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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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Thalassictis montadai; hyaeninae; carnivora; taxonomy; miocene

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

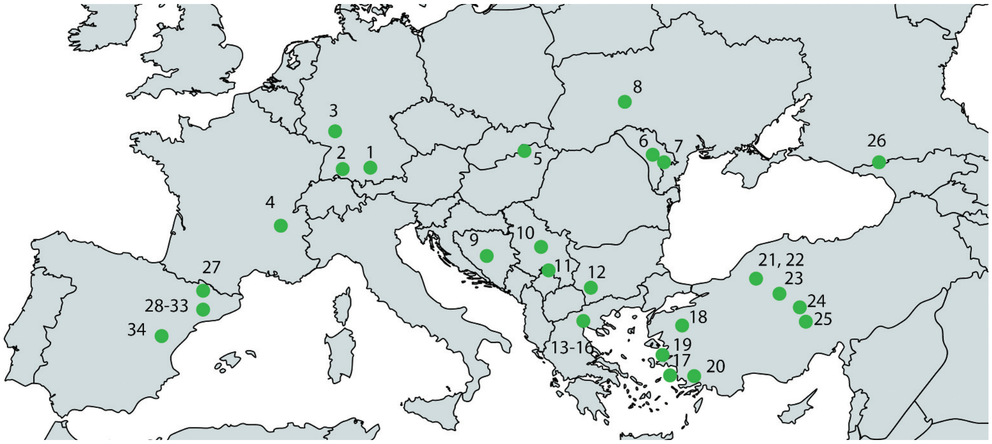

Figure 1. Map depicted the localities of: 1 – Hammerschmiede, 2 – Höwenegg, 3 – Dorn-Dürkheim, 4 – La Grive-Saint Alban, 5 – Rudabánya, 6 – Kishinev, 7 – Kalfa, 8 – Gritsev, 9 – Gračanica, 10 – Brajkovac, 11 – Prebreza, 12 – Oranovo, 13 – Diavata, 14 – Xirochori, 15 – Ravin des Zouaves, 16 – Ravin de 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 *Tunguricti*s (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)	-
		Akkaşdaği[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)	
		Akkaşdaği[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)	

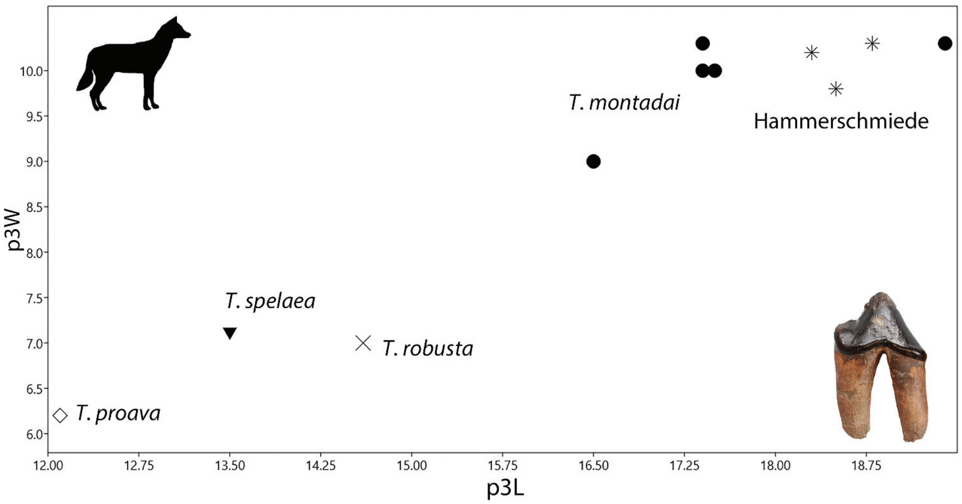

Figure 3. Comparison of p3 dimensions of several species of *Thalassictis*: stars – Hammerschmiede specimens of *Thalassictis montadai*; dots – other *Thalassictis montadai* specimens; X – *Thalassictis robusta*; Inverted triangle – *Thalassictis spelaea*.

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.

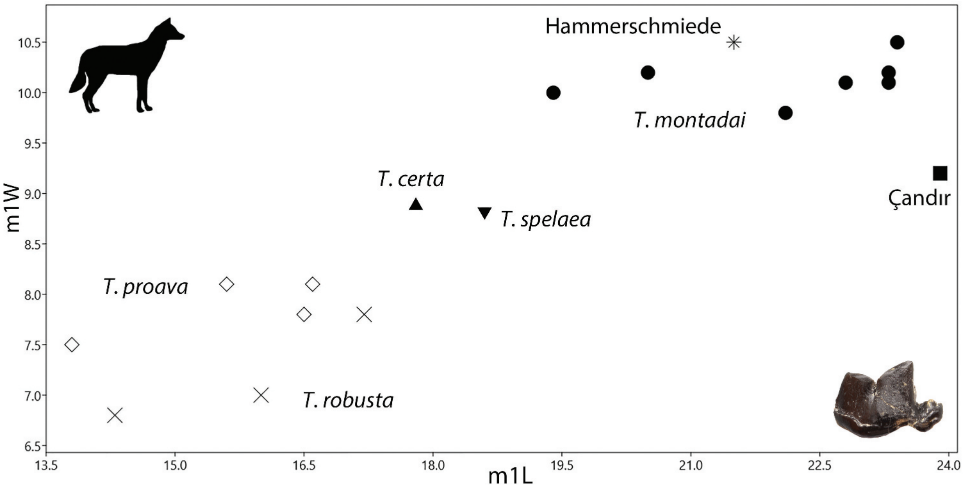

Figure 4. Comparison of m1 dimensions of several species of *Thalassictis*: star – Hammerschmiede m1 of *Thalassictis montadai*; dots – other *Thalassictis montadai* specimens; square – *Thalassictis* cf. *montadai* from Çandir; Triangle – *Thalassictis certa*; Inverted triangle – *Thalassictis spelaea*; 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).

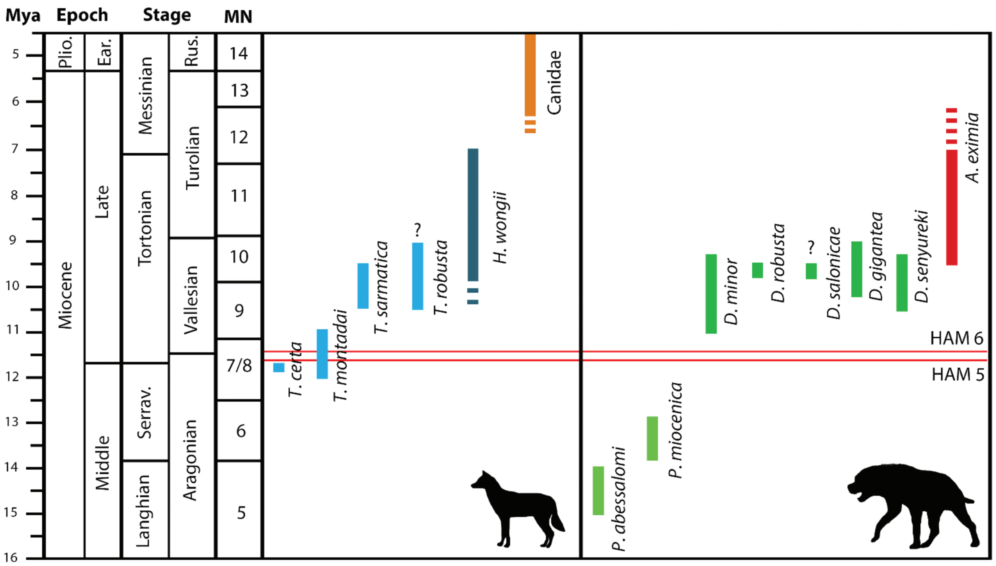

Figure 6. The stratigraphical replacements of the large ictitheres and crocutoid hyenas in Europe and Anatolia between the Middle Miocene and Early Pliocene. Data from: Schmidt-Kittler (1976), Werdelin and Solounias (1991), Spassov and Koufos (2002), Viranta and Werdelin (2003), Turner et al. (2008), 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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