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RESEARCH PAPER

Hyaenid remains from the Late Miocene of Kutschwan (Shanxi Province, China)

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Abstract

The hyaenid family reached its peak of spatial range and taxonomic diversity during the Late Miocene, including a very wide range of different forms that were spanning throughout the Old World. Particularly, the fossil record of the family in the Balkans and China has been extremely variable during that time. The present paper deals with cranial and postcranial hyaenid material from the Late Miocene locality of Kutschwan (Shanxi Province, China). The specimens were identified as *Hyaenictitherium wongii*, a widespread species with well-known occurrences throughout Eurasia during the Vallesian and the Turolian. The material presents some notable features, such as the enlarged M1, M2 and m2 that point towards a more basal form of the species. However, the statistical analysis of the variability of these characters points towards intraspecific divergence based on selective release, instead of taxonomically significant adaptive traits. The postcranial material conforms very well to the known material of *H. wongii* from other localities, indicating an agile cursorial hunter. This species is the only carnivoran found in Kutschwan, based on the current data.

Keywords Hyenas · Neogene · *Hyaenictitherium* · *wongii* · *hyaenoides* · Eurasia

Abbreviations

GPIMH	Geological and Palaeontological Institute and Museum, Hamburg, Germany
GPIT	Palaeontological collection of the University of Tübingen, Germany
MGL	Musée de Géologie de Lausanne, Switzerland
NHMA	Natural History Museum of Aegean, Mytilinii, Samos, Greece
NHMBA	Naturhistorisches Museum, Basel, Switzerland
NHMBE	Naturhistorisches Museum, Bern, Switzerland
NHMW	Naturhistorisches Museum, Wien, Austria
NMNHS	National Museum of Natural History, Sofia, Bulgaria
SNSB-BSPG	Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany

Introduction

The family Hyaenidae Gray, 1869, today includes only four species that are restricted to Africa and Southwest Asia (e.g. Westbury et al. 2021). However, the fossil record of the family includes numerous species that cover a very wide range of different forms (e.g. Werdelin 1991; Werdelin and Solounias 1991; Turner et al. 2008). The hyaenids reached their maximum diversity and dominance in the Old-World ecosystems during the Late Miocene (Werdelin 1991; Werdelin and Solounias 1991; Turner et al. 2008). Many different Late Miocene hyenas are attributed to the group of ictitheres, which included forms that were similar in morphology to the extant canids (Thenius 1966; Crusafont Pairó and Petter 1969; Semenov 1989, 2008; Werdelin and Solounias 1991; Turner et al. 2008; Coca-Ortega and Pérez-Claros 2019; Pérez-Claros and Coca-Ortega 2020; Kargopoulos et al. 2021, 2023).

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The Late Miocene fossil record of China includes several of these forms, belonging to the genera *Ictitherium* Wagner, 1848, and *Hyaenictitherium* Kretzoi, 1938. However, it also includes some more derived (non-ictithere) hyaenids, such as *Palinhyaena* Qiu et al., 1979, *Lycyaena* Hensel, 1862, *Chasmaporthetes* Hay, 1921, *Adcrocuta* Kretzoi, 1938, and *Dinocrocuta* Schmidt-Kittler, 1976, and some more basal forms, such as *Tunguritis* Colbert, 1939, and the recently erected genus *Gansuyaena* Galiano et al., 2022 (Zdansky 1924; Colbert 1939; Werdelin and Solounias 1991; Tseng and Wang 2007; Galiano et al. 2022).

The herein presented material was collected by Dr Albert Tafel, during his expedition in China and Tibet in 1905 (Tafel 1914). During his studies in the locality of Kutschwan (Shanxi Province, China), Tafel collected some fossil mammalian remains from the red clays of the Chinese Loess Plateau along the Yellow River. Unfortunately, the exact geographic location of the site as well as the taphonomical data from the excavation are not known. The material was transported to Tübingen, where it was firstly studied by Killgus (1922, 1923), who reported the presence of rhinos, hipparions, giraffids, bovids and hyenids in the locality. A more recent study by Kampouridis et al. (2022) reviewed the holotype material of the rhinocerotid *Parelasmotherium schansiense* Killgus, 1923, recovered from Kutschwan. Killgus (1922, 1923) reported some hyaenid remains from the locality as "*Palhyaena hipparionum*". No other carnivoran specimens were discovered in the material from Kutschwan. As discussed in Werdelin and Solounias (1991), this name is now considered a nomen dubium and material initially published under this name possibly corresponds to a range of different forms. The aim of the present study is to review these specimens, ascribe them to a taxonomically valid species and compare them to all relevant hyaenid forms.

Material and methods

All the material is stored in the Palaeontological Collections of the Eberhard Karls University of Tübingen (Germany). All measurements were taken using a digital calliper and rounded in the first decimal point. Dental nomenclature and measurements follow Werdelin (1988a). Statistical analysis was performed in PAST 4.03 (Hammer et al. 2001), and the figures were edited in Adobe Photoshop. Structures that are present in more than one specimen and do not exhibit morphological divergences are described in a common frame, while deviations from the standard morphology are furtherly noticed.

Systematic palaeontology

Class **Mammalia** Linnaeus, 1758

Order **Carnivora** Bowdich, 1821

Family **Hyaenidae** Gray, 1821

Genus ***Hyaenictitherium*** Kretzoi, 1945

Hyaenictitherium wongii (Zdansky, 1924)

Material. Partial skull—GPIT-PV-86045; partial skull and mandible—GPIT-PV-86046; partial skull—GPIT-PV-86047; right proximal radius—GPIT-PV-122894; right calcaneus—GPIT-PV-86044; left tarsus with astragalus, scaphoid, cuboid, cuneiforms and the proximal MtII–MtIV—GPIT-PV-122893; left tarsus with scaphoid, cuboid, cuneiforms and MtI–MtV—GPIT-PV-86048.

Description. The specimens GPIT-PV-86046 (Fig. 1c) and GPIT-PV-86047 (Fig. 1a) retain the mesial part of the skull, including the premaxilla, maxilla, upper dentition, nasals and part of the zygomatic, frontal and temporal bones. On the other hand, the specimen GPIT-PV-86045 (Fig. 1b) preserves the distal part of the skull, including the distal part of the maxilla and upper dentition, as well as the whole braincase.

The rostrum is relatively long and narrow. Its minimum width is at the plane the diastema between P1 and P2. The anterior palatine foramina are relatively short, and they are situated at the plane of the canines. The posterior palatine foramina are far smaller, and they are situated at the plane of the distal accessory cusp of P2. The suture between the maxilla and the palate is at the plane of the contact between P3 and P4. There is a deep pit in the maxilla, distolingually of the upper carnassial. The pyriform is moderately wide and high. The infraorbital foramen is relatively large, and it is situated above the distal part of P3. Above the paracone of P4, there is a deep infraorbital pit (shallower in GPIT-PV-86046). The postorbital processes of the zygomatic and the frontal are relatively well developed. The postorbital constriction is well marked, and two faint converging temporal lines are present. The mesial part of the braincase is slightly compressed laterally, but the remaining part indicates the presence of a relatively wide braincase and zygomatic arches. The sagittal crest is not very well developed. The palate ends slightly distally to the plane of M2. The choana is relatively long and narrow. The postglenoid process is high, narrow and hook-like. The basioccipital is relatively flat and triangular. The auditory and occipital regions are mostly damaged or absent. The only remaining features include the damaged eustachian opening and foramina ovale and rotundum, as well as a small mastoid process. Cranial measurements can be found in Table 1.

The three incisors are very similar to each other, even though there is some considerable size difference between them. Their main cusp is spatulate and forms a distal shelf

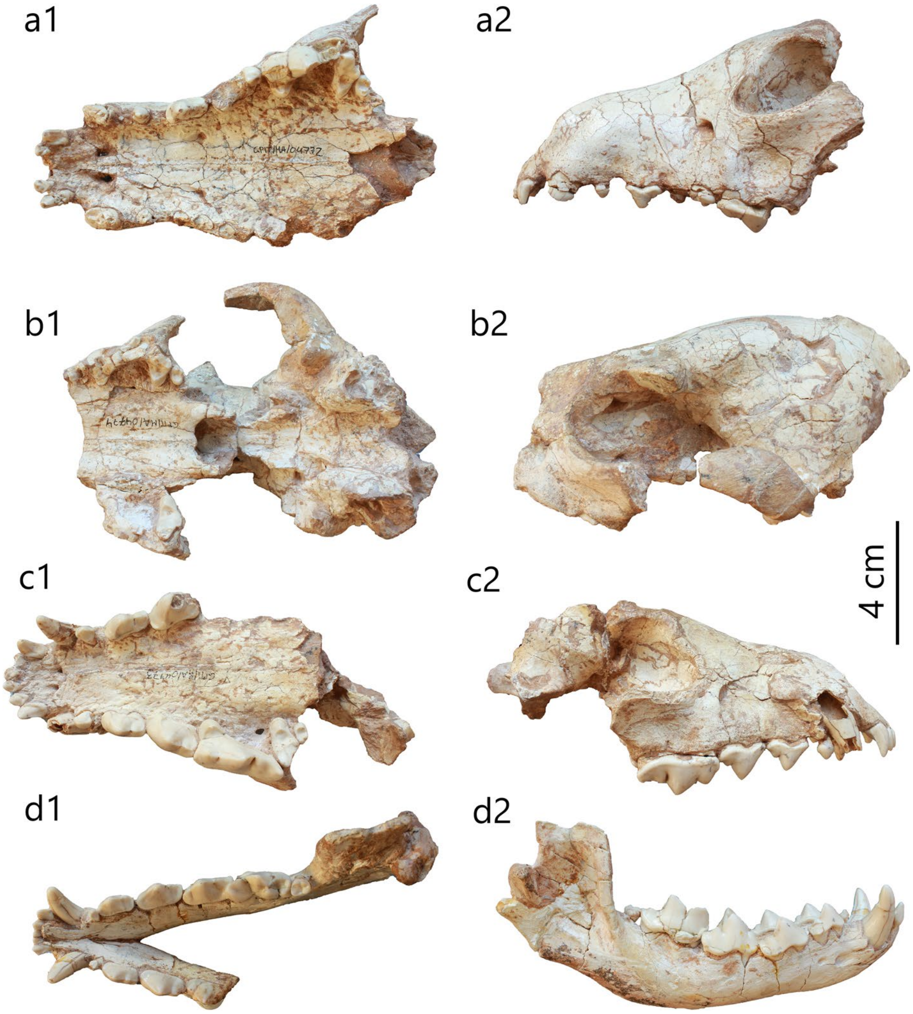

Fig. 1 Cranial material of *Hyaenictitherium wongii* from the Late Miocene of Kutschwan in (1) occlusal and (2) lateral views: **a** GPIT-PV-86047, skull, **b** GPIT-PV-86045, skull, **c–d** GPIT-PV-86046 skull and mandible

Table 1 Measurements (in mm) of the skulls of *Hyaenictitherium wongii* from Kutschwan. Measurements in parentheses were taken in approximation, due to specimen damage

	GPIT-PV-86047	GPIT-PV-86046	GPIT-PV-86045
Nasal length	78.4	61.1	
Palate length	(118.0)		
Basioccipital length			28.4
Premolar row length	70.9	68.0	
Molar row length	15.4	14.9	13.5
Width at I3	25.9	26.1	
Width at C	44.0		
Minimum palate width	38.0	33.7	
Width at P4			68.5
Preorbital constriction	45.4		37.1
Postorbital constriction			34.5
Choana breadth			13.8
Mastoid breadth			58.9
Endocranium width			55.9
Endocranium height			54.9

that covers the whole distal base of the tooth. This shelf is symmetrical in I1 and I2, but stronger in the lingual part of the tooth in I3, which has a more buccally bent main cusp. Additionally, I3 exhibits a fine crest in its buccal side that runs through most of the tooth's surface. The canines are damaged in GPIT-PV-86047 and not fully erupted in GPIT-PV-86046. However, their preserved parts indicate that, in regard to the general hyaenid morphology, they are relatively long and narrow with a crest in their distal part. The cheek teeth exhibit finely wrinkled enamel and have well-developed cingula that are more evident in their distolingual sides. The first premolar is also spatulate and intermediate in size between I2 and I3, even though its lingual part is not as concave as in the incisors. The second and third premolars are very similar to each other. They have a high and acute main cusp, followed by a moderately developed distal accessory cusp. A strong crest runs from the tip of the main cusp towards the mesiolingual part of the cingulum. Their only differences are the larger size and the wider distal part of P3. The upper carnassial is long and high. The highest cusp is the paracone, followed by the metastyle and the lower parastyle. The paracone and the metastyle are separated by a deep carnassial notch. The parastyle has a small crest in the base of its mesiolingual part. The protocone is well developed, and it is situated approximately at the same plane as the parastyle. The M1 is relatively well developed, and it has three roots. The highest cusp is the protocone, which is followed buccally by a wide and shallow valley. The paracone and the metacone have approximately the same size, and they are connected by a low crest. An additional buccolingual crest is present lingually of the paracone. The buccal side of the tooth is far more expanded in the level of the paracone than in the level of the metacone. The second upper molar is oval and far smaller than M1, and it has two roots in GPIT-PV-86046 and possibly three in GPIT-PV-86047. Similarly to the latter, it has three cusps: a lingual protocone, a mesiobuccal paracone and a distobuccal metacone that have approximately the same size. A deep valley is present at the middle of the tooth. Measurements of the upper dentition can be found in Table 2.

The specimen GPIT-PV-86046 preserves a mandible (associated to the aforementioned skull) that is lacking the distal part of the left hemimandible and is slightly damaged in the right coronoid process (Fig. 1c). Part of it has been restored using gypsum. The mandibular condyle is relatively strong and is clearly situated above the level of the toothrow. Based on the shallow masseteric fossa, the very tight arrangement of the cheek teeth, the not fully erupted canine and the absence of dental wear, it probably belongs to a relatively young individual, in agreement with the morphology of the relevant skull. The hemimandible is relatively slender and short in terms of height. There are no distinct diastemata, with the exception of that of c–p1. The mandibular symphysis is relatively long, reaching the middle/distal plane of p2. There are two oval mental foramina ventrally to the second premolar: a smaller distal one and a larger mesial one. The size difference between the two foramina is greater in the left hemimandible in comparison with the right one. The ventral profile of the mandible presents two deepened points: a smaller one ventrally to p2 and a larger one below m2–p4, forming a structure similar to a subangular lobe. The masseteric fossa is relatively shallow, and its mesial border hardly reaches the distal border of the toothrow. The remaining part of the coronoid process is slender and high. The angular process and the mandibular condyle are relatively damaged, and they do not allow a detailed description. Mandibular measurements can be found in Table 3.

The preserved lower dentition is complete in the right hemimandible, whereas the left hemimandible is missing the i3, part of p3 and the p4–m2. The first incisors are asymmetrical, having a groove in their buccal side that expands in both the mesial and distal faces of the teeth. Additionally, their occlusal profile is approximately flat or slightly inclined in mesiodistal view. On the other hand, the second incisors exhibit a central cuspid (creating an acuter occlusal profile), which is far more developed in the third incisor. In the latter, there is a distinct lingual cuspid. The incisors are gradually larger and exhibit more robust cingulids that are not very prominent. The canines are not fully erupted. They are long, high, slightly curved, buccally inclined, and they exhibit a clear ridge in their distal part. Their enamel is faintly wrinkled, as in the larger cheek teeth. The first premolar is single-rooted, spatulate, resembling the i1 and i2, but its overall shape is more rhomboidal. The second and third premolars are very similar to each other, being asymmetric with a high main cuspid and moderately developed distal accessory cuspid and distal cingulid. The third premolar is relatively longer and the distal end of its cristid joins the cingulid in a structure that resembles a tiny cuspulid. The fourth premolar is surrounded by a more developed cingulid that is stronger in its distal part. The tooth exhibits a secondary distal accessory cuspid. The lower carnassial is long and high, with a strong cingulid in its buccal side. The trigonid is relatively high, covering most of the tooth's length, with the protoconid being the largest cuspid followed by the comparably large paraconid. The metaconid is moderately developed, and most of its buccal side is confluent to the protoconid. The talonid is relatively small, with a restricted valley that is lower lingually than buccally. The developed entoconid and the hypoconid form the lingual and buccal walls of the talonid, respectively, whereas a tiny hypoconulid is present in its distal border. Finally, the second molar is oval in occlusal view, with the exception of a buccal extension that creates a more triangular dental profile. The lingual border of the tooth is straighter, and it hosts a large metaconid

Table 2 Metrical comparison of the upper dentition (in mm) of *Hyaenictitherium wongii* from Kutschwan to other material of this species, as well as *Hyaenictitherium hyaenoides*, *Palinhyaena reperta* and *Lycyaena dubia* from various localities in China. Comparative data from Werdelin (1988a)

	GPIT-PV-86047		GPIT-PV-86046		GPIT-PV-86045		*Hyaenictitherium wongii*	*Hyaenictitherium hyaenoides*	*Palinhyaena reperta*	*Lycyaena dubia*
	L	R	L	R	L	R				
I1L		5.1	4.5	4.9						
I1W		4.7	4.4	4.0						
I2L	5.1			5.6						
I2W	4.8			4.8						
I3L	6.7		7.3	7.4						
I3W	6.4		6.8	6.8						
CL		12.5								
CW		8.0								
P1L	5.6		6.1	5.9			4.8–6.2 5.4 (*n* = 12)			
P1W	5.2			5.4			3.8–4.8 4.4 (*n* = 10)			
P2L	14.1		15.3	14.8			11.1–15.1 13.3 (*n* = 83)	14.0–17.2 15.4 (*n* = 19)	12.5–15.0 13.7 (*n* = 9)	15.4–17.8 16.5 (*n* = 8)
P2W	6.5			7.3			5.4–7.7 6.5 (*n* = 99)	7.4–10.0 8.6 (*n* = 19)	7.1–8.6 7.9 (*n* = 10)	8.1–9.4 8.8 (*n* = 8)
P3L	18.3			18.7			14.3–19.0 16.7 (*n* = 91)	18.0–22.5 19.7 (*n* = 19)	17.0–19.5 18.0 (*n* = 10)	19.6–22.5 20.8 (*n* = 9)
P3W				9.8			7.4–10.8 9.0 (*n* = 108)	9.8–13.1 11.4 (*n* = 22)	10.0–12.6 11.4 (*n* = 11)	10.7–12.3 11.6 (*n* = 9)
P4L				27.3			23.1–29.2 25.5 (*n* = 100)	27.4–33.4 30.0 (*n* = 17)	24.4–28.7 26.8 (*n* = 10)	31.1–34.7 32.0 (*n* = 8)
P4Wa	14.2			15.5			11.2–16.8 14.0 (*n* = 92)	15.5–19.2 17.0 (*n* = 21)	12.9–16.4 15.1 (*n* = 11)	15.5–18.4 17.3 (*n* = 9)
P4Wbl				10.2			7.2–10.6 8.6 (*n* = 107)	9.1–11.8 10.4 (*n* = 19)	8.5–10.3 9.5 (*n* = 10)	9.1–11.0 10.0 (*n* = 9)
M1L	9.1			10.5		8.8	6.0–9.2 7.9 (*n* = 82)	7.0–8.9 8.0 (*n* = 14)	5.5–7.4 6.5 (*n* = 9)	6.0–8.1 7.3 (*n* = 5)
M1W	16.1			16.5		14.3	13.2–18.1 15.0 (*n* = 82)	14.3–18.7 16.3 (*n* = 14)	12.1–15.8 14.2 (*n* = 6)	14.6–17.5 16.2 (*n* = 4)
M2L	4.1			4.0	4.0		3.1–5.6 4.5 (*n* = 73)	3.1–5.0 4.1 (*n* = 12)	3.3–3.8 3.5 (*n* = 6)	
M2W	6.7			6.8	6.4		4.5–8.6 6.9 (*n* = 79)	4.7–6.2 5.6 (*n* = 13)	3.5–6.4 5.2 (*n* = 8)	

and a smaller entoconid, whereas the buccal border is more semicircular, and it hosts a shorter and higher hypoconid and a longer and lower protoconid. Measurements of the lower dentition can be found in Table 4.

The specimen GPIT-PV-122894 (Fig. 2a) is a right proximal radius, broken at the midshaft and damaged in the proximal epiphysis. The remaining part of the proximal epiphysis is oval with a deeper central part. The mesial part of the epiphysis is marked by a distally bending border. Two tuberosities can be found distally of the proximal epiphysis: a larger lateral one and a smaller posteromedial one. The anterior face of the radius is convex, whereas the posterior face is straight to convex.

The calcaneus (GPIT-PV-86044; Fig. 2b) is slightly damaged in the posterior part (possibly due to the young age of the individual), and the sustentaculum tali is completely broken. It is relatively high and narrow with a very marked ridge posteriorly to the articular surfaces for the astragalus. The latter is divided in two surfaces: the ectal facet, which is preserved, and the sustentacular facet, which is destroyed. However, it base remains and it is evident that it was situated far from the distal part of the calcaneus. In the same sense, the space between the ectal facet and the articular surface for the cuboid is relatively long and large, marked by faint grooves. The peroneal tubercule is present, and the groove for peroneus longus is well marked. Finally, the articular

Table 3 Measurements (in mm) of the *Hyaenictitherium wongii* mandible of GPIT-PV-86046 from Kutschwan

	GPIT-PV-86046
Condyle to symphysis	134.2
Angular process to symphysis	137.4
Mandibular corpus height at p3	19.7
Mandibular corpus height at p4	21.5
Mandibular corpus height at m1	26.0
Mandibular corpus height at m2	26.2
Premolar row length	51.9
Molar row length	28.6
Cheek teeth length	76.2
Toothrow length	96.4
Dentary length	126.9
Proximal masseteric border to symphysis	100.7

surface for the cuboid is almost oval in shape, but its medial border is bent mesially.

The remaining two specimens (GPIT-PV-122893 and GPIT-PV-86048; Fig. 2c and d, respectively) correspond to two articulated tarsi. The description concerns both specimens. The astragalus is present only in GPIT-PV-122893, and it is moved from its natural position, as it has fallen distally, with its dorsal side lying on dorsal part of the remaining tarsus. The head of the astragalus is wide and is divided from the rest of the bone through a short neck. The plantar surface is marked by two articular surfaces: a long and narrow medial sustentacular facet and a short and wider lateral ectal facet. The two surfaces are separated by a deep groove. The scaphoid is partially destroyed in GPIT-PV-86048, so the description is based mainly on GPIT-PV-122893. The proximal articular surface for the astragalus is oval and elongated with a distinct rim and a shallow middle part. Its plantar surface hosts two tubercules: a larger lateral one and a smaller medial one. The scaphoid reaches its maximum height in its dorsomedial part. The cuboid is relatively high and wide, with a strong plantar oblique tuberosity that is followed distally by a deep groove. The first cuneiform (entocuneiform) is better preserved in GPIT-PV-86048, being relatively elongated and tightly attached to the rest of the tarsus. Its medial face is divided by a faint crest. Its distal articular surface is oblique, convex and smooth. A small rudimentary MtI can be traced in its distal end. The remaining bones (cuneiforms and metatarsals) are very densely packed, and they do not allow for a description of articular surfaces. It is worth mentioning that the entocuneiform is enlarged with a large hook with the groove for peroneus longus. The metatarsals are also elongated with convex dorsal and concave plantar surfaces. The MtIII and MtIV are longer than MtII and MtIV, but the absence of the distal epiphyses of the MtIII–MtIV does not allow for any measurements. The remaining distal epiphyses (in MtII and MtV) are globular, enlarged and with a strong plantar sagittal crest. Measurements of the postcranial material can be found in Table 5.

Discussion

Comparisons

There are several medium-sized hyaenid species in the Late Miocene of China, as already noted in the introduction. The genera that are considered herein for comparisons are *Chasmaporthetes*, *Palinhyaena*, *Lycyaena*, *Ictitherium* and *Hyaenictitherium*. The much smaller-sized and primitive *Tungurictis* and *Gansuyaena* as well as the much larger-sized and derived *Dinocrocuta* and *Adcrocuta* do not belong to this group, and they are excluded from the comparisons, based solely on size and evolutionary stage. The remaining genera are dealt with in more detail below, based on respective literature sources and personal observations.

The genus *Chasmaporthetes* is a dominant hyaenid during the Pliocene and Pleistocene, but its reports in the Miocene are far less frequent. Detailed reviews of the characteristics and the temporospatial range of this genus can be found in Kurtén and Werdelin (1988), Werdelin et al. (1994) and Tseng et al. (2013). The only Late Miocene species of *Chasmaporthetes* from China is the fragmentary known *Chasmaporthetes exitelus* Kurtén and Werdelin, 1988. The Kutschwan specimens differ from this species, and the genus *Chasmaporthetes* in general, in the following characteristics: smaller size, longer rostrum, non-stepped frontal profile, presence of M2 and m2, less developed P4 metastyle in regard to the paracone, m1 metaconid present and m1 talonid with three cuspids.

The species *Palinhyaena reperta* Qiu et al., 1979, is the only species of the genus *Palinhyaena*. It consists of a transitional form between the cursorial meat/bone eaters (*Lycyaena*, *Chasmaporthetes* and *Hyaenictis*) and the true bone-cracking crocutoids (e.g. *Adcrocuta*) (Qiu et al. 1979; Werdelin and Solounias 1991; Coca-Ortega and Pérez-Claros 2019). This form can be differentiated from the material from Kutschwan by its shorter rostrum, the more mesially situated palatine foramina, the absence of a diastema between C and P1 in adult individuals and the much wider upper and lower premolars (Tables 2 and 4; Fig. 3).

The genus *Lycyaena* is represented in the Late Miocene of China by the species *Lycyaena dubia* Zdansky, 1924, which has been found in numerous localities (Zdansky, 1924; Werdelin 1988a; Werdelin and Solounias 1991). This is the East Asian counterpart of the European *Lycyaena chaeretis* (Gaudry, 1861). These two forms are very

Table 4 Metrical comparison of the lower dentition (in mm) of *Hyaenictitherium wongii* from Kutschwan to other material of this species, as well as *Hyaenictitherium hyaenoides*, *Palinhyaena reperta* and *Lycyaena dubia* from various localities in China. Comparative data from Werdelin (1988a)

	GPIT-PV-86046		*Hyaenictitherium wongii*	*Hyaenictitherium hyaenoides*	*Palinhyaena reperta*	*Lycyaena dubia*
	L	R				
i1L	3.9					
i1W	2.7	2.6				
i2L	5.0					
i2W	3.9	3.8				
i3L		5.6				
i3W		5.8				
cL	10.5	10.7				
cW	8.9	9.0				
cH	19.9	20.5				
p1L	3.3	3.6				
p1W	3.4	3.5				
p2L	13.4	12.9	10.6–13.6 12.2 (*n* = 77)	12.4–15.7 14.3 (*n* = 14)	11.9–13.0 12.3 (*n* = 7)	14.8–16.7 15.5 (*n* = 5)
p2W	6.5	6.4	5.0–7.0 5.9 (*n* = 83)	7.1–8.8 7.7 (*n* = 15)	7.2–8.0 7.6 (*n* = 8)	6.8–7.3 7.1 (*n* = 5)
p3L	16.6	17.2	13.4–17.1 15.3 (*n* = 77)	15.5–19.2 17.5 (*n* = 14)	15.0–16.7 15.6 (*n* = 8)	18.7–19.1 18.9 (*n* = 3)
p3W		7.9	6.2–8.5 7.3 (*n* = 85)	8.2–10.3 9.5 (*n* = 16)	9.0–10.0 9.5 (*n* = 10)	9.0–9.8 9.5 (*n* = 5)
p4L		19.3	14.7–19.0 17.0 (*n* = 66)	18.3–21.8 20.1 (*n* = 13)	16.4–17.8 17.1 (*n* = 11)	21.2–22.4 21.9 (*n* = 4)
p4W		9.1	7.1–10.3 8.2 (*n* = 74)	8.8–11.3 10.1 (*n* = 18)	8.7–10.1 9.6 (*n* = 12)	9.8–10.2 10.1 (*n* = 4)
m1L		22.9	17.7–23.1 20.3 (*n* = 66)	19.0–25.1 22.9 (*n* = 14)	20.3–21.5 20.9 (*n* = 7)	22.4–23.8 23.1 (*n* = 4)
m1Ltr		16.7	13.0–14.9 14.1 (*n* = 14)	13.7–19.6 17.6 (*n* = 14)	15.3–18.6 16.5 (*n* = 9)	17.3–18.8 18.1 (*n* = 4)
m1Wtr		10.7	7.4–10.2 8.6 (*n* = 63)	9.0–11.2 10.1 (*n* = 15)	8.3–9.3 9.2 (*n* = 8)	9.0–10.0 9.5 (*n* = 4)
m1Wta		9.4				
m2L		6.7	4.8–7.0 5.8 (*n* = 36)	4.7–6.6 5.4 (*n* = 7)	4.5–4.9 4.7 (*n* = 3)	
m2W		6.7	4.0–5.8 5.1 (*n* = 36)	4.3–5.6 5.0 (*n* = 7)	4.2–4.4 4.3 (*n* = 3)	

similar to each other, and they may be conspecific (Zdansky 1924; Werdelin 1988a; Werdelin and Solounias 1991). There are several differences between these two species and the herein described material. In particular, *Lycyaena* is characterized by considerably larger size (Tables 2 and 4; Fig. 3), shorter rostrum, more developed accessory cusps and cuspids, more developed lingual side of P3, absence of M2 and very restricted M1 in comparison with the Kutschwan hyaenid.

The genus *Ictitherium* includes several species expanded through Late Miocene, the most common form being *Ictitherium viverrinum* Roth and Wagner, 1854 (Werdelin 1988b; Semenov 1989; Werdelin and Solounias 1991). Even though these forms exhibit a wide range of size and an equally wide spectrum of morphological traits, the present material can be differentiated from them based on the comments of Semenov (2008): temporal lines merging relatively caudally, ventrally protruding mental edge of the mandible, P4 protocone not protruding mesially to the parastyle and relatively small m1 talonid with reduced cuspids. The less protruding mental edge of the mandible (GPIT-PV-86046) is attributed to the relatively young age of the individual. Semenov (2008) also mentions some more distinguishing characters between the two groups, including the presence of the alisphenoid canal and the larger size of M2, m1 talonid and m2 based on some ratios in Ictitheriinae. However, these traits do not seem to have strong differentiative value. The alisphenoid canal is present in several specimens of *H. wongii*, such as SNSB-BSPG-2008-XXXIV-38 (from Maragheh, Iran; Late Miocene) and MGL-82842 (from Samos, Greece; Late

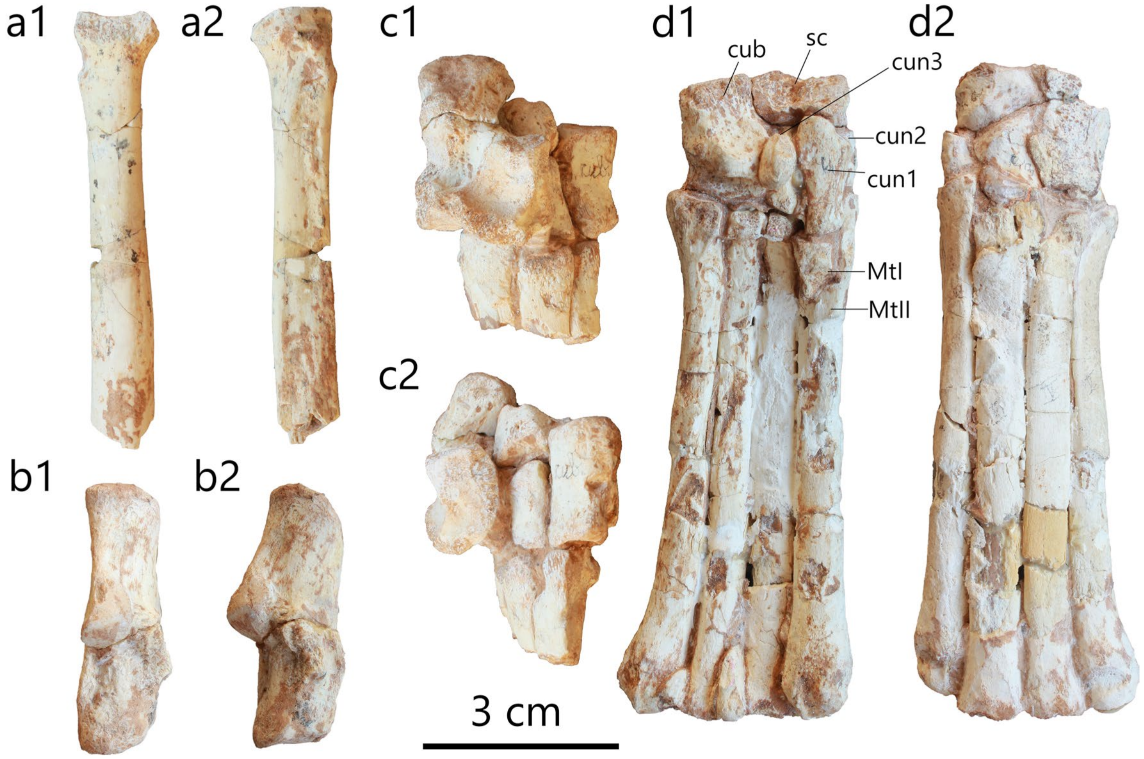

Fig. 2 Postcranial material of *Hyaenictitherium wongii* from the Late Miocene of Kutschwan: **a** GPIT-PV-122894, right proximal radius in **a1** anterior and **a2** posterior views, **b** GPIT-PV-86044, right calcaneus in **b1** anterior and **b2** anterolateral views, **c** GPIT-PV-122893, left tarsus and metatarsus in **c1** anterior and **c2** lateral views, **d** GPIT-PV-86048, left tarsus in **d1** plantar and **d2** dorsal views showing the cuboid (cub), scaphoid (sc), cuneiforms (cun), MtI and MtII

Table 5 Measurements of the postcranial material of *Hyaenictitherium wongii* from Kutschwan in mm. Measurements in parentheses were taken in approximation, due to specimen damage

Element	Code	H	APDp	TDp	APDm	TDm	APDd	TDd
Radius	GPIT-PV-122894		14.0		11.0	6.6		
Calcaneus	GPIT-PV-86044	(48.0)	(13.0)		18.6	11.0	13.3	
Astragalus	GPIT-PV-122893	27.4	9.7	14.3				18.1
Cuboid	GPIT-PV-122893	18.0	8.1	11.2		8.9	9.0	12.5
	GPIT-PV-86048	18.1	9.0	10.9	12.4			11.7
Scaphoid	GPIT-PV-122893	9.8			15.6	14.1		
	GPIT-PV-86048	10.2						
Entocuneiform	GPIT-PV-122893	15.3						
	GPIT-PV-86048	16.6	6.4	9.2		6.0		6.2
Mesocuneiform	GPIT-PV-122893							
	GPIT-PV-86048	8.3		5.2	6.8		7.5	
Ectocuneiform	GPIT-PV-122893				19.3			
MtI	GPIT-PV-86048	9.3		6.1				
MtII	GPIT-PV-122893		12.7					
	GPIT-PV-86048	80.7			6.9	7.2	10.1	10.2
MtIII	GPIT-PV-122893		14.1					
	GPIT-PV-86048		15.0		7.7	6.7		
MtIV	GPIT-PV-122893		11.7	6.2				
	GPIT-PV-86048		12.3					
MtV	GPIT-PV-122893	81.9	10.3		5.9	7.0	9.8	9.3

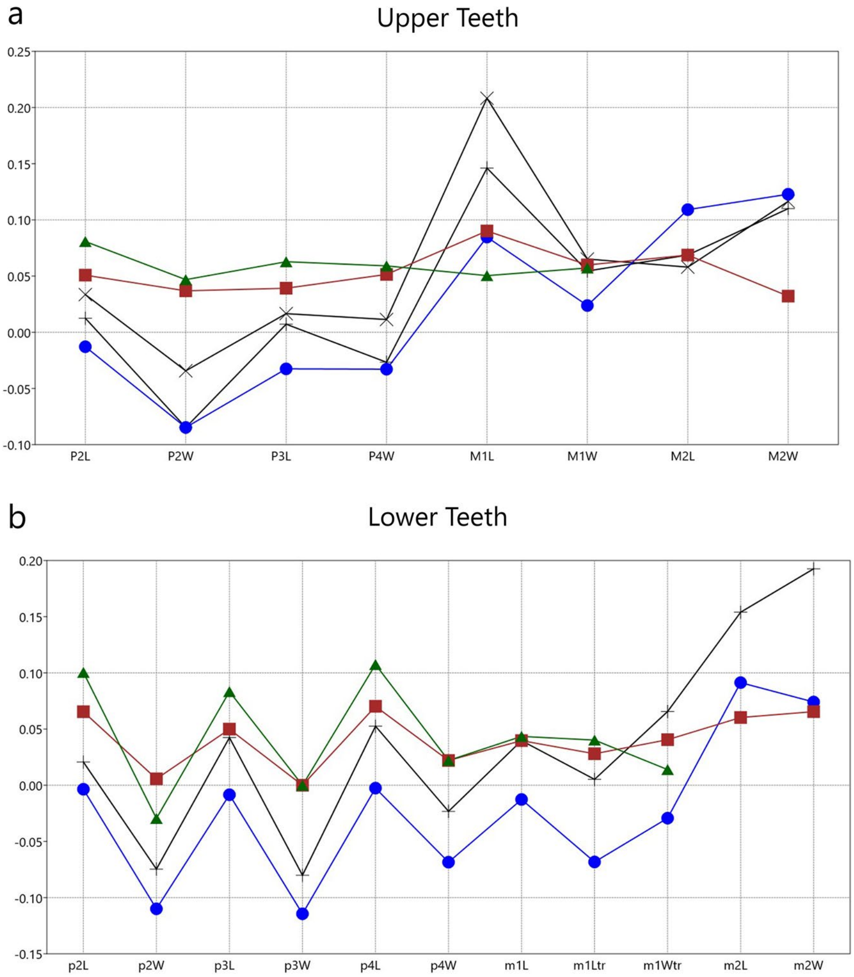

Fig. 3 Simpson's diagram comparing the measurements of the **a** upper and **b** lower teeth of the material from Kutschwan (black X and cross for GPIT-PV-86046 and 86047, respectively) to the mean values for *Palinhyaena reperta* (standard), *Hyaenictitherium wongii* (blue dots), *Hyaenictitherium hyaenoides* (red squares) and *Lycyaena dubia* (green triangles). Comparative data from: Werdelin (1988a), as also shown in Tables 2 and 4

Miocene). Additionally, the ratios provided by Semenov (2008) for quantifying the relative size of M2, m1 talonid and m2 do not seem to fit to the dataset collected by the authors. As discussed below, there are numerous specimens of *H. wongii* from Samos that exhibit relatively well-developed distal molars. Therefore, these characters are herein not considered as taxonomically significant, at least concerning the present material.

Semenov (1989) erected the genus *Hyaenotherium* Semenov, 1989, to include "*Hyaenotherium magnum*" Semenov, 1989, and "*Hyaenotherium wongii*". Through the diagnosis and the comparisons he provided, he differentiated *Hyaenotherium* from *Hyaenictitherium* based on the undivided posterior bony lip of the external auditory canal, the shorter and blunter jugal (paraoccipital) process, the lack of a hook on the pterygoid and the possession (usually) of a three-rooted M2 in the former. However, these differentiations, even though notable, are herein considered insufficient for the establishment of a new genus. As mentioned before, the intraspecific variability of the size of M2, including the number of its roots, is very high and it does not present clear patterns between different forms. The pterygoids are very rarely preserved in fossil specimens, especially the hook at their distal end, so it would be highly impractical to rely on such a trait to distinguish two genera. The remaining two traits are also not easily discriminated, and it would be unfeasible to be unable to distinguish two genera if this region is missing or destroyed. Therefore, it is herein preferred to consider *Hyaenotherium* as a junior synonym of *Hyaenictitherium*, following the approach of Zhang et al. (2002), de Bonis et al. (2005) and Tseng and Wang (2007). Additionally, as Werdelin and Solounias (1991) noted, "*Hyaenotherium magnum*" exhibits no significant differences from *H. wongii*, especially when the huge variability of the latter is taken into account. Therefore, the synonymy of these forms is also followed here.

In general, the morphology of the specimens fits perfectly with that of the species *Hyaenictitherium wongii*. The species *H. wongii* is known from several other localities in the Late Miocene of Eurasia and particularly of China (Zdansky 1924; Werdelin 1988a; Werdelin and Solounias 1991; Tseng and Wang 2007). Even though the measurements are higher than the average values for the species (Fig. 3), they are inside the known metrical range based on material from various localities in China (Tables 2 and 4; data from Werdelin 1988a). The most noteworthy characters that differentiate the Kutschwan material from the average form of the species are the relatively narrow p3 (p3W/p3L = 45.9%; stage 0 of character 12 in Tseng and Wang 2007), the more developed m2 and the relatively large M1 (P4L/M1W = 165%; stage 1 of character 5 in Tseng and Wang 2007). However, given the apparent presence of considerable intraspecific variability in this species (Werdelin 1988a), these traits (even though they are worth mentioning) are considered to have no taxonomic value. Similar values are evident in several specimens of the same species from the island of Samos (Late Miocene, Greece) studied in several museum collections (e.g. NHMW, NHMA, MGL, NHMBE). The relatively large M1 (P4L/M1W ≤ 165%) has also been seen in the specimens NHMW-1911/0001/0019, NHMA-MTLA-200 (also published by Koufos 2009), MGL-82849, MGL-82957, MGL-82843, MGL-82842, MGL-39697, NHMBE-5047 and NHMBA-Sam 36. Additionally, the relatively narrow p3 (p3W/p3L ≤ 47%) has been found in NHMW-1911/0005/0779, GPIMH-3013a (published by Lehmann 1984, but based on personal measurements), MGL-82834 and MGL-82851. Therefore, both deviations from the norm of the species are known and are to be expected in a large dataset. Additionally, the morphology and metrics of the postcranial material fits very well to material of this species from Samos housed in MGL.

The species *Hyaenictitherium hyaenoides* is very similar to *Hyaenictitherium wongii* (Tseng and Wang 2007). Additionally, the two species have been known to be contemporary (Fig. 3 of Tseng and Wang 2007) and even coexisting in the several localities throughout Asia (Werdelin and Solounias 1991), including some localities from their type material (Zdansky 1924). However, these two forms represent a transition from a more plesiomorphic ecomorph (*H. wongii*) towards a larger, bone-cracking ecomorph (*H. hyaenoides*). Concerning the size differentiation between the two forms, *H. hyaenoides* is larger than *H. wongii* (Tables 2 and 4; Fig. 3). However, the specimens from Kutschwan occupy an intermediate position between the two species, fitting both to the higher values of *H. wongii* and the lower values of *H. hyaenoides*. The dental morphology is more informative in terms of specific discrimination as *H. hyaenoides* has developed a more derived dentition, including less developed upper molars (stage 3 of character 5 in Tseng and Wang 2007) and more robust premolars (characters 12–14 in Tseng Wang 2007). These characteristics present the aforementioned trend towards the bone-cracking ecomorph (Werdelin and Solounias 1991; Turner et al. 2008; Coca-Ortega and Pérez-Claros 2019). In this sense, the specimens from Kutschwan clearly fit to the morphology of *H. wongii*. In fact, as stated above, the upper molars in the recovered material are considerably large, and the premolars are relatively narrow in comparison with *H. hyaenoides*.

Evolutionary interpretation of the intraspecific variability

The variability of the relative size of the proximal premolars and distal molars of the genus *Hyaenictitherium* is herein investigated as significantly important for the ecological and evolutionary study of this genus. Werdelin (1988a, Tables 3 and 4) studied a very wide sample of individuals of *H. wongii* and *H. hyaenoides* from various localities in Eurasia and provided the summary statistics for their dental measurements. A very important innovation of this paper was the consideration of the coefficient of variation (V) of the datasets, which is widely ignored in the literature due to the low number of individuals in palaeontological studies. Werdelin (1988a) calculated the *V* of dental measurements, not only in fossil hyaenids, but also in extant ones, discussing the possibilities of high variability in a specific character inside the range of a species. A similar approach was also followed for other hyaenid forms (Werdelin 1988b, 1990; Werdelin et al. 1994). The V values for the upper and lower teeth of *H. wongii* and *H. hyaenoides* are herein depicted in Fig. 4.

It is evident that the proximal premolars (P2 and p2) and the distal molars M2 and m2 exhibit the highest values of *V*, whereas the "central" cheek teeth (P3–M1 and p3–m1) have lower values. This differentiation is also proven correct by using t test comparison between the two groups of teeth for both species (p value < 0.01; Table 6). Similar patterns can be seen in other hyaenid species (Werdelin 1988a, 1988b, 1990; Werdelin et al. 1994).

Darwin (1859) noted that "an organ, when rendered useless, may well be variable, for its variations cannot be checked by natural selection". This is a principle that has been used in evolutionary and ecomorphological studies concerning many different living forms. For example, one application of this principle concerns the shape and size variability of the bony labyrinth of mammals. Billet et al. (2012) discovered considerably high variability in the inner ear of the three-toed sloths (in comparison with other xenarthrans), since these animals do not require elaborate sense of balance and speed. On the other hand, Mennecart and Costeur (2016) noted that the labyrinth variability in a tragulid species was low, indicating that balance and pace were important for this form.

A term that is closely associated with the principle of Darwin is Probable Mutation Effect (PME) as stated and defined by Brace (1964) and margined by Byles (1972). PME defines that when a biological structure is not functional, the relaxation of selective pressure allows mutations on the genes responsible for this structure to flourish inside

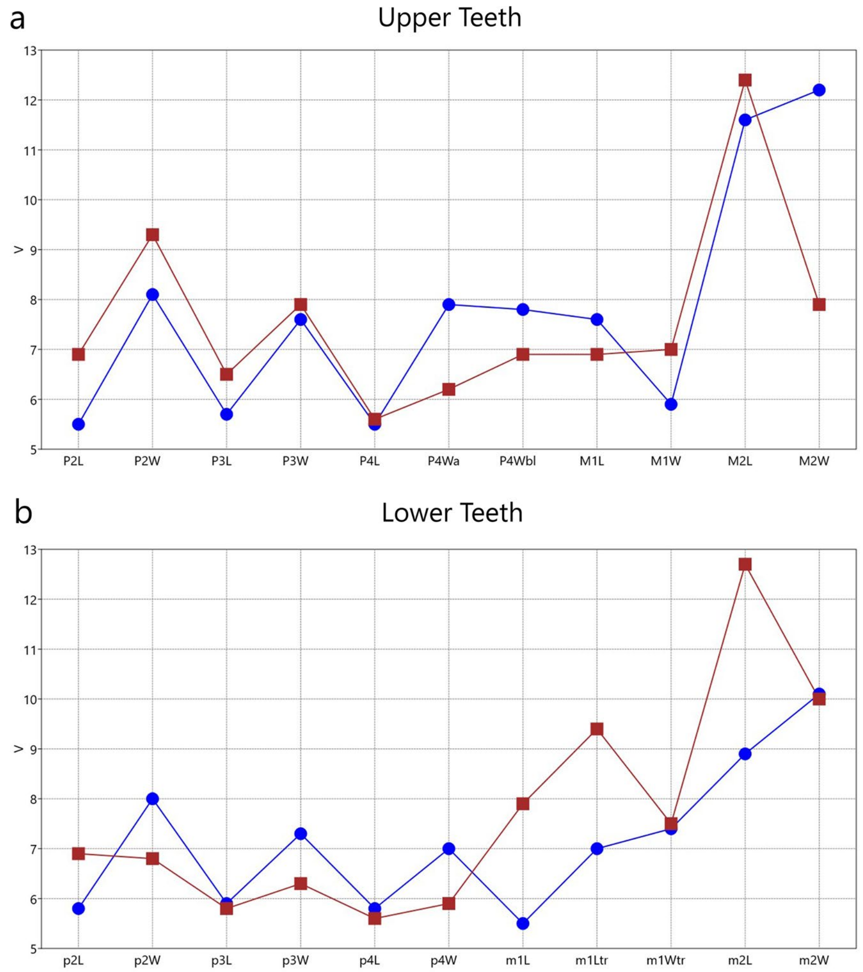

Fig. 4 Values of coefficient of variation for dental measurements of the **a** upper, and **b** lower teeth for *Hyaenictitherium wongii* (blue dots) and *Hyaenictitherium hyaenoides* (red squares) based on the data of Werdelin (1988a)

a certain population. This term has mainly been used to discuss reductions in human dentition, and the exact details of the model have been debated (Calcagno and Gibson 1988). However, its basic principle remains consistent to that of Darwin, and it has been used in non-human taxa. Tague (2002) compared the variability in the lengths of metacarpals in some primates, in order to infer their developmental and evolutionary significance. Wilkens (1988) reported high variability in the eyes of cave populations of a characid fish, as vision became insignificant for their biological needs.

All the aforementioned studies converge in the main essence of Darwin's assumption, noting that high variability of a character is linked to selective release, which is associated with the restricted functionality of this feature. In the case of ictitheres, the high variability in terms of dental size could be interpreted as an indicator of the release of selective pressure in the proximal premolars and the distal molars. In fact, most ecomorphological studies for carnivorans (including ictitheres, other hyaenids or canids) have been focused on the upper and lower carnassials as main indicators of diet (Crusafont-Pairó and Truyols-Santonja 1956; Meloro and Raia 2010; Tarquini et al. 2020). Even when premolars are considered, usually only the largest lower premolar (p3 or typically p4) is studied (e.g. Van Valkenburgh 1989; Van Valkenburgh and Koepfli 1993). Consequently, the ecomorphological significance of the mesial premolars and the distal molars was not considered as indicative, at least for this taxonomic group.

Table 6 Results of t test comparison between the V values of the variable teeth (P2, p2, M2 and m2) and the stable teeth (P3, P4, M1, p3, p4, m1) for *H. wongii* and *H. hyaenoides* based on the data from Werdelin (1988a)

	Hyaenictitherium wongii		*Hyaenictitherium hyaenoides*	
	Variable	Stable	Variable	Stable
N	8	14	8	14
Mean	8.775	6.7071	9.1125	6.8143
Difference between means	2.0679		2.2982	
t	2.8558		3.0927	
p	0.00977		0.00574	

Fig. 5 Comparison of the upper dentition of **a** *Hyaenictitherium wongii* (GPIT-PV-86046) to that of **b** *Canis lupus* (NMNHS-460). Not in scale

If this line of thought is followed for the ictitheres, there are two results that can be inferred. Firstly, it is evident that the larger size of these teeth in the Kutschwan specimens (as well as in the other similar specimens mentioned before) cannot be interpreted as a taxonomically significant character, as it is clearly not an adaptation (sensu Leitch 2017; and references therein), but merely a result of selection release. Secondly, these teeth seem to be less significant for the dietary needs of these animals. It is evident from their morphology that they are far less robust than the respective teeth of the large canids, e.g. *Canis lupus* Linnaeus, 1758 (Fig. 5). Therefore, it can be deduced that ictitheres were not using their distal cheek teeth for durophagous feeding or for grinding food particles at the degree that the large canids do today. However, this is a hypothesis that needs to be tested through various methods in the future.

Based on this discussion, it can be deduced that the specimens from Kutschwan would fit to a more basal position in this ecomorphological trend. This is based mostly on the large size of the upper molars. Unfortunately, the absence of detailed stratigraphic data does not enable a more thorough temporospatial analysis of this trend. However, as more data are published on these forms, it is inevitable to discuss these notes in more depth.

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Data availability The authors confirm that the data supporting the findings of this study are available within the article.

Declarations

Conflict of interest There is no conflict of interest.

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