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Hyaenidae (Carnivora, Mammalia) from the Late Miocene (MN 9/10) Dinotheriensande

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Running title

Hyaenids from the late Miocene of the Dinotheriensande

Kurzfassung

Hyaenidae (Carnivora, Mammalia) aus dem Oberen Miozän (MN 9/10) der Dinotheriensande

In dieser Arbeit wird der Neufund einer Hyäne, ein Mandibelfragment mit p3-4, aus dem Oberen Miozän (MN 9/10) von Eppelsheim beschrieben. Auf Basis seiner Morphologie gehört es zu *Protictitherium crassum* (FILHOL, 1883), wofür geringe Mandibelhöhe, schlanke Prämolaren und relative hohe posteriore Nebenhöcker des p4 sprechen. *P. crassum* ist ein gut bekanntes, zeitlich und räumlich weit verbreitetes miozänes Hyäntaxon. Das neue Stück erlaubt auch eine Zuordnung eines Eppelsheimer Mandibelragments zu *P. crassum*, das KOENIGSWALD (1928) als *Ictitherium robustum* beschrieb. Obwohl beide Stücke das obere Ende der Größenvariabilität der Art repräsentieren, schließt ihre Morphologie bzw. ihre zu geringe Größe eine Zuordnung zu anderen Hyänenarten wie *Ictitherium viverrinum* oder *Thalassictis robusta* aus. Solche großen Vertreter von *P. crassum* wurden als eigene Art (*P. arambourgi*) beschrieben, inzwischen aber mit *P. crassum* synonymisiert. „*Ictitherium*“ *tauricum* ist in Größe und Morphologie ebenfalls ähnlich, aber auch diese Art stellt ein mögliches Synonym von *P. crassum* dar. *P. crassum* ist das bisher einzig bekannte Hyäntaxon aus den Dinotheriensanden.

Abstract

A new hyaenid specimen, a fragmentary mandible with p3-4 from the Late Miocene (MN 9/10) of Eppelsheim, is described and discussed. It is assigned to *Protictitherium crassum* (FILHOL, 1883) based on its morphology, especially low mandible height, slenderness of premolars, and height of distal accessory cuspids in p4. *P. crassum* is a well-known, temporally and spatially widespread Middle and Late Miocene hyaenid carnivoran. The analysis of the new specimen allows the re-assignment of another mandible fragment from Eppelsheim to *P. crassum* which was described as “*Ictitherium robustum*” by KOENIGSWALD (1928). Though both specimens represent the upper dental size range of the species, their morphology and small size exclude other hyaenid taxa, such as *Ictitherium viverrinum* or *Thalassictis robusta*. Very large specimens of *P. crassum* were previously described as separate species (*P. arambourgi*), but this taxon is now thought to be a synonym of *P. crassum*. The same is true for “*Ictitherium*” *tauricum*, which is also similar in size and morphology, but might be synonymous with *P. crassum*, as well. *Protictitherium crassum* remains the only hyaenid taxon known from the Dinotheriensande.

Key Words

Dinotheriensande, Germany, *Protictitherium*, *Ictitherium*, size variation

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1. Introduction

The hitherto only described hyaenid from Eppelsheim was published by KOENIGSWALD (1928), who assigned a mandible fragment with damaged p3, p4, damaged m1, and alveolus of m2 to "*Ictitherium*" *robustum* (NORDMANN in GERSVAIS, 1850) based on morphology. *Thalassictis robusta* was constantly confused with *Ictitherium viverrinum* ROTH & WAGNER, 1854 (DE BONIS 2004, SEMENOV 2008) until KURTÉN (1982) described the characters differentiating these two taxa (and the genera *Ictitherium* and *Thalassictis*). KOENIGSWALD (1928) already noted the small size of the specimen from Eppelsheim for *T. robusta* and interpreted it as a very small female. ZAPFE (1948) corroborated the assignment to this species, but recognized that the mandible of the specimen is much lower than in other specimens of *T. robusta* (or *I. viverrinum*). Until now, however, this specimen has been interpreted as the smallest known representative of *T. robusta*, and occurs in faunal lists of Eppelsheim under this name (KOENIGSWALD 1929, TOBIEN 1955, FRANZEN et al. 2003b). In NOW, the New and Old Worlds Database of Fossil Mammals, however, the specimen is noticed as *Protictitherium crassum*, presumably through an update by Suvi VIRANTA in 2000. *Ictitherium* was also reported from the Dinotheriensande of the Wissberg (WAGNER 1947a). The only related specimen (HLMD Din 1156), however, is much too large to belong here. Instead, it represents a right P4 of a small individual of *Amphicyon eppelsheimensis*.

A second hyaenid specimen, a fragmentary mandible with p3 and p4 of about the same size as the specimen described by KOENIGSWALD (1928) was unearthed in Eppelsheim during the 2011 excavation campaign of the MNHM. In this contribution, we describe this specimen and discuss its systematic relationships.

2. Material and Methods

Measurements were taken with digital calipers to the nearest 0.1 mm. Terminology and nomenclature of the tooth morphology is taken from SMITH & DODSON (2003). Herein, length

refers to the greatest mesiodistal length of the tooth crown and width refers to the greatest labiolingual width of the tooth. Comparative material is mentioned in the text.

3. Abbreviations

- HLMD – Hessisches Landesmuseum
Darmstadt, Germany
- MNCN – Museo Nacionales des
Ciencias Naturales, Madrid,
Spain
- MNHM – Naturhistorisches Museum
Mainz/Landessammlung für
Naturkunde Rheinland-Pfalz,
Mainz, Germany
- SMF – Senckenberg Museum und
Forschungsinstitut,
Frankfurt a. M., Germany.

4. Geography and Age of Eppelsheim

Eppelsheim represents one of the oldest historic localities in Europe from which finds of Miocene mammals have been published (Fig. 1). Locals have worked in the fluvial deposits of the Proto-Rhine system in Rheinhessen at least since the 18th century (WAGNER 1947b). The sediments are known as "Dinotheriensande", because *Dinotherium* was first described from Eppelsheim (KAUP 1829), but were also named "Eppelsheim Formation" (e. g., FRANZEN in GRIMM et al. 2011, BÖHME et al. 2012). From 1996 to 2000, scientific excavations at Eppelsheim have taken place annually by the SMF, financially supported by the MNHM. Since 2001 these excavations are carried out by the MNHM and since 2017 these are being continued in close cooperation with the Generaldirektion Kulturelles Erbe Rheinland-Pfalz, Direktion Landesarchäologie. These long-term excavations have largely enhanced our knowledge of the geology, stratigraphy (FRANZEN et al. 2003b, SOMMER et al. 2009), and fauna of the site. Since 2001, sands and gravels of the Proto-Rhine River covering the "Basiston" in the channel 1.5 km NNW of Eppelsheim have

been documented in detail by 160 profiles (parallel and transverse to the former flow direction of the river) and numerous photos (Fig. 2). Details on the applied documentation techniques in the Eppelsheim excavations are outlined in LISCHESKY (2018). The three-dimensional analysis shows an extremely complex fabric: Besides numerous small sediment units, documenting rapidly changing sedimentation conditions, two gravel beds cut diagonally through the Vallesian channel filling, marking important erosional events. The

upper one documents the youngest erosional event at the excavation site. The specimen described herein was embedded within this uppermost gravel horizon on the top of tectonically tilted marly limestone banks, about 80 cm away from and 10 cm below the top of the steep limestone and marl complex forming the right river bank.

Age determination of the Eppelsheim sediments is based on biostratigraphical information. While the existence of a Proto-Rhine River at Eppelsheim can be traced back at

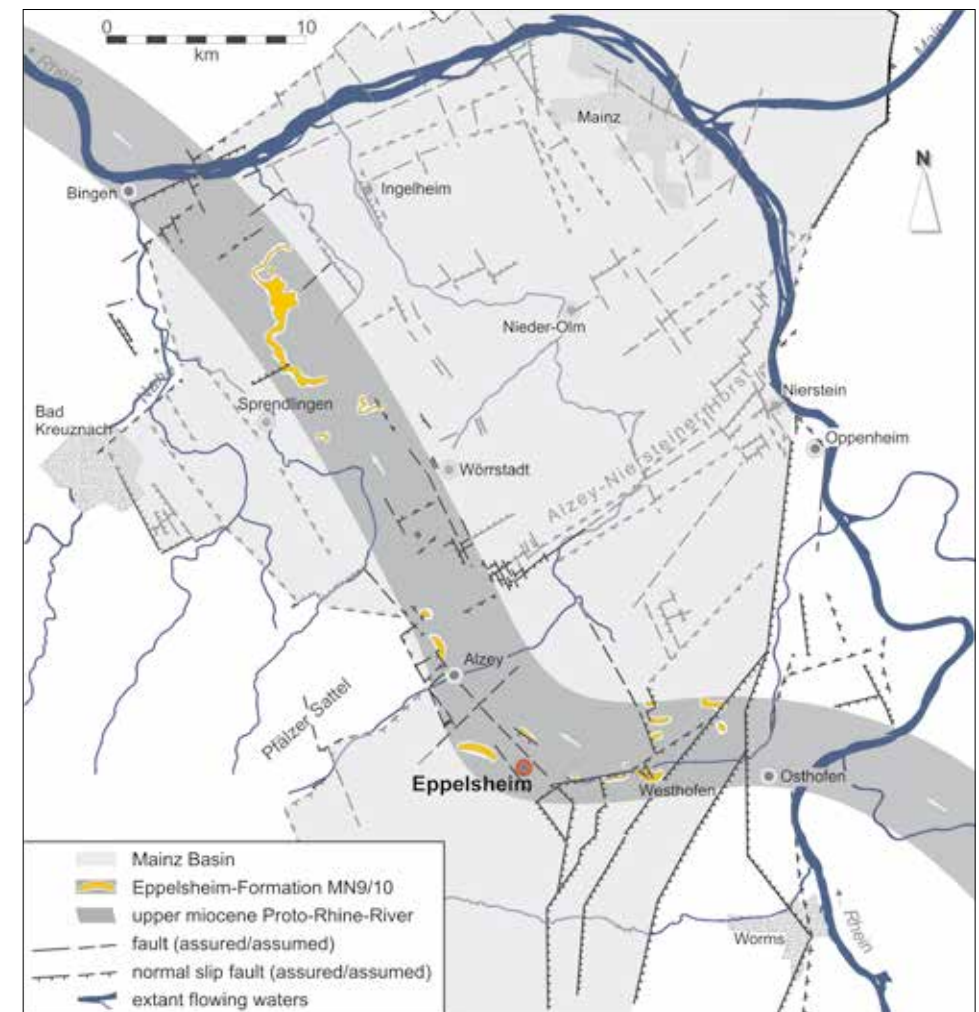


Fig. 1: Map of Eppelsheim location within the Dinotheriensande. Scale bar 10 km.

least to the Late Serravallian (MN 7/8; GRIMM et al. 2012, 2014), the fauna is considered to be mainly of Vallesian age, MN 9 (FRANZEN et al. 2003b, SOMMER et al. 2009, PICKFORD & POURABRISHAMI 2013), and may reach into MN 10 (FRANZEN et al. 2003a, b). However, re-worked fossils from the Middle Miocene might also be present in the Dinotheriensande (KLÄHN 1922, BÖHME et al. 2012, PICKFORD & POURABRISHAMI 2013). The absolute age of the Eppelsheim sediments thus spans from 11.1 Ma (beginning MN 9, STEININGER 1999), demonstrated by a *Hippotherium* molar found close to the base of the sediments, to at least 9.7 Ma (ending MN 9, STEININGER 1999).

5. Systematic Paleontology

Carnivora BOWDICH, 1821

Hyaenidae GRAY, 1821

Uctitheriinae TROUESSART, 1897

Protictitherium KRETZOI, 1938

Diagnosis: The latest diagnoses of the genus were provided by WERDELIN & PEIGNÉ (2010) and FRAILE (2015), with small size, low mandi-

ble body, relatively large posterior cuspids in p4, and viverrid-like m1 with well-developed metaconid being the most relevant diagnostic characters of the lower dentition. However, WERDELIN & SOLOUNIAS (1991) found no synapomorphies to unite the (then) described species and therefore considered the genus possibly paraphyletic.

Remarks: Number and diagnosis of the included species is highly debated. The specimens of Eppelsheim do not add evidence to this discussion, but it can be stated that *P. crassum* is consistently referred to as largest species of the genus (FRAILE 2015, KOUFOS et al. 2018), if *P. arambourgi* (OZANSOY, 1965) is regarded as conspecific (SCHMIDT-KITTLER 1976, SEMENOV 1989, 2001, WERDELIN & SOLOUNIAS 1991, WERDELIN & PEIGNÉ 2010, KOUFOS et al. 2018).

Protictitherium crassum (FILHOL, 1883)

Holotype: “*Herpestes crassus*”, mandible fragment with canine, alveoli of p1 and p2-3 (FILHOL 1883: pl. 4, figs. 10-11). DEPÉRET (1892: pl. 1, figs. 14-17) added a P4 and two mandible fragments to the hypodigm of the type locality.

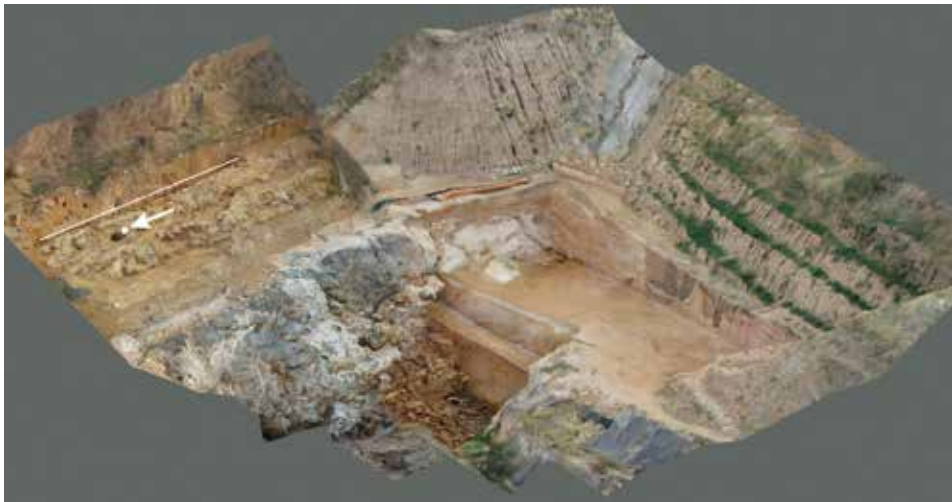


Fig. 2: Part of the excavation site of Eppelsheim. Right river banks on the left hand side of the image. The arrow points to the position where MNHM PW2019/3-LS, *Protictitherium crassum* (FILHOL, 1883), was embedded in the right river banks. The center of the picture shows the famous “Dinotheriensand basis conglomerate” representing the riverbed on the deepest floor of the pit. Flow direction of the river was from the right upper to the left lower corner of the image. Scale bar above the excavated top of the riverbank 10 m.

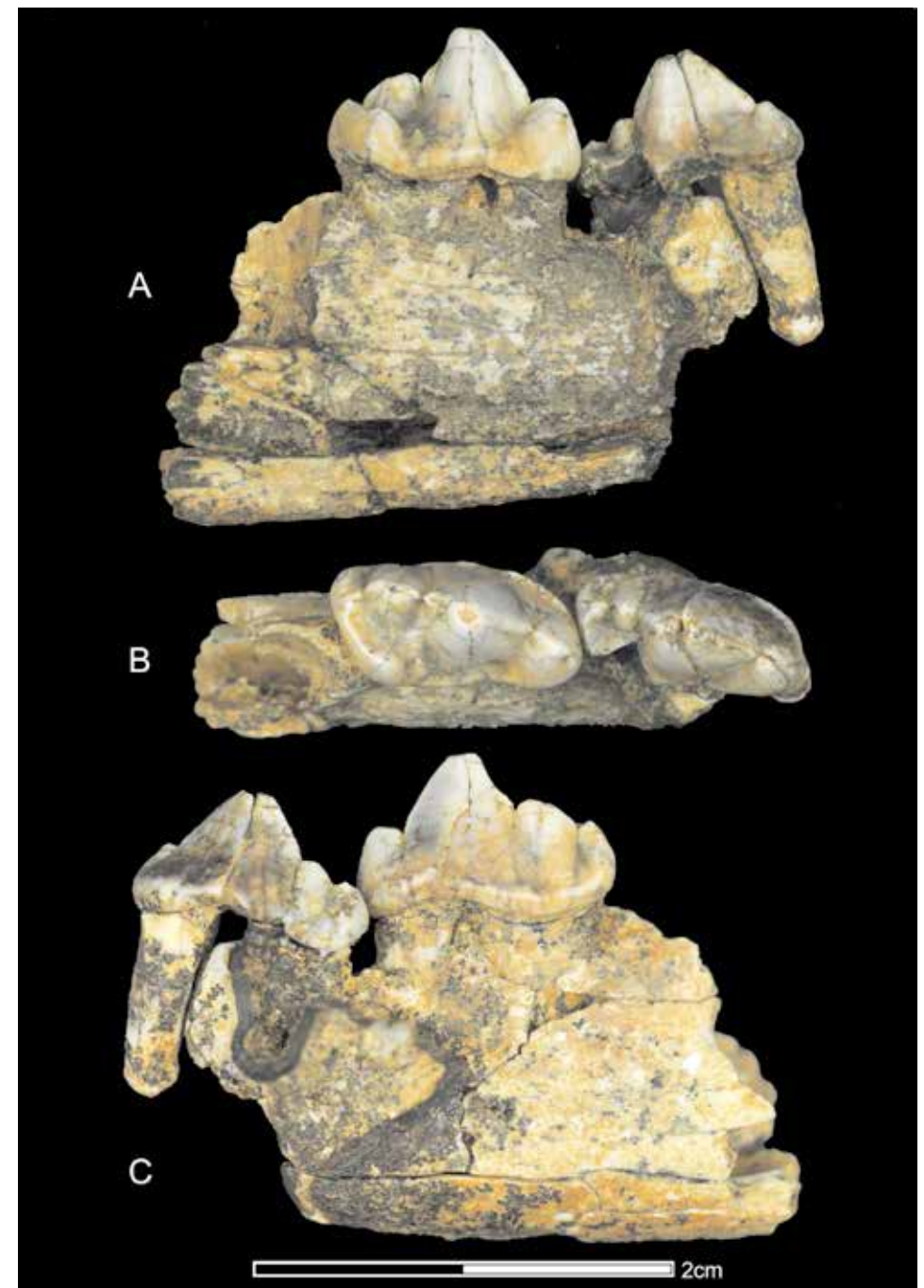


Fig. 3: MNHM PW 2019-03/LS, *Protictitherium crassum* (FILHOL, 1883) from MN 9/10 of Eppelsheim. Fragment of left mandible with p3 and p4 in A: lingual, B: occlusal, C: labial view.

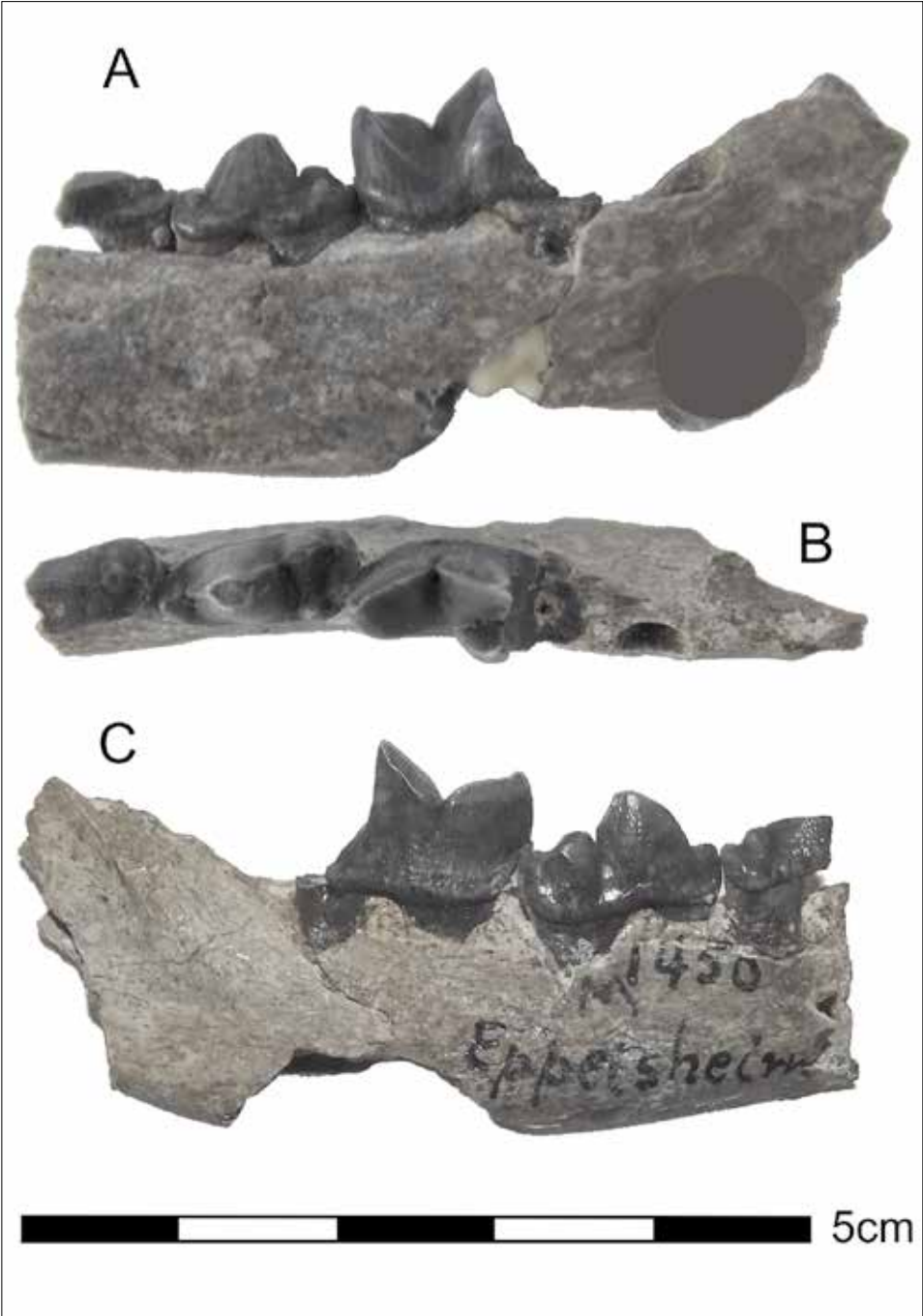


Fig. 4: SMF M 1450, *Protictitherium crassum* (FILHOL, 1883), fragment of right mandible with damaged p3, p4, damaged m1, and alveolus of m2 (KOENIGSWALD 1928: figs 1-3) in A: lingual, B: occlusal, C: labial view.

Table 1: Measurements of p3 and p4 [in mm] of hyaenids from the Dinotheriensande and comparative material. ¹KOUFOS et al. (2018), ²SENYÜREK (1960), ³NAKAYA et al. (1984), ⁴BORISSIAK (1915), ⁵ZAPFE (1948).

taxon	Specimen/location	p3		p4	
		length	width	length	width
Eppelsheim hyaenid	MNHM PW 2019-03/LS	12.0	6.0	12.9	6.5
	SMF M 1450			12.5	6.5
" <i>P. arambourgi</i> "	holotype from Middle Sinap, Turkey ¹	11.9	5.5	-	6.6
cf. <i>P. crassum</i>	from Küçükyozgat, Turkey ²	11.6	4.6	12.3	5.3
<i>Protictitherium</i> sp.	from Samburu Hills, Kenya ³	11.0	5.5	12.7	6.3
" <i>I.</i> " <i>tauricum</i>	holotype from Sebastopol, Ukraine ⁴	11.0	6.0	12.5	6.5
<i>I. viverrinum</i>	from MN 9 of Vösendorf, Austria ⁵	14.0	7.0	15.0	7.5

Type locality: La Grive Saint Alban, France, MN 7/8.

Distribution: MN 4 to MN 13 from France (FILHOL 1883, DEPÉRET 1892), Spain (FRAILE 2015), Greece (KOUFOS 2000, 2009, 2011), Turkey (VIRANTA & WERDELIN 2003, DE BONIS 2004, 2005, KOUFOS et al. 2018), Germany (MORLO 1997), Moldova and Ukraine (WERDELIN & SOLOUNIAS 1991, SEMENOV 1989, 2001).

Known specimens: SMF M 1450 from Eppelsheim (Fig. 4). Fragment of right mandible with damaged p3, p4, damaged m1, and alveolus of m2 (KOENIGSWALD 1928: figs 1-3). SMFM 1451 from Eppelsheim. Fragment of a right lower canine, associated to the mandible fragment.

New specimen: MNHM PW 2019/03-LS from Eppelsheim (Fig. 3). Fragment of left mandible with p3, p4, and the anterior alveolus of m1.

Comparative description: The mandible body is relatively low in both specimens. The height at p4 is 14 mm in SMF M 1450 and 15 mm in the new specimen, and is thus less than twice as high as the p4. This is similar to the mandible height of *P. crassum* from the Spanish Batallones (FRAILE 2015), *P. "arambourgi"* (see KOUFOS et al. 2018: figs. 3g-i), and "*Ictitherium tauricum*" (see SENYÜREK 1960: figs. 9-10), but differs from *I. viverrinum* (e. g., DE BONIS 2005: fig. 5), where the mandible is about 2.5 times as high as the p4, and also differs from *T. robusta* (e. g., SEMENOV 2008: fig. 4b), where this index is still higher than 2.

A mental foramen is only visible in SMF M 1450. It is situated below p3.

From the tooth crown of the canine fragment almost nothing is preserved. It can be assigned to *P. crassum* only because it comes from the same mandible as the cheek teeth (KOENIGSWALD 1928).

The p3 is laterally compressed but relatively slightly broader than most *P. crassum* from Batallones. It has an anterior accessory cuspid that is shifted lingually. This configuration also occurs in other specimens of *P. crassum* (e. g., MNCN B-450) and to a lesser degree in the holotype of *I. tauricum*. A labial cingulid is developed. Directly posterior to the slightly horizontally abraded protoconid, a low distal accessory cuspid is developed in both specimens. It is a little bit lower than in most other *P. crassum* (including "*P. arambourgi*") and not shifted distinctly labially like in most other specimens of the species, but similar to the holotype of "*I. tauricum*" and the Turkish specimen attributed to that species by DE BONIS (2004). In this Turkish specimen, however, the distal accessory cuspid is higher and resembles the configuration in most *P. crassum*. On the other hand, a specimen from the Mytilinii Basin (KOUFOS 2009: fig. 7a) is very similar to the Eppelsheim hyaenid in having the distal accessory cuspid as high and not shifted labially. The posterior cingulid builds a small basal cuspid postero-lingual to this accessory cuspid. A lingual enlargement of the posterior cingulid was present, but its size is obscured by tooth breakage in the new specimen. Such an enlargement is not visible in the holotype of "*I. tauricum*".

The p4 described by KOENIGSWALD (1928) is morphologically identical to that of MNHM PW 2019/3-LS, but is slightly shorter and thus appears stouter. Both p4 resemble p3 in morphology, but show stronger accessory cusps and cingulids. Strong, well developed accessory cusps and cingulids are seen in most *P. crassum* (e. g., MNCN BAT1'01-C6-146 DER, FRAILE 2015: fig. 7.9), but not in *I. viverrinum* and *T. robusta*. WERDELIN (1988) considered a weak anterior accessory cuspid in p4 as diagnostic for the genus *Ictitherium*. In this respect, the holotype of "*I. tauricum*" and the Kenyan "*Ictitherium*" sp. (WERDELIN & PEIGNÉ 2010) fit to *Ictitherium*. However, the Turkish "*I. tauricum*" has an even stronger anterior accessory cuspid than the Eppelsheim hyaenid or "*P. arambourgi*". Compared to *T. robusta*, both p4 from the Dinotheriensande are smaller and more slender due to a relatively longer anterior accessory cuspid and a relatively longer area posterior to the protoconid. In both specimens, a strong distal accessory cuspid is developed that is higher than that in *T. robusta* (see MORLO 1997: fig. 16). The labial shift of the distal accessory cuspid is variable. It is located directly posterior to the horizontally abraded protoconid in MNHM PW 2019/3-LS, but also in the Spanish specimen MNCN BAT-1'02-D5-85, and in a specimen

from Greece, where this character varies even within the same individual (KOUFOS 2009: fig. 7a). A basal lingual cuspid is formed by the cingulid directly lingual to the distal accessory cuspid. In most *P. crassum*, this basal lingual cuspid is placed more posteriorly, but exceptions exist (e. g., MNCN B-2378). In the holotype of "*I. tauricum*" this cuspid seems to be located at the postero-lingual corner of the tooth. Both p4 from Eppelsheim also have a basal cuspid posterior to the distal accessory cusp built by the posterior cingulid, namely at the most posterior point of the tooth. It resembles that of other *P. crassum* in height and position.

The m1 described by KOENIGSWALD (1928) has only the trigonid preserved. It is characterized by a high, very pointed metaconid as it is typical for *Protictitherium*. It is as tall as the paraconid. In *Ictitherium* and *Thalassictis* the metaconid is more robust, lower, and less pointed (DE BONIS 2004). As in other *P. crassum*, the m1 also displays a strong lingual cingulid that surrounds the anterior tip of the tooth.

Remarks: Based on general morphology, both specimens match ictitherine hyaenids. They are of unusual size, however. The large data set of hyaenid tooth measurements provided by COCA-ORTEGA & PÉREZ-CLAROS

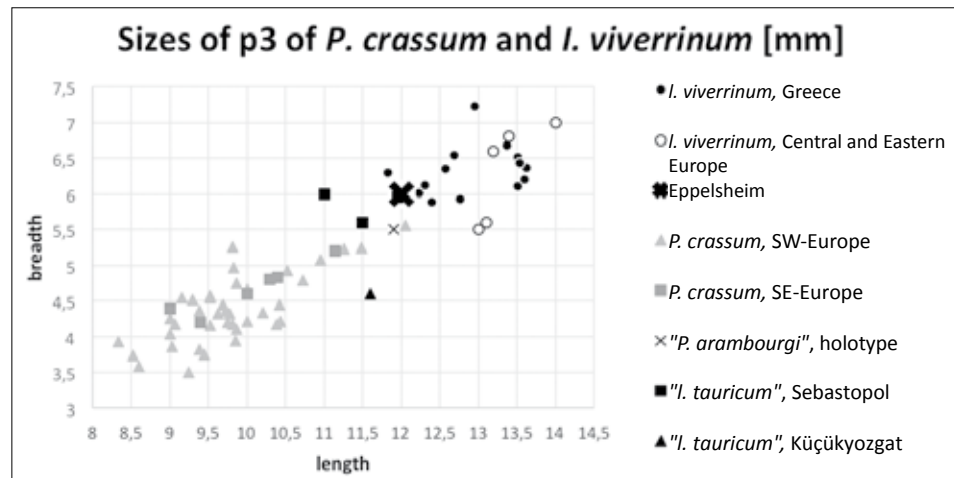


Fig. 5: Sizes of p3 of the Eppelsheim hyaenid and comparative material. Data taken out of BORISSIAK (1915), SENYÜREK (1960), SEMENOV (1989), FRAILE (2015), and KOUFOS et al. (2018).

(2019) reveals only two European species with specimens of similar size: *Protictitherium crassum* (largest p3: 12.05:6.0, largest p4: 13.0:6.5) and *Ictitherium viverrinum* (smallest p3: 12.0:5.5, smallest p4: 13.0:6.5). Compared to other data sets, the specimens from Eppelsheim however, are clearly larger (figs. 5-6) than nearly all of the abundant material of *P. crassum* from Batallones (FRAILE 2015: tables 6.4.4 and 6.4.5), Greece (KOUFOS 2009: tabl. 4), and Turkey (KOUFOS et al. 2017: fig. 4). Exceptions are a single specimen from Xirochori 1, Axios valley, Greece (KOUFOS 2000), one specimen from Batallones with a large p3 (MNCN BAT-3'13-427, FRAILE 2015), and the holotype of *P. "arambourgi"* (OZANSOY, 1965) from Yassiören, Middle Sinap of Turkey.

Protictitherium crassum (including *P. "arambourgi"*) is the largest species of the genus. It is well known from the Middle and Late Miocene (MN 4 to MN 13) throughout Europe and Asia Minor (e. g., SCHMIDT-KITTLER 1976, MORLO 1997, GINSBURG 1999, VIRANTA & WERDELIN 2003, KOUFOS 2009, FRAILE 2015, KOUFOS et al. 2018). KOUFOS (2000, 2009), FRAILE (2015), and KOUFOS et al. (2018) published the latest detailed analyses on the species. KOUFOS et al. (2018) stated that the anterior accessory cusps in the premolars of *P. "arambourgi"* are slightly smaller than

in *I. viverrinum* from Pikermi, while the materials of *P. crassum* from Eppelsheim and Batallones demonstrate the variation in this character to be size independent. For GINSBURG (1977), the lower premolars of *P. "arambourgi"* are too thick and massive to belong to *Protictitherium*, and he placed the taxon into *Ictitherium*. However, length and breadth of p3-4 also vary greatly in *P. crassum* (Figs. 5-6). Due to its very large variability concerning size and morphology (e. g., FRAILE 2015, KOUFOS et al. 2018), we follow SCHMIDT-KITTLER (1976), SEMENOV (1989), WERDELIN & SOLOUNIAS (1991), WERDELIN & PEIGNÉ (2010), FRAILE (2015), and KOUFOS et al. (2018) in regarding *P. "arambourgi"* and *P. crassum* as conspecific. It should be noted that KOUFOS et al. (2018) characterize its size and morphology as "in between *P. crassum* and *I. viverrinum*". This exactly describes the configuration of the Eppelsheim hyaenid.

"*Ictitherium*. cf. *arambourgi*" from Morocco is based on isolated upper and lower dental elements of a juvenile specimen (GINSBURG 1977). It was declared to be too derived to belong to *Protictitherium* due to the morphology of M1 (WERDELIN & SOLOUNIAS 1991) or was placed into *P. crassum* (WERDELIN & PEIGNÉ 2010). Recently, WERDELIN (2019) stated that the Moroccan specimen is similar to

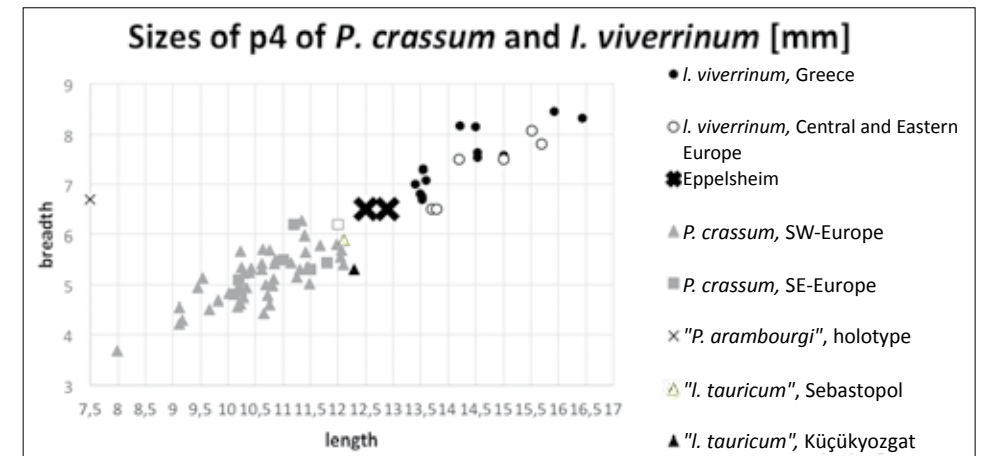


Fig. 6: Sizes of p4 of the Eppelsheim hyaenid and comparative material. Data taken out of BORISSIAK (1915), SENYÜREK (1960), SEMENOV (1989), FRAILE (2015), and KOUFOS et al. (2018). Length of p4 of the holotype of *P. arambourgi* cannot be measured (KOUFOS et al. 2018). To be visible on the chart we set it to 7.5 mm.

P. punicum (KURTEN, 1978) from Tunisia. Both specimens from Morocco and Tunisia are slightly larger than most *P. crassum* and thus of comparative size to the Eppelsheim hyaenid. However, no dental element of “*I. cf. arambourgi*” or *P. punicum* can be compared directly to the Eppelsheim specimens. We therefore do not further discuss the assignment of these African specimens.

“*Ictitherium*” sp. from the Late Miocene Samburu Hills of Kenya (NAKAYA et al. 1984: pl. 1 figs. 3-4) is another African specimen attributed to *Protictitherium* by WERDELIN & PEIGNÉ (2010). It has a much shorter and narrower p3 than in MNHM PW 2019/3-LS, but its p4 is of comparable size. Judging by the pictures, p4 has a shorter anterior accessory cuspid and a lower distal accessory cuspid than in the Eppelsheim hyaenid. Due to the limited information given, we do not further discuss possible specific assignments of this specimen, but agree with WERDELIN & PEIGNÉ (2010) that it may belong to *Protictitherium*.

Ictitherium tauricum BORISSIAK, 1915, is regarded to be the smallest species of *Ictitherium* as being similar in size to *P. “arambourgi”* and thus of the same size as the largest *Protictitherium* (DE BONIS 2004). “*Ictitherium tauricum*” was placed into *Protictitherium* by KRETZOI (1938) and synonymized with *P. crassum* by SCHMIDT-KITTLER (1976), SEMENOV (1989, 2001), and FRAILE (2015), but according to WERDELIN & SOLOUNIAS (1991), the P4-protcone is placed more anteriorly than in *P. crassum*. Consequently, these authors (followed by DE BONIS 2004, but not DE BONIS et al. 2010) regarded the species still to belong to *Ictitherium*. It should be noted, though, that P4-protcone position varies in the numerous material of *P. crassum* from Batallones (FRAILE 2015: MNCN BAT-3’13-1261, figs. 6.1.3 vs. MNCN B-1990, fig. 6.1.5 and fig. 6.3.1), which decreases the importance of this character for generic assignments. The holotype of “*I. tauricum*” comes from Sebastopol in the Ukraine. KOENIGSWALD (1928) regarded it to be close to the Eppelsheim hyaenid mainly due to its size. Additionally, material from the Turkish site Küçükyozgat (SENYÜREK 1960) was assigned to “*I. tauricum*” by DE BONIS (2004).

The species is said to differ from *P. “arambourgi”* in having the premolars relatively broader (WERDELIN & SOLOUNIAS 1991) and p4 more symmetrical (DE BONIS 2004). Looking at the Eppelsheim hyaenid, differences concerning relative breadth of p4 are contradictory: the p4 of SMF M 1450 has the same dimensions as in the holotype of “*I. tauricum*”, while p4 of MNHM PW 2019/3-LS is of the same breadth, but longer. The Turkish p4, on the other hand, is much narrower than the other specimens, but only slightly shorter. The same pattern is visible in p3: in MNHM PW 2019/3-LS it is as broad as in the holotype of “*I. tauricum*” but longer, while the Turkish specimens are much narrower, but only slightly shorter. Concerning morphology, p4 of the Eppelsheim hyaenid and of *P. “arambourgi”* (see KOUFOS et al. 2018: figs. 3g-i) differ from the Turkish p4 in having a shorter preprotocristid and thus are “less symmetrical” in the sense of DE BONIS (2004). The p3 of the Turkish specimens shows a higher distal posterior cuspid than in MNHM PW 2019/3-LS, SMF M 1450, and *P. “arambourgi”* (see KOUFOS et al. 2018: figs. 3g-i). All these morphological differences, though, fall into the variability visible in *P. crassum* from Batallones. This renders a synonymy of the holotype of “*I. tauricum*” to *P. crassum* to be highly probable even though the longer premolars of the new specimen in relation to the holotype of “*I. tauricum*” are closer to specimens of *P. crassum*. The Turkish specimen of “*I. tauricum*”, on the other hand, has very slender premolars and a high distal accessory cuspid in p3. In these characters, it is much closer to *P. crassum* from Batallones than to the Eppelsheim hyaenid, raising the possibility that the Turkish specimen also represents *P. crassum*. This is additionally supported by a P4 protocone position similar to some *P. crassum* from Batallones, even though SENYÜREK (1960) states this character to be similarly developed in P4 of the “*I. tauricum*” holotype and the Turkish specimen. We therefore tentatively assign the specimens from Küçükyozgat to *P. crassum* and regard a synonymy of “*I. tauricum*” to *P. crassum* to be probable (following SCHMIDT-KITTLER 1976, SEMENOV 1989, 2001, and FRAILE 2015), thereby corroborating DE

BONIS et al. (2010) who considered the morphology of “*I. tauricum*” to differ greatly from the type species of *Ictitherium*, *I. viverrinum*.

The smallest *Ictitherium viverrinum* may also reach the size of the Eppelsheim hyaenid (figs. 4-5, COCA-ORTEGA & PÉREZ-CLAROS 2019). The species is recorded in Eurasia mainly from MN 9 to MN 13 with localities geographically reaching from France to China (NOW). The oldest record comes from MN 6 of China (QI 1989, WANG et al. 1998), but this was questioned by WERDELIN & SOLOUNIAS (1991). Specimens of *I. viverrinum* from MN 9 (e. g., ZAPFE 1948, for a specimen from the Austrian Vösendorf) are larger than the Eppelsheim hyaenids (Figs. 5-6, KURTEN 1982, KOUFOS 2000, KOUFOS et al. 2018: fig. 4), have a higher mandible body, and less high posterior accessory cuspids in p4.

Ictitherium viverrinum was often confused with *Thalassictis robusta*, which also explains the assignment of the Eppelsheim hyaenid to “*Ictitherium robustum*” by KOENIGSWALD (1928). *Thalassictis robusta* is less abundant than *I. viverrinum* and known from MN 9 to MN 11, ranging from Spain to Bulgaria. In Germany, it is reported for MN 9 of Höwenegg and MN 11 of Dorn-Dürkheim (MORLO 1997). SEMENOV (2008) provided the latest detailed analysis of the species. *T. robusta* is even larger than *I. viverrinum* (KURTEN 1982) and differs significantly from *Protictitherium* in its much more robust premolars and a lower metaconid in m1.

6. Discussion

Our analysis of the hyaenid specimens from Eppelsheim reveals that an assignment to a large-sized *Protictitherium crassum* is the most probable. This species varies greatly in morphology and size, which additionally allows inclusion of *P. “arambourgi”*, the Turkish record of “*Ictitherium tauricum*”, and also the holotype of “*I. tauricum*” into *P. crassum* (following SCHMIDT-KITTLER 1976, SEMENOV 1989, 2001, and FRAILE 2015).

Protictitherium crassum was a small hyena with a viverrid-like appearance. It is very well-known

from many sites in Europe and Asia Minor, but no undoubted record from outside of this area exists. The only possible record from Africa (“*Ictitherium cf. arambourgi*” in GINSBURG 1977) was regarded to closely resemble African *Protictitherium punicum* by WERDELIN (2019).

With an estimated body mass of about 8 kg (FRAILE 2015), *P. crassum* was the size of a recent fox (*Vulpes vulpes*), but presumably lived in larger groups as is indicated by the numerous findings in Batallones (FRAILE 2015). Analysis of postcranial material points to a terrestrial, cursorial type of locomotion (CRUSAFONT-PAIRO & PETTER 1969, GINSBURG 1999, FRAILE 2015).

The species is very abundant in Late Miocene locations reflecting more arid environments (Spain, Greece, and Turkey). It is, however, also found in localities interpreted to reflect a more humid environment in France (DEPÉRET 1892), Germany (MORLO 1997) or Slovakia (SABOL & HOLEC 2002), but it never is numerous in such sites. This is also the case for Eppelsheim, from where *P. crassum* is the only known hyaenid, yet with only two specimens. Even though large to very large carnivorans are well known from these sediments (TOBIEN 1955), it was only after the Vallesian crisis that larger, bone-cracking hyaenids arrived in Germany, as is verified by the diverse record of hyaenids and percrocitids from MN 11 of Dorn-Dürkheim (MORLO 1997). Before their arrival, bone consuming carnivorans were represented in the Dinotheriensande by amphicyonids and ursid hemicyonines like *Amphicyon eppelsheimensis* WEITZEL, 1931, *Dinocyon teilhardi* JOURDAN, 1861 (see TOBIEN 1955), and “*Pseudocyon sansaniensis* aff. *serus*” (KUSS 1965).

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