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Research Paper

The carnivoran guilds from the Late Miocene hominid locality of Hammerschmiede (Bavaria, Germany) ☆

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ABSTRACT

The Late Miocene locality of Hammerschmiede has yielded an astonishing diversity of vertebrates, including 28 different carnivoran species. The main layers HAM 5 (11.62 Ma) and HAM 4 (11.44 Ma) have been found to host 21 and 17 carnivoran species, respectively. Herein we perform a guild structure analysis aiming to unravel their ecomorphological role. A rarefaction analysis showed that such a high representation of carnivorans is comparable only to the fissure fillings of La-Grive-Saint-Alban. The First and Last Occurrence Dates of several genera and species are reported in the locality. The profile of the locality concerning the Numbers of Species and Individuals per family is unique among the Miocene localities of Europe. The discovered carnivorans were attributed to palaeoecological categories based on their body mass, locomotor pattern, and diet preferences. Ecomorphological comparison revealed that most species were able to reduce competition by occupying different ecological niches, but some cases of ecological overlap were found. This shows that the ecosystem of Hammerschmiede offered diverse resources that allowed the subsistence of a plethora of carnivorans. Finally, the two main layers exhibit some differences in their carnivoran components, with HAM 4 dominated by small-/medium-sized piscivores/generalist carnivores, whereas HAM 5 also includes large-sized durophagous/hypercarnivorous forms.

1. Introduction

The locality of Hammerschmiede is situated in the southwestern part of Bavaria (Germany), near the town of Pforzen. Since the works concerning the fauna of Hammerschmiede by Fahlbusch and Mayr (1975) and Mayr and Fahlbusch (1975), many vertebrates have been discovered in the locality, including mammals, birds, reptiles, amphibians and fish. The centrepiece of the Hammerschmiede fauna is *Danuvius guggenmosi*, a hominid that shows locomotor patterns that include bipedalism (Böhme et al., 2019, 2020). Concerning the carnivorans of the locality, the first reports come from Mayr and Fahlbusch (1975), followed by preliminary faunal lists by Kirscher et al. (2016) and Böhme et al. (2019). Recent studies of the carnivoran material revealed an astonishing diversity of different forms (Kargopoulos, 2022; Kargopoulos et al., 2021a, 2021b, 2022a, 2022b, under review). Such a rich assemblage offers the great opportunity to study the carnivoran guild of the locality as a whole and to discuss its importance for the faunal transition from the Middle to the Late Miocene in Europe.

The purpose of the present study is to provide a preliminary analysis of the carnivoran guilds of Hammerschmiede, in order to contribute to the bigger picture of the ecosystems of the locality. The carnivoran component of Hammerschmiede is compared to

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that of other localities from the Miocene of Europe to reveal its particular characteristics.

2. Material and methods

2.1. Material

The material studied herein 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 and Fahlbusch (1975) and it is hosted in the collections of SNSB-BSPG (Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany). The material from HAM 4 and HAM 5 comes from the excavations organized by the Eberhard Karls University of Tübingen. Finally, the material from HAM 6 comes from private collections. The specimens from HAM 4, HAM 5 and HAM 6 is currently at GPIT (Paleontological Collection of the University of Tübingen, Germany).

The total number of the studied specimens is 367 for all three layers (HAM 1: 13; HAM 4: 171; HAM 5: 181; HAM 6: 2). A very large percentage of the material is identified as "Carnivora indet." and 124 specimens (34%) were identified at genus- or species-level. This has happened because of two main reasons. First, most of the material is at least partially damaged. Especially the postcranial material is primarily broken and deformed, due to taphonomic or excavation/preparation effects. This made the identification in a lower taxonomic level impossible. Additionally, the discovered craniodental specimens uncovered an extraordinary diversity of carnivorans (especially of small size) in the locality. Even though this made the study of these remains 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 was not possible to attribute it to a particular species. A similar problem was faced concerning the isolated incisors and canines. Finally, adding to this problematic situation was the fact that several forms are known only from dental specimens in the literature and their postcranial morphology is not known. In general, 59% of the material includes teeth or jaws and 41% postcranial elements. In HAM 4, the postcranial elements were slightly more frequent (44%) in comparison to HAM 5 (41%), whereas the specimens from HAM 1 and HAM 6 are exclusively dental.

2.2. Methods

The Species Diversity of the Hammerschmiede guild was estimated using Individual Rarefaction analysis in comparison to the data for Eppelsheim and Dorn-Dürkheim 1 (Germany; Morlo et al., 2022), Rudabánya (Hungary; Werdelin, 2005; Kargopoulos et al., 2022b), Wintershof-West (Germany; Dehm, 1950), Steinheim (Germany; Helbing, 1936; Heizmann, 1973; Morlo et al., 2020), La Grive-Saint Alban (France; Viret, 1951) and Sansan (France; Ginsburg, 1961a; Peigné, 2012). Despite the fact that the localities of Can Ponsic and Can Llobateres (Spain) were included in the other analyses of this article, they were not added to this particular analysis, because the exact number of specimens per species remains unclear for these localities. The analysis was performed using Species Richness and Shannon Index. The only deviation from the use of rarefaction by Morlo et al. (2022) 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 (such as similar ecosystems, similar sampling methods, similar means of chronology, similar taphonomic conditions, and homogenous distribution of the species; e.g., Chao et al. 2020, for sampling inconsistences). 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 at three levels: (*i*) including all the aforementioned localities, (*ii*) including all the aforementioned localities but excluding Wintershof-West because of the very high number of specimens, and (*iii*) including only Hammerschmiede, Rudabánya and Steinheim (since the material from Eppelsheim and La Grive-Saint-Alban is considered to be a mixture from several stratigraphic intervals spanning over considerable time; Mein and Ginsburg, 2002; Böhme et al., 2012).

The guild analysis was approached based on three palaeoecological parameters: body mass, locomotor pattern, and dietary preference. The differentiation of the categories of each parameter is based mostly on Morlo et al. (2010), Kargopoulos (2019) and references therein, and a more detailed discussion is held in a non-quantitative frame. Body Mass groups include the following six categories: < 1 kg, 1–3 kg, 3–10 kg, 10–30 kg, 30–100 kg, and >100 kg. Locomotor Pattern is divided into the following six groups: Generalized Terrestrial (GT), Semi-aquatic (SA), Semi-fossorial (SF), Scansorial (Sc), Arboreal (Ar), and Cursorial (Cu). Finally, Dietary Preference includes the seven following categories: Hypercarnivorous (HC), Carnivorous (C), Durophagous (D), Piscivorous/Mollusc-eater (PM), Hypocarnivorous (hC), Insectivorous (I), and Herbivorous (He). Attributions to these categories for the small-sized carnivorans taxa follow Kargopoulos et al. (2022b). The remaining forms are discussed in more detail herein.

The discovered species were plotted in biplots of the body mass category (x-axis) and dietary preferences (y-axis) including the locomotor pattern (different symbols) for Hammerschmiede, HAM 4 and HAM 5, in order to depict the niche partitioning between carnivoran species.

3. Results

3.1. Attribution to ecomorphological categories

The small carnivorans of Hammerschmiede have already been ascribed to ecomorphological categories in Kargopoulos et al. (2022b). The remaining forms are discussed in more detail herein.

A large amphicyonid has been discovered with one DP4 from HAM 6 and one McIII from the HAM 5 layer. It is difficult to estimate the body mass based on these two specimens. However, the preserved DP4 (length = 13.8 mm; width = 15.5 mm) is similar in length and width 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 Hammerschmiede amphicyonid (total length = 78.2 mm) is longer 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 justified. The metacarpal is relatively short and broad, indicating 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. 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 taxon might have been at least occasionally durophagous.

The diet of the ailuropodine bear *Kretzoiarctos beatrix* is discussed in detail by Kargopoulos et al. (under review), showing that it was an opportunist with occasional consumption of both hard plants and vertebrates. Following the equation of Van Valkenburgh (1990) for the m1 of ursids, the estimated body mass for this species (based on the specimens from Nombrevilla, Abocador de Can Mata and Hammerschmiede) would be approximately 85 kg. However, the dental measurements (length and width) of *Kretzoiarctos* are similar to that of *Ursus arctos arctos* (personal data based on specimens from Bulgaria housed at the NMNHS). This does not 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 tentative attribution to the >100 kg body mass category is considered. Extant bears are able to exhibit a very wide range of locomotor behaviours, 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 the possibility that it could exploit many different parts of the ecosystem.

Some isolated phocid teeth have been found in both HAM 4 and HAM 5 (Kargopoulos, 2022). Unfortunately, the material of this taxon in Hammerschmiede is very restricted. Additionally, the isolated status of the teeth prevents a secure identification of the exact position of the teeth in the toothrow. However, based on dental dimensions (length and width), the specimens are slightly larger than the respective teeth of *Phoca vitulina*. The adult body mass for this species is approximately 100 kg (Walker and Bowen, 1993), so the Hammerschmiede phocid is attributed to the > 100 kg body mass category. Since all phocids are semi-aquatic, it is reasonable to suggest that this form also followed the same lifestyle. Additionally, all extant phocids today are mainly feeding on fish and molluscs. Considering the tooth morphology, the same can be expected for the Hammerschmiede seal. Moreover, 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 molluscs.

The felid *Pseudaelurus quadridentatus* is represented by two teeth and a partial skeleton in the HAM 5 layer. Morlo et al. (2010) placed this species in 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. 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). Like all felids, this form is considered to be a hypercarnivore.

A metailurine cat larger than *Pseudaelurus quadridentatus* is represented by one upper canine from HAM 5. 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 at the transition between two categories. Based on the skull length equation (using the values of *M. major* provided by Roussiakis, 2001), the estimated body mass is approximately 75 kg. Therefore, the 30–100 kg category is herein preferred. This form is larger than *Pseudaelurus quadridentatus*, but 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. As other felids, this form is considered to be hypercarnivorous.

A large barbourofelid is represented by a humerus in HAM 5 (Kargopoulos, 2022) and an upper canine in HAM 4. Morlo et al. (2010) suggested that *Albanosmilus jourdani* should be included in 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 transverse diameter of the diaphysis of the discovered barbourofelid humerus is 66.1 mm, whereas that of *S. palmidens* is 51.7 mm. Therefore, the Hammerschmiede form is larger than the one from Sansan, so the attribution to the *A. jourdani* body mass category (>100 kg) is preferred. Not much can be said about the locomotor pattern of this form. The barbourofelids are mainly considered to be generalized terrestrial carnivorans (Morlo et al., 2010). However, until more material comes to light, it is preferred to retain a doubtful attribution to this category for this taxon. Barbourofelids have developed hypercarnivorous adaptations, such as sabre-canines and serrated teeth.

The remains of *Thalassictis montadai* from HAM 4, HAM 5, and HAM 6 were presented in Kargopoulos (2022) and Kargopoulos et al. (2022a). 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 and Golpe Posse, 1973), the body mass is estimated to the approximately 23 kg. Therefore, this species is attributed to the 10–30 kg category. Viranta and Werdelin (2003) described some postcranial elements of this species from various sites in Sinap (Turkey). They mentioned that the limb bones of this form are stouter than those of *Hyaenictitherium wongii*, noting that there are not 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. 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.

A very large hyaenid has been found in HAM 5, being similar in size (but slightly larger) to *Adcrocuta eximia* (Kargopoulos et al., 2022a). The dimensions of this species are considerably larger than that of the extant *Crocuta crocuta* (Werdelin and Solounias, 1990; Beke, 2010), which ranges from 40 to 80 kg (Hayssen and Noonan, 2021). Therefore, based on the significant difference in I3 dimensions, the Hammerschmiede hyaenid is attributed to the >100 kg body mass category. Since the exact affinities of this form are unknown and there are no postcranial remains from Hammerschmiede that can be attributed to it, its locomotor pattern remains unknown. 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., 2022a).

3.2. Guild diversity

It is clear that the locality of Hammerschmiede has yielded an astonishing variability of carnivoran remains, resulting in a total of 28 different taxa. 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 on findings from 2021. The detailed list of the discovered carnivorans and their distribution among the studied layers is presented in

Table 1
The carnivorans of Hammerschmiede and their distribution in different layers, including number of individuals per layer, estimated body mass (BM), locomotor pattern (LP), and dietary preferences (DP) 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 nov. 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	1		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
Incertae sedis	*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	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**	**17**	**2**			
Number of individuals		**6**	**28**	**32**	**2**			

Table 1. Additionally, the minimum number of individuals (MNI), the estimated body mass group (BM), locomotor pattern (LP), and dietary preference (DP) of each form are given.

The two main layers (HAM 5 and HAM 4) have yielded approximately the same number of individuals (28 and 32 respectively), but HAM 5 has provided more taxa (21 vs. 17). 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 10 (36%) are known from both of them. This is very interesting concerning the biochronology and palaeoecology of some forms. The other two layers (HAM 1 and HAM 6) have only yielded 5 and 2 taxa, respectively. However, the meagre carnivoran record from HAM 1 has been valuable, since it confirmed the presence of two forms that are not present in any of the other three layers: "*Martes*" sp. and *Proputorius pusillus*.

Such a high number of carnivoran species is definitely noteworthy, especially considering that at least 21 of them were syntopic in HAM 5. Table S1 (Appendix A) presents the number of carnivoran species in 53 localities based on the lists presented by Kargopoulos (2022) from the Miocene of Europe, Anatolia, and North Africa. Hammerschmiede appears as the third richest locality in carnivoran species, following only Wintershof-West (30 species) and La Grive-Saint Alban (41 species), which are both fissure fillings. This makes it the richest stratified locality in this region. When the MN zonation is considered as a comparative factor, based on Mein and Ginsburg (2002), the MN 7 fissures from La Grive contain 26 carnivoran species, whereas the MN 8 fissures contain 19, so both stratigraphic intervals are less rich than Hammerschmiede as a whole. A comparable number of carnivorans can also be seen in a handful of localities: Paşalar (n = 27), Vieux-Collonges (n = 25), Can Llobateres 1 (n = 25), Dorn-Dürkheim 1 (n = 23), Artenay (n = 21), and Sansan (n = 21) (see Kargopoulos, 2022 for faunal sources). The other 44 localities (83%) have yielded less than 20 carnivoran species. Of course, some localities (including Hammerschmiede and Sansan) consist of several different layers (e.g., different fluvial channels in Hammerschmiede) and different fissures (as in the case of La Grive-Saint Alban and potentially also for Vieux-Collonges), 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 on our knowledge of the fossil record.

A problem that occurs while comparing the species diversity between two localities is the unequal number of compared specimens. For example, the locality of Wintershof-West (that includes only two more carnivoran species than Hammerschmiede) has yielded almost 2000 carnivoran specimens identified at genus level (Dehm, 1950) in comparison to the 124 specimens from Hammerschmiede. A methodology that has been used in order to overcome this inequality is rarefaction analysis. Fig. 1 and Figs. S1, S2 (Appendix A) depict the interpolated Species Richness and Shannon H index in different sets of localities.

As demonstrated in these figures, the Species Diversity in Hammerschmiede is distinctively higher than that of Steinheim, Rudabánya, Dorn-Dürkheim 1, Eppelsheim, and Sansan. La-Grive-Saint-Alban (despite not including an exceptionally high number of specimens) has yielded many different taxa, because of the lumping of fissures with different ages. 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 from La-Grive, in order to make a more direct comparison in a stratigraphically meaningful way (Mein and Ginsburg, 2002). Finally, Wintershof-West has yielded a tremendous amount of carnivoran specimens (Dehm, 1950), but the Shannon H index is estimated to be lower than

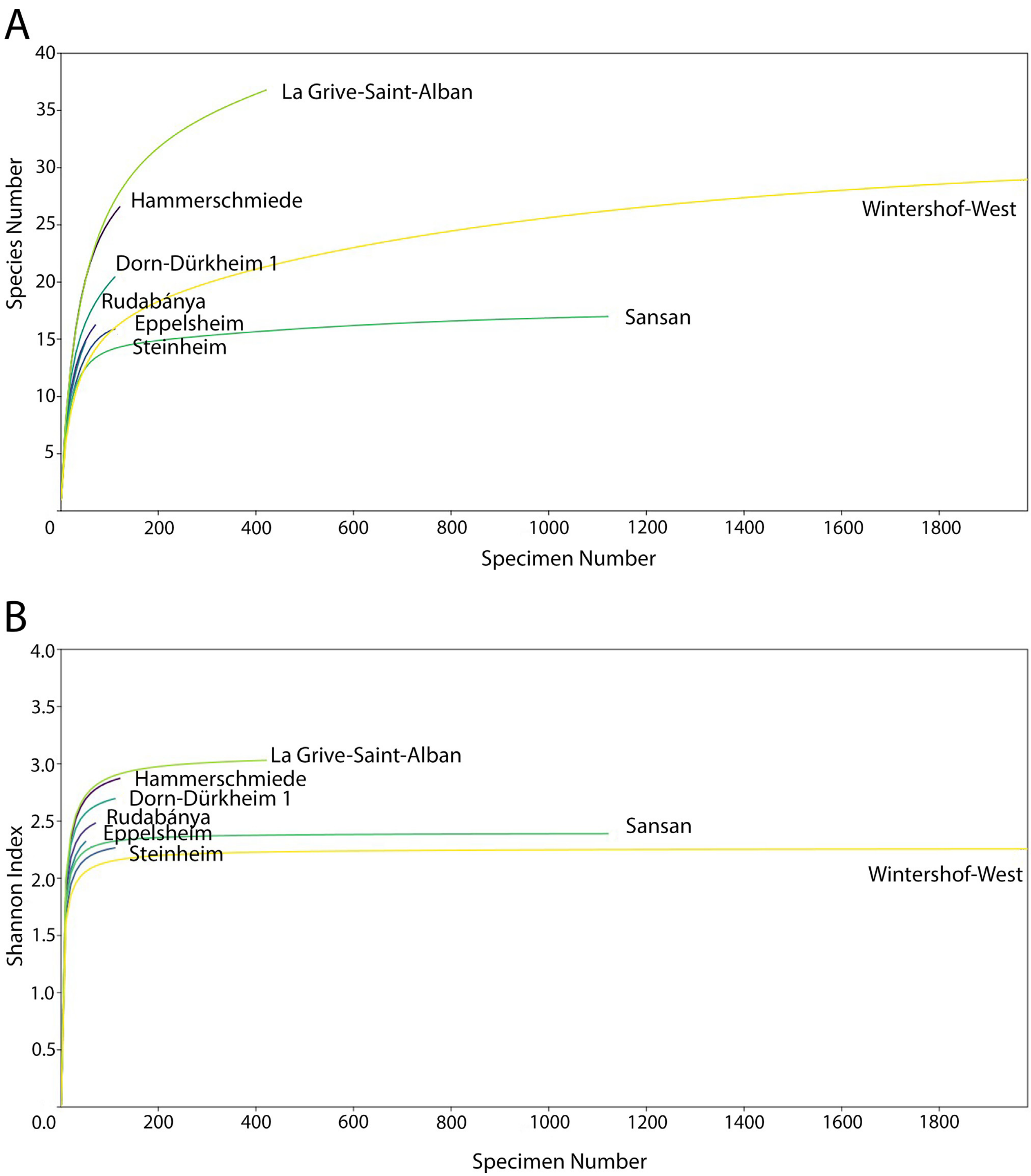

Fig. 1. Individual Rarefaction analyses using Species Richness (**A**) and Shannon H index (**B**) for Hammerschmiede, Steinheim, Eppelsheim, Dorn-Durkheim, Rudabánya, Sansan, La-Grive-Saint-Alban, and Wintershof-West (data from Kargopoulos, 2022 and references therein).

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 is also biased by the stratigraphic mixture of specimens in this locality (Böhme et al., 2012).

4. Discussion

4.1. Biostratigraphy

The locality of Hammerschmiede is (among other reasons) very interesting in terms of age. It is stratigraphically placed at the very base of the Late Miocene (Tortonian; Kirscher et al., 2016). 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, Fig. 2 depicts the range of the discovered carnivorans at the species and genus levels. The carnivorans that have been identified in a taxonomic rank higher than that of the genus are not included in this analysis.

In terms of species, the locality of Hammerschmiede includes two species that have not been reported from any other locality: *Circamustela hartmanni* and *Vishnuonyx neptuni*. Furthermore, the Last Occurrence Dates (LODs) of the following species are reported in Hammerschmiede: "*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 presented herein. Concerning the genera, 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, which agrees with the age of the locality, ca. 0.5 myr before the arrival of hipparionine horses in Europe (Kirscher et al., 2016). However, the coexistence in HAM 4 and HAM 5 of Aragonian and Vallesian taxa 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 age difference of 180 kyr between HAM 4 and HAM 5 (Kirscher et al., 2016) does not provide a key-point on the gradual dominance of the Vallesian forms.

4.2. Guild contents

Pie diagrams were constructed in order to depict the relative diversity and abundance of the discovered families in Hammerschmiede as a whole, in HAM 4 and in HAM 5 (Fig. 3). When observing the relative diversities of the carnivoran families of Hammerschmiede (Fig. 3(A, C, E)), 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 by only 1 species (3%).

As also noted in Table 1, HAM 4 has fewer taxa than HAM 5, which is represented also at the family level. The mustelids make up the majority of discoveries in this layer (8 species; 47%), followed by the viverrids (3 species; 18%), whereas the felids, ursids, phocids, and ailurids are represented by only 1 species (6%) each. HAM 5 includes all the families found in the locality, resulting in a much more complex graph (Fig. 3(E, F)). Again, mustelids are the most diversified family with 7 species (37%), followed by hyaenids and felids (2 species each; 11%), whereas all other families are represented by only one species. Therefore, the common pattern between the three graphs in Fig. 3 involves that mustelids are by far the most diverse family. However, when the relative number of individuals (relative abundance) per family is studied in a similar way, the results are considerably different in the locality as a whole, but also in the two main layers (Fig. 3(B, D, F)).

Concerning the locality as a whole, there are no major differences between the charts of relative diversity and abundance. The main difference concerns the presence of many more individuals of viverrids (12 individuals; 20%). However, 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*. In particular, the relative abundance of viverrids in HAM 4 is the only number that approaches that of mustelids (Fig. 3). The relative abundance and diversity charts of HAM 5 are also similar to each other. The only noteworthy difference is in the higher percentage of mustelids, which could be explained 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. 4 depicts these relationships in some of these localities, based on the carnivoran lists given in Kargopoulos (2022). Comparison of these 6 guilds to that of Hammerschmiede reveals that every locality has its own profile, exhibiting several differences compared to the others. Hammerschmiede includes the phocid and *Potamotherium* (Kargopoulos, 2022; Kargopoulos et al., 2022b), which are absent in the other localities. Sansan (Peigné, 2012) and La-Grive (Viret, 1951) include herpestids and lophocyonids that are not present as a family in Hammerschmiede. The amphicyonids are always present in these localities, even reaching 25% of the guild's species in Steinheim (Morlo et al., 2020). 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 very 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 equally distributed 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 (Robles et al., 2013b). However, despite their presence in Hammerschmiede, they are extremely rare (only two specimens) given the proven richness of the locality. Summarizing, in comparison to these six 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 Mustelidae and Viverridae. These characteristics will be discussed further below.

4.3. Competition

Different approaches have been employed in order to analyse 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

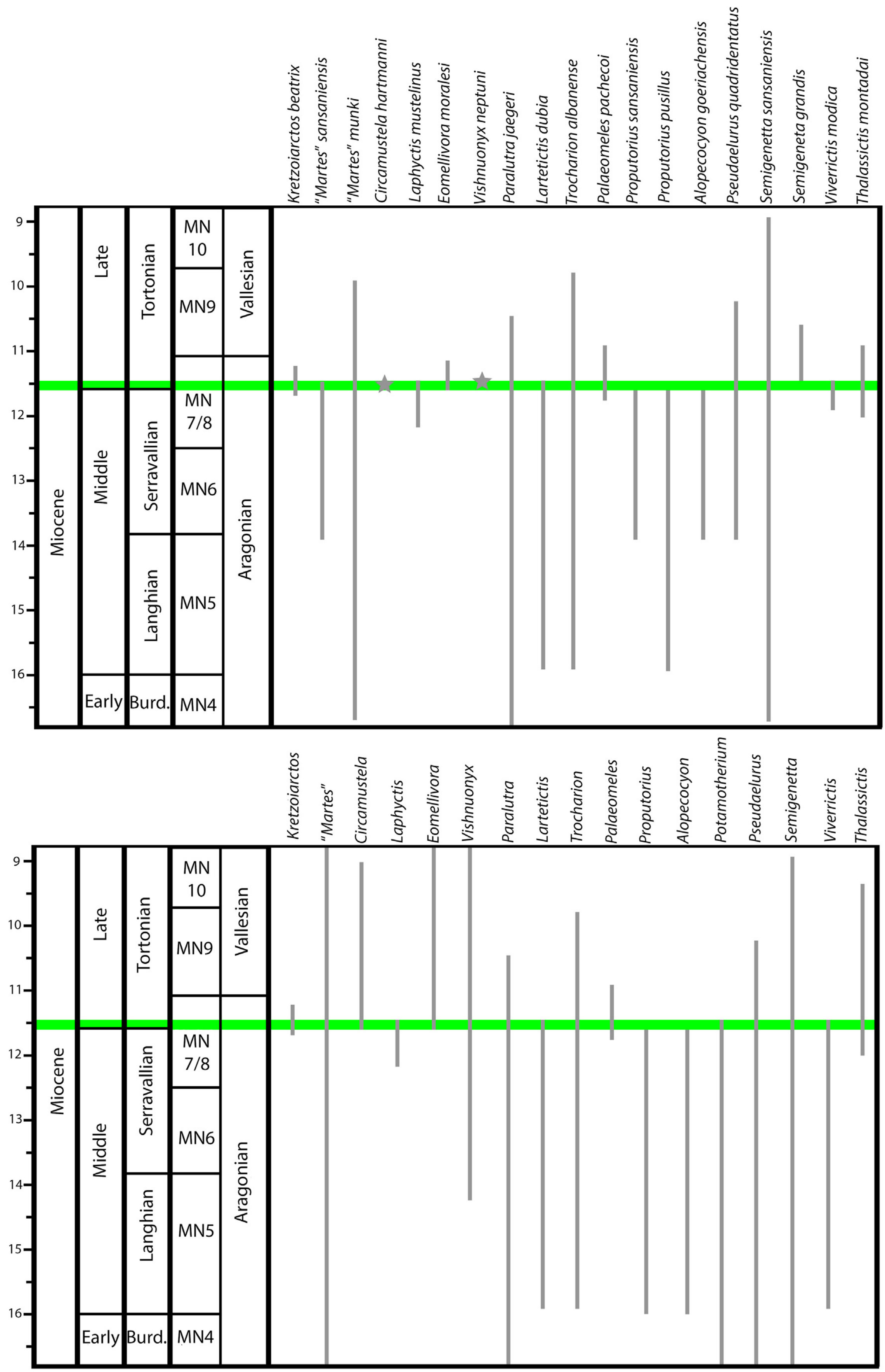

Fig. 2. Biostratigraphic distribution of the carnivoran species and genera found in Hammerschmiede. The green line represents Hammerschmiede. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

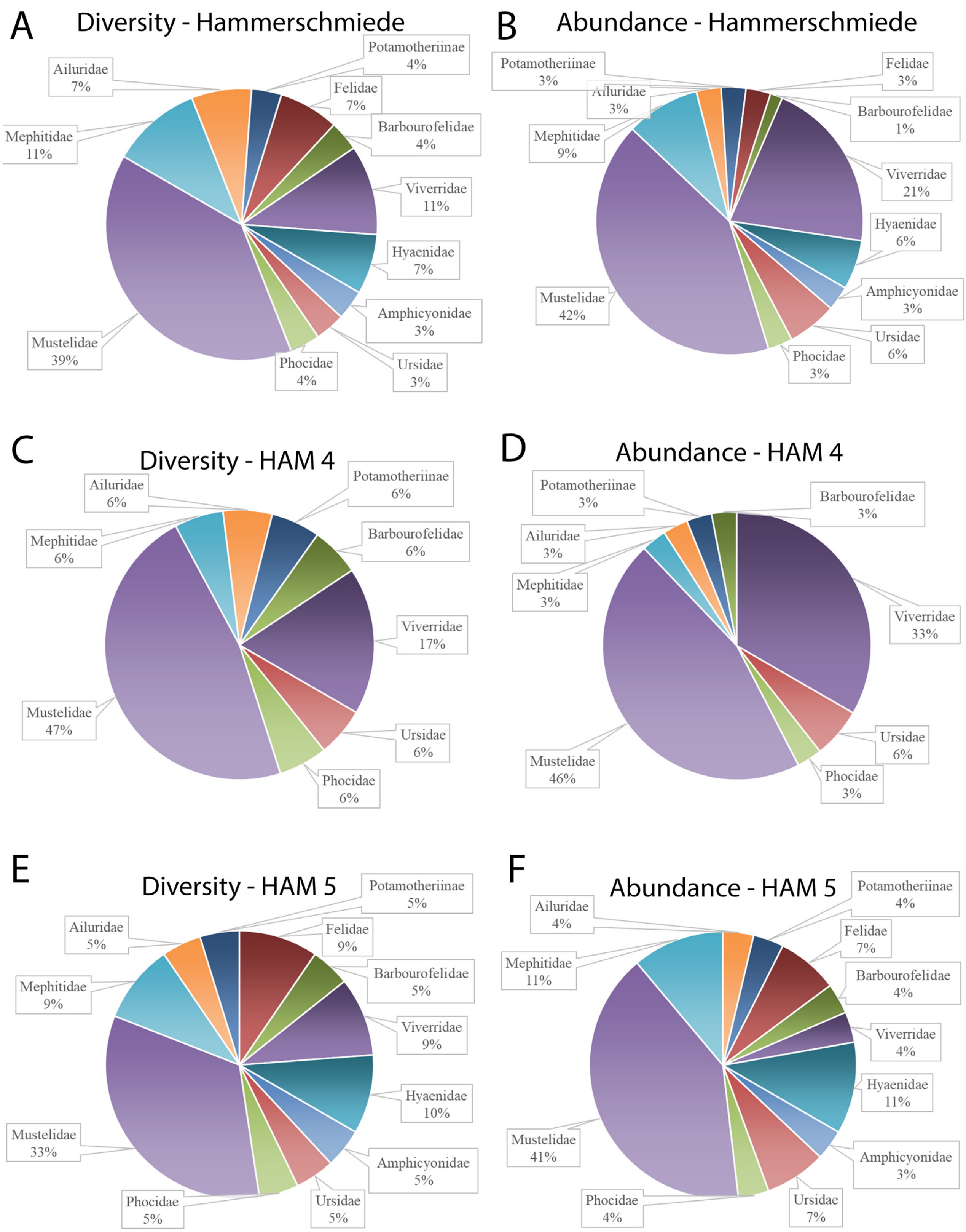

Fig. 3. Relative diversity (**A, C, E**) and abundance (**B, D, F**) of the carnivoran families for Hammerschmiede in total (A, B), HAM 4 (C, D) and HAM 5 (E, F).

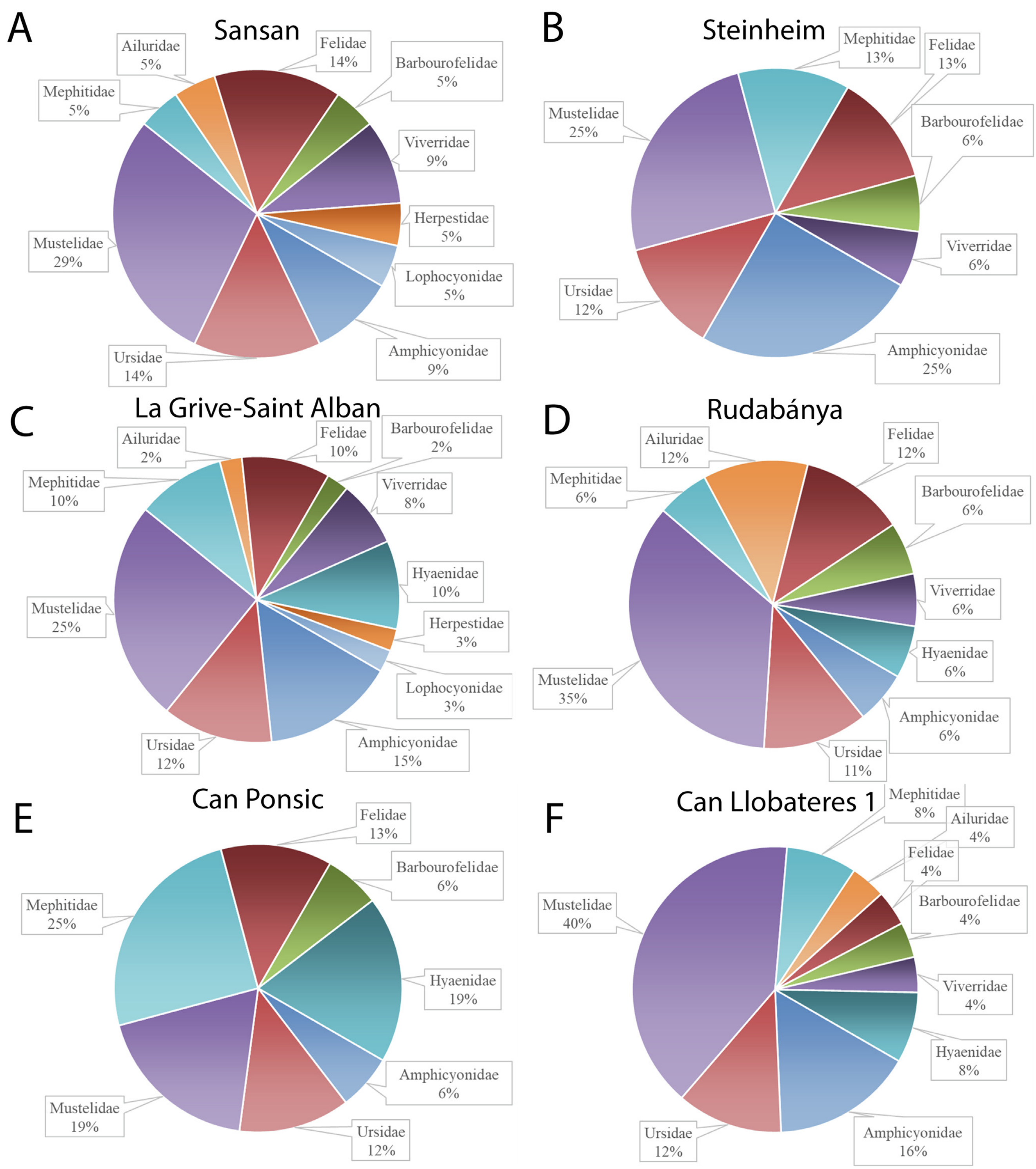

Fig. 4. Relative abundance of the carnivoran families found in Sansan (**A**), Steinheim (**B**), La Grive-Saint Alban (**C**), Rudabánya (**D**), Can Ponsic (**E**), and Can Llobateres 1 (**F**).

for the locality as a whole, as well as for HAM 4 and HAM 5 separately (Fig. 5).

Concerning the body mass, the distribution of the species is resembling an expected normal distribution in its lower values (Fig. 5(A)). 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*, the barbourofelid, and the phocid. Unfortunately, the large forms are known only from fragmentary remains, so their exact taxonomic position remains uncertain. However, if this distribution is not biased, then this difference in the distribution of large carnivorans' between the two main layers surely is a fact that needs to be investigated in further detail.

Concerning dietary preferences, most species are carnivorous or hypercarnivorous. The piscivores/mollusc-eaters are also abun-

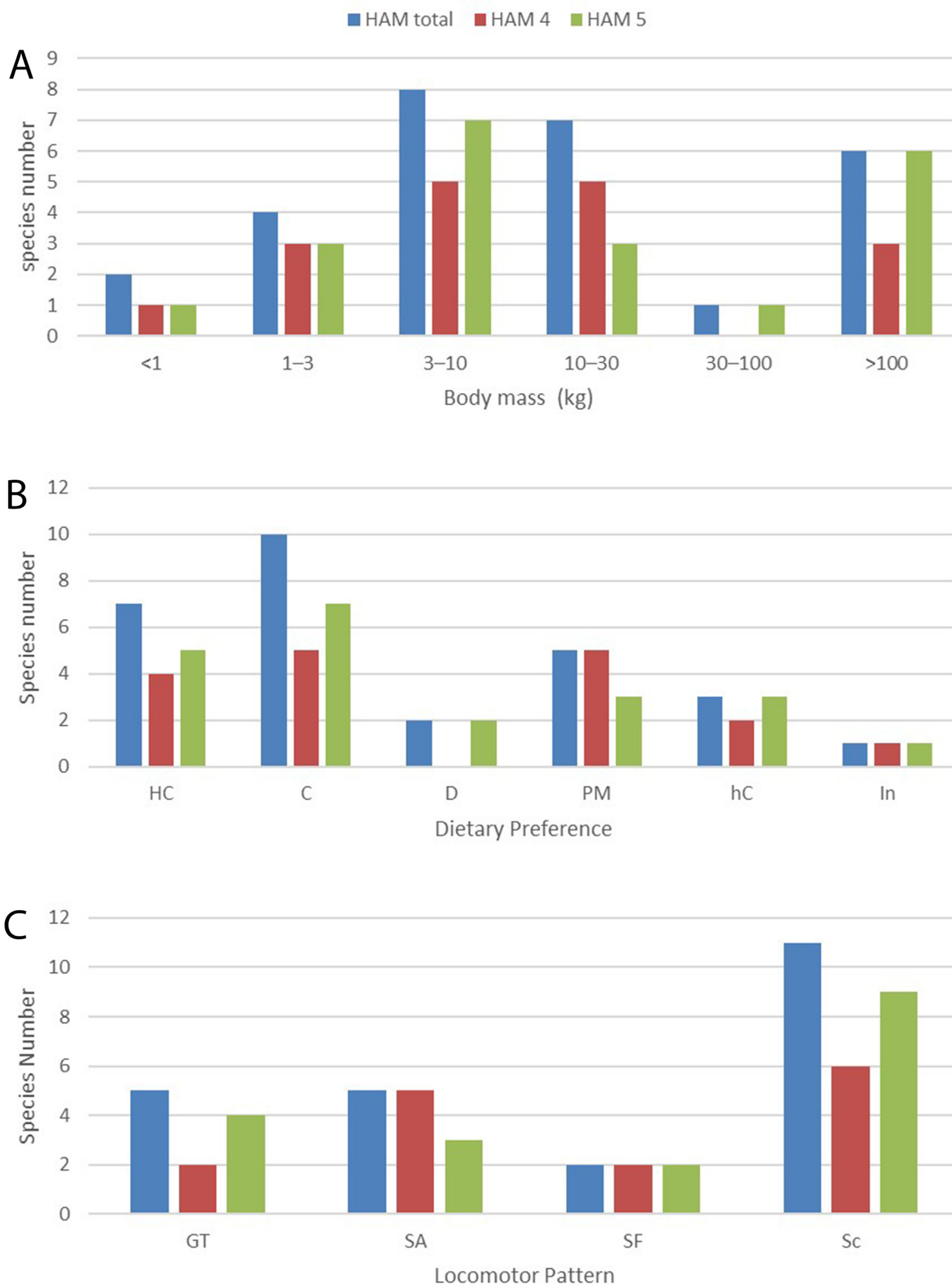

Fig. 5. Column charts depicting the distribution of the carnivorans in their respective categories of body mass (**A**), dietary preferences (**B**), and locomotor pattern (**C**) for Hammerschmiede in total (blue), HAM 4 (red) and HAM 5 (green). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

dant, indicating a plethora of river-originating dietary resources. One interesting difference between the two main layers is the absence of durophagous carnivorans (hyaenids) in HAM 4, despite the abundant finds of splinter bones from medium-sizes ungulate long bones (Lechner, 2024), as well as the lower frequency of hypercarnivores (mainly 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 patterns, the influence of the forested part of the ecosystem is evidenced by the abundance of scansorial taxa. 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, Fig. 5 points 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/mollusc-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 lower diversity of large-sized species, the absence of durophagous species and the lower diversity of 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. A way to depict this are biplots using body mass category in the x-axis, dietary preferences in the y-axis and presenting the different locomotor patterns by using different symbols (Fig. 6). Again, the plot was made for Hammerschmiede, HAM 4 and HAM 5.

Fig. 6 shows that despite the exceptionally high number of carnivoran species in the locality, cases 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 and Morlo, 1998; Valenciano et al. 2020). However, as also stated in Kargopoulos et al. (2022b), 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 (n = 12) with size-ranges between 5 and 130 cm total body length (pers. data, M. Böhme) in Hammerschmiede and the abundance of bivalves support this suggestion.

The barbourofelid, the Metailurini and *Pseudaelurus* are also closely placed on the plot. The latter differs from the other two in its smaller size. The felids are differentiated in the sabertooth features from the barbourofelid. This means that the barbourofelid was perhaps focusing on larger prey, without using the neighbouring trees as a hunting terrain. On the contrary, the metailurine was possibly more agile and able to use the trees, 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* (Kargopoulos, 2019).

Palaeomeles and the undetermined gulonine are also similar in body mass and dietary preferences and they coexist in HAM 5. However, the opportunistic foraging generally characterizing hypocarnivorous species creates more feeding choices and, consequently, reduces potential trophic conflicts. Therefore, even though these species most probably covered a broadly similar niche, they possibly reduced/avoided competition, because the ecosystem can easily support two small-/medium-sized carnivoran species (Haines et al., 2022). Nevertheless, both species are relatively rare in the locality (Table 1).

Another case of overlapping species is that of *Laphyctis* and *Semigenetta grandis* that co-occur in HAM 4. It is possible that these two species did not act only as hypercarnivorous predators, but also as scavengers, similar to the extant *Gulo* and *Canis*, respectively (Kargopoulos et al., 2022b). In this sense, these forms can be seen as the replacements of the durophagous species (hyaenids) seen in HAM 5. The high diversity of the Hammerschmiede ecosystem would inevitably result to a considerable number of available carcasses, so the presence of scavengers is expected.

Perhaps the clearest case of competition in the locality is that between "*Martes*" *sansaniensis* and *Semigenetta sansaniensis*, which is enhanced by *Alopecocyon goeriachensis* in HAM 5. These species cover the niche of scansorial opportunistic carnivores of 3–10 kg. Nevertheless, based on details of their dentition they are differentiated to a certain degree: (*i*) *Alopecocyon* has an elongated m2 and M2, (*ii*) "*Martes*" exhibits a typical gulonine morphology, and (*iii*) *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 (Popowics, 2003; Friscia et al., 2007). This differentiation perhaps could have been controlled 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 at their specific characteristics (Haines et al., 2022). 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 taxa. Finally, since excavations in Hammerschmiede are ongoing, it is very possible that the results of the diversity, abundance, and occurrences might change with future discoveries.

5. Conclusions

Hammerschmiede has yielded a very rich carnivoran assemblage with unique components, and it offers a valuable window for the evolution of carnivorans during the transition between the Middle and Late Miocene. The discovered carnivoran fauna is distinct from that of any other known locality in the Miocene of Europe. Ecomorphological comparisons inside the guild showed that most species occupied distinct niches, but some cases of ecological overlap and subsequent competition were also found.

CRediT authorship contribution statement

Nikolaos Kargopoulos: Conceptualization, Methodology, Visualization, Writing – original draft, Writing – review & editing, Investigation. **Alberto Valenciano:** Conceptualization, Investigation, Writing – original draft, Writing – review & editing. **Juan Abella:** Conceptualization, Investigation, Writing – original draft, Writing – review & editing. **Michael Morlo:** Conceptualization, Investigation, Writing – original draft, Writing – review & editing. **George E. Konidaris:** Conceptualization, Investigation, Writing – original draft, Writing – review & editing. **Panagiotis Kam-**

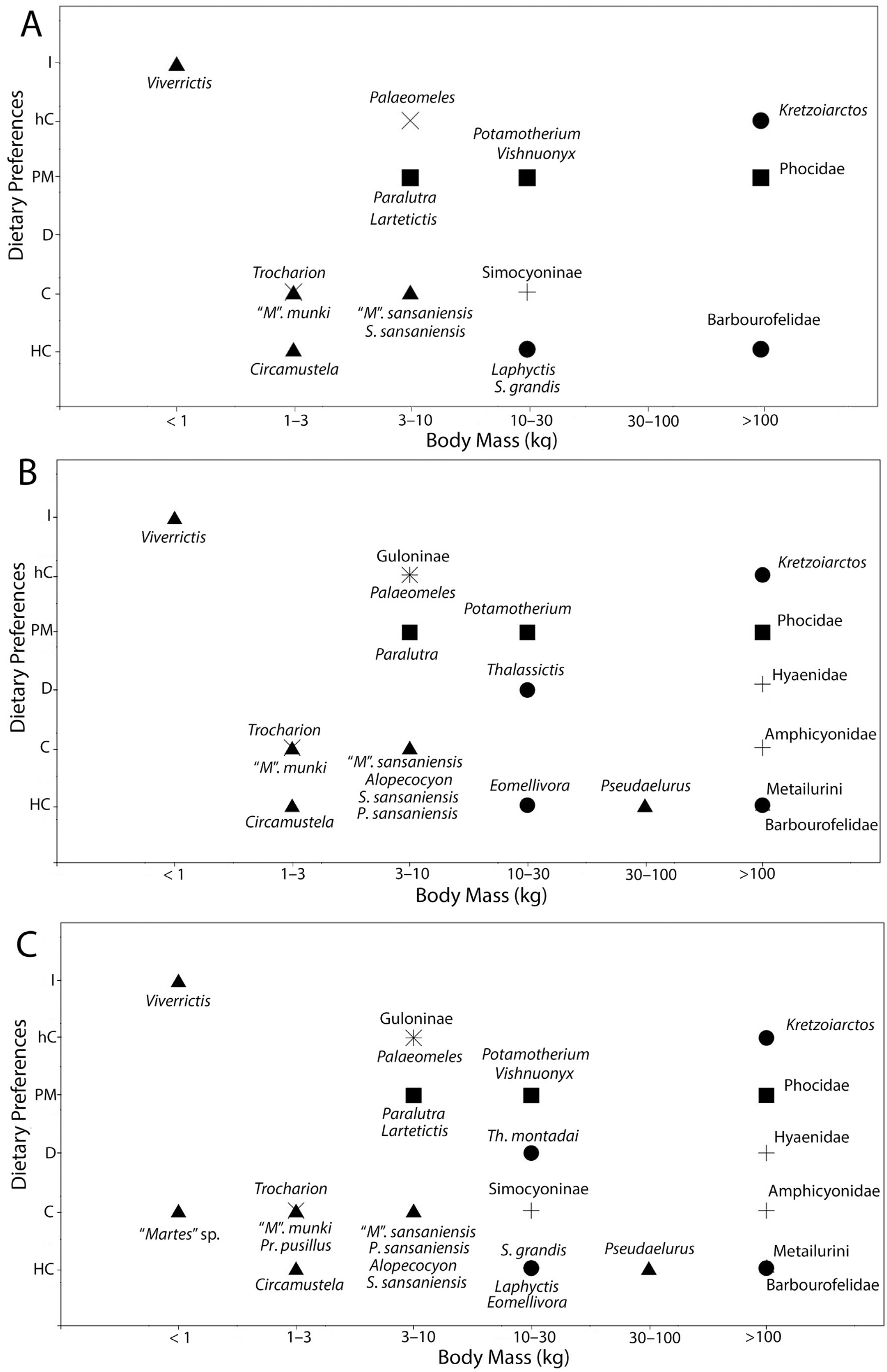

Fig. 6. Distribution of ecomorphological variables among carnivoran body mass categories for HAM 4 (**A**), HAM 5 (**B**), and Hammerschmiede as a whole (**C**). Symbols: triangle, scansorial; square, semi-aquatic; circle, generalized terrestrial; ×, semi-fossorial; +, unknown.

pouridis: Conceptualization, Investigation, Writing – original draft, Writing – review & editing. **Thomas Lechner:** Conceptualization, Investigation, Writing – original draft, Writing – review & editing. **Madelaine Böhme:** Conceptualization, Investigation, Resources, Supervision, Writing – original draft, Writing – review & editing.

Data availability

No data was used for the research described in the article.

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Appendix A. Supplementary material

Supplementary information (including Table S1 and Figs. S1 and S2) associated with this article can be found, in the online version, at https://doi.org/10.1016/j.geobios.2024.02.003.

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