentatus*, Metailurini indet. (1 species), Barbourofelidae indet. (1 species), *Thalassictis montadai* and Hyaenidae indet. (1 species). This long list makes the locality the third most speciose in the Miocene of Europe, exhibiting significantly high rarefaction curves, given the relatively low number of specimens.

The locality consists of the FOD for 2 genera (*Circamustela* and *Eomellivora*) and two species (*Semigenetta grandis* and *Eomellivora moralesi*), as well as the LOD for 6 genera (*Laphyctis*, *Lartetictis*, *Proputorius*, *Alopecocyon*, *Potamotherium* and *Viverrictis*) and 7 species (“*Martes*” *sansaniensis*, *Laphyctis mustelinus*, *Lartetictis dubia*, *Proputorius sansaniensis*, *Proputorius pusillus*, *Alopecocyon goeriachensis* and *Viverrictis modica*). Therefore, the Aragonian influence is stronger than the Vallesian one in the current guild. The abundance and diversity profiles of the locality and the two main layers don’t resemble any of the well-known Middle and Late Miocene localities of Europe.

Most of the carnivorans are small- to medium-sized scansorial opportunists or semi-aquatic piscivores/mollusk-eaters. This conforms to the forested river environment that has been proposed for the locality. Most of the species occupy distinct ecological niches avoiding competition, despite the high diversity. The HAM 5 layer has yielded more carnivoran species, including several large-sized forms that are for the time being absent in HAM 4, indicating possible taphonomic differences between the two layers.

Future Objectives

The present Thesis has covered several aspects of the taxonomy, biostratigraphy, palaeogeography and palaeoecology of the discovered carnivorans. However, there are still several interesting tasks that can be completed in the future:

- Despite the considerable amount of papers that have been published the past 50 years for Hammerschmiede, there are still many questions about this locality. Several taxa have not been published yet, while a detailed study on the taphonomy of the locality and the environmental conditions during that time are still unknown.
- The excavations in the main layers must continue, in order to recover more material of the enigmatic forms of the guild, such as the amphicyonid, the large metailurine and the barbourofelid.
- Since, no taxon was found to be similar to the unidentified gulonine, it is possible that new material will support the erection of a new taxon for this form.
- More material of *Lartetictis* may reveal that this form must belong to a new species. The already pointed small size and mixed characteristics between *L. dubia* and *L. pasalarensis*, together with the fact that Hammerschmiede is the LOD for the genus point towards this direction.
- The excellent skull of “*Martes*” *sansaniensis* can be invaluable for the review of this lineage and its relationship to the extant martens. Additionally, it can provide a reliable endocast of the brain of the species, enabling a paper on this topic.
- The coprolite record and the bite marks that have been discovered in several specimens in the locality can be studied in more detail.
- The guild analysis can be combined to more data from other Miocene localities of Europe and be published, when a more complete view of the enigmatic forms has been established.

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