

First Record of *Hoplictis* (Carnivora, Mustelidae) in East Asia from the Miocene of the Ulungur River Area, Xinjiang, Northwest China



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Abstract: The first unequivocal remains of medium to large-sized mustelids from the middle Miocene Halamagai and Kekemaideng formations have been found in the Ulungur River area, Xinjiang, northwestern China. These new fossils are referred to the hypercarnivorous mustelid *Hoplictis* Ginsburg, 1961 and denote the first record of the genus in East Asia. We define *Hoplictis baihu* n. sp., for the mustelid from Tiersihabahe (Halamagai Fm.), which represents the smallest species of the genus. This primitive form is closer to *H. florancei* and *H. noueli* than to *H. anatolicus* and later, larger and more derived *Hoplictis* spp., from Europe and North America. A large toothless mandible from Duolebulejin (Kekemaideng Fm.) is assigned to *Hoplictis* cf. *helbingi*, and it presumably might represent the first record of *H. helbingi* outside Western Europe. The systematic position of *Hoplictis* in relation to *Ischyriactis* with which it is similar is clarified. The occurrence in East Asia of two species of *Hoplictis* greatly expands the known distribution and diversity of the genus, and supports a Palaearctic Neogene dispersal event of carnivorans between Europe and Asia during the late Shanwangian–early Tunggurian equivalent to MN5–6 in Europe, and indication of another dispersal event from Europe to North America, through Northwest China during the late Tunggurian, equivalent to MN7–8 in Europe.

Key words: vertebrate paleontology, paleobiogeography, hypercarnivore, *Hoplictis*, *Ischyriactis*, Miocene, Xinjiang

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1 Introduction

The Mustelidae represent the largest living family of carnivorans and possesses an abundant fossil record in the early and middle Miocene of Europe and North America (e.g. Blainville 1842; Filhol 1872; Depéret 1892; Mayet 1908; Viret 1933, 1951; Helbing 1928, 1930, 1936; Dehm 1950; Ginsburg 1961, 1999, 2002; Roth 1989; Ginsburg and Morales 1992; Baskin 1998, 2005, 2017; Nagel et al., 2009; Peigné 2012; Valenciano et al., 2016, 2018). However, our understanding of Asiatic forms is more limited (Babbitt 1999, Peigné et al., 2006), despite Asia being located between the two continents. Early Miocene mustelid remains from Asia are poorly documented (Peigné et al., 2006); they include *Mustela* sp. and *Proputorius* from the Xiejia and Sihong Faunas in China

(Qiu and Qiu 1995; Hunt 1996), the leptarctine Mustelidae *Kinometaxia guangpui* Wang et al., 2004 from Danghe, Tabenbuluk area of the northern Tibetan Plateau (Wang et al., 2004), an unidentified small mustelid from the DM16 locality in Damiao, Inner Mongolia (Zhang et al., 2011), and a P4 of another unidentified small mustelid from Kazakhstan (Kordikova et al., 2000: fig. 4e, f). The record of these forms in China during the middle Miocene is more complete. Mustelids from the Tunggur Formation (Fm.) in Inner Mongolia, of middle Miocene age, yield a better understanding of the family and the entire order (Qiu et al., 2013a and references herein). The local fauna of carnivores includes the immigrant North American mustelids *Leptarcus neimenguensis* Zhai, 1964, and *Sthenictis neimenguensis* Tseng et al., 2009, as well as *Melodon?* sp. (Colbert 1939). In Damiao, the Tunggurian DM01 locality, several mustelids are present, but no details were published by Zhang et al. (2011). The middle

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Miocene Halamagai Fm., located in Northwest China, is an additional significant formation in the country, which has yielded an interesting and rich assemblage of carnivorans (Wang et al., 1998; Bi et al., 1999; Ye et al., 2001a, b; Wu et al., 2003; Ye et al., 2005; Qiu et al., 2013b; Jiangzuo et al., 2018). This assemblage comprises the ailurids *Alopecocyon goeriachensis* (Toula, 1884) and *Simocyon* sp., the amphicyonids *Amphicyon ulungurensis* Qi, 1989, *Gobicyon zhegallo* Gabunia, 1981, *Cynelos* cf. *bohemicus* Schlosser, 1899, *Cynelos* aff. *helbingi* Dehm, 1950, and cf. *Cynelos* sp., the nimravid *Nimravus* sp., the felid *Pseudaelurus cuspidatus* Wang et al., 1998, as well as the hyaenids *Tungurictis spocki* Colbert, 1939, *Protictitherium intermedium* Schmidt-Kittler, 1976, *Protictitherium* sp., and *Thalassictis chinjiensis* (Pilgrim, 1932). The single mustelid described from the Halamagai Fm. is a fragmentary mandible of a juvenile with deciduous teeth and premolar germs, reported by Wang et al. (1998) as *Oligobunis?* sp., which could represent the first oligobunine mustelid found in the Old World. However, more material is needed to corroborate this important find. Neither the mustelids nor the other carnivoran remains from the Kekemaideng Fm. have been described.

The newly discovered fossil specimens reported herein from the middle Miocene of China are referred to the genus *Hoplictis* Ginsburg, 1961. This genus represents a hypercarnivorous mustelid recorded from the early Miocene to the early late Miocene of the Northern Hemisphere (Mayet 1908; Helbing 1930; Viret 1951; Bryant 1968; Crusafont-Pairó 1972; Edwards 1976; Gabunia 1973; Schmidt-Kittler 1976; Roth 1989; Baskin 1998, 2005; Pickford et al., 2000). Six species has been attributed to it: *Hoplictis florancei* (Mayet, 1908), from Pontlevoy-Thenay (type locality), France, early middle Miocene, MN5 (European Neogene Land Mammals Ages), and from Erkertshofen 2, Germany, late early Miocene (MN4) (Roth 1989); *Hoplictis noueli* (Mayet, 1908) from Artenay, France, (MN4); *Hoplictis anatolicus* (Schmidt-Kittler, 1976) from Çandır (type locality), Paşalar, and Mordogan in Turkey (MN5–6) (Gürbüz 1992; Kaya et al., 2003; Nagel 2003), and from Belometchetskaya in Belarus (MN6) (Gabunia 1973; Pickford et al., 2000); *Hoplictis helbingi* (Viret, 1951) from La Grive (type locality, MN7–8, France) and Castell de Barberà, Vallès-Penedès Basin, Spain, early late Miocene (MN9) (Crusafont-Pairó 1972); *Hoplictis?* *petteri* Crusafont-Pairó, 1972 from Can Llobateres I, Spain (MN9); and *Hoplictis* (= *Beckia*) *grangerensis* (Bryant, 1968) in North America during the late Clarendonian (North American Land Mammal Ages, c. MN9–10) both from Granger Clay Pit, Washington, and in the locality V6107 in the Contra Costa Group, Los Angeles, USA (Edwards 1976). Furthermore, the genus is present in the Love Bone Bed, Florida as *Hoplictis* sp. (Baskin 2005). In spite of this great diversity, the available material is scarce and comprises predominantly mandibular remains and isolated lower teeth, with the exception of an M1 of *H. noueli* from Artenay (Helbing 1930, fig. 3), a P4 of *H. helbingi* from La Grive (Viret 1951, pl. II, fig. 13), and quite a complete skull with mandibles and some

postcranial remains of *H. anatolicus* from Çandır (Schmidt-Kittler, 1976, fig. 20–24, pl. IA, B).

The aim of this work is to describe some of the unpublished remains of large mustelids from the Halamagai and Kekemaideng formations in Xinjiang, comparing them with small to large mustelids from the late Oligocene to late Miocene elsewhere in Asia, Europe, North America and Africa.

2 Localities and Formations

The Ulungur River area in the northern Junggar Basin (for location see Fig. 1) is one of the most important fossil site assemblages in Western China, with deposits ranging in age from the late Eocene to the late Miocene. The middle Miocene Halamagai Fm. has already produced abundant evidence of Carnivora, including so far five to seven amphicyonid species, two species of ailurids, one mustelid species, three species of hyaenids, one felid species and one possible nimravid species (Qi 1989; Wang et al., 1998, Jiangzuo et al., 2018). The base of the formation was estimated to be 17 Ma on the basis of palaeomagnetic correlation (Ye et al., 2012), and therefore the main part of the Halamagai Fm. corresponds to the late Shanwangian–early Tunggurian or MN5–6 in Europe (Qiu et al., 2013a). The Kekemaideng Fm., which overlies the Halamagai Fm. is thought to be late Tunggurian in age, equivalent to MN7–8 in Europe (Ye et al., 2012).

3 Material and Methods

The materials were collected by Sijian Xu and Jie Ye in 2017. All the material of *Hoplictis* from China studied here is housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP). For comparison we studied the original fossils of *Namibictis senuiti* Morales et al., 1998 from Arrisdrift, early-middle Miocene of Namibia (Morales et al., 1998, 2003) housed at the Museum of the Geological Survey of Namibia; *Iberictis azanzae* Ginsburg and Morales, 1992 from Artesilla, Spain, early Miocene, MN4 (Ginsburg and Morales 1992; Valenciano et al., 2018) housed at MPZ; *Iberictis buloti* Ginsburg and Morales, 1992 from els Casots, Spain, early Miocene, MN4 (Valenciano et al., 2018) housed at ICP; *Laphictis mustelinus* (Viret, 1933), from Can Mata 1 (Villalta Comella and Crusafont Pairó 1943; Petter 1963), Spain, middle Miocene MN7–8, housed at ICP; *Hoplictis helbingi* from Castell de Barberà (Crusafont-Pairó 1972), Spain, early late Miocene, MN9, housed at ICP; *Eomellivora fricki* (= *Hoplictis petteri*) from Can Llobateres I (Crusafont-Pairó 1972), Spain MN9, housed at ICP. We also studied *Martes munki* Roger, 1900 from La Grive, France, MN7–8, and *Martes burdigaliensis* Beaumont, 1974 from Vieux-Collonges, France, MN5 by casts housed at MNCN and a cast of *Hoplictis* (= *Beckia*) *grangerensis* (Bryant, 1968) from Granger Clay Pit, housed at AMNH. We further inspected photographs of *Dehmictis vorax* (Dehm, 1950) from Wintershof-West, early Miocene, MN3, Germany housed at BSPG; *Martes sansaniensis* (Lartet, 1851) and *Ischyricictis zibethoides* (Blainville, 1842) from Sansan, France, middle Miocene,



Fig. 1. Map localizing the fossil sites in the Halamagai and Kekemaideng formations, including the type localities of the new *Hoplictis* spp., in Xinjiang, Northwestern China.

MN6, such as *Hoplictis noueli* from Artenay, France, early Miocene, MN4, housed at NMB and MNHN, the early middle Miocene *Hoplictis florancei* from Erkerthofen 2, Germany, late early Miocene MN4, and Pontlevoy-Thenay, France, early middle Miocene, MN5 housed at BSPG and MNHN respectively; *Hoplictis anatolicus* from Candir, Turkey, middle Miocene, MN6 housed at BSPG; and *Hoplictis helbingi* from La Grive, France, MN7–8, housed at FSL.

Dental nomenclature follows Ginsburg (1999) and Smith and Dodson (2003). Measurements were made with digital calipers accurate to 0.02 mm.

Institutional abbreviations. AD, Arrisdrift collection, Museum of the Geological Survey of Namibia, Windhoek, Namibia; BSPG, Bayerische Staatssammlung für

Paläontologie und Geologie, Munich, Germany; FSL, Université Claude Bernard Lyon 1; GSI, Geological Survey of India, Kolkata, India; MNCN, Museo Nacional de Ciencias Naturales Madrid, Spain; MNHN: Muséum National d'Histoire naturelle, Paris, France; MPZ, collection of the former Museo Paleontológico de la Universidad de Zaragoza, currently housed at the Museo de Ciencias Naturales Universidad de Zaragoza, Zaragoza, Spain; NMB, Naturhistorisches Museum Basel, Switzerland; ICP, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Spain; IPS, collections from the ICP (formerly 'Institut de Paleontologia de Sabadell'); V, vertebrate collection housed at IVPP (Institute of Vertebrate Paleontology and Paleoanthropology), Chinese Academy of Sciences,

Beijing, China.

4 Systematic Paleontology

Order Carnivora Bowdich, 1821
 Suborder Caniformia Kretzoi, 1943
 Infraorder Arctoidea Flower, 1869
 Superfamily Musteloidea Fischer, 1817
 Family Mustelidae Fischer, 1817
 Genus *Hoplictis* Ginsburg, 1961

Type species. *Hoplictis florancei* (Mayet, 1908) from Pontlevoy-Thenay, France, early middle Miocene (MN5).

Referred species and type localities. *Hoplictis noueli* (Mayet, 1908) from Artenay (MN4, France), *Hoplictis anatolicus* (Schmidt-Kittler, 1976) from Çandır (MN6, Turkey), *Hoplictis baihu* n. sp. (Tieersihabahe, Halamagai Fm., c. MN5–6, China); *Hoplictis helbingi* (Viret, 1951) from La Grive (MN7–8, France) and *Hoplictis grangerensis* (Bryant, 1968) from Granger Clay Pit (Clarendonian, USA).

Original diagnosis. Modified from Ginsburg and Morales (1992), and Ginsburg (1999). Mustelid close to *Ischyriactis* but with a more hypercarnivorous tendency, with lingual part of M1 reduced, m1 slightly higher, narrower, and without metaconid and entoconid.

Emended diagnosis. Hypercarnivorous mustelid with long P4 with reduced protocone; M1 with metacone and lingual platform reduced; deep mandibular corpus; p4 high with posterior accessory cuspid; m1 relatively high, with metaconid reduced or absent, and slender talonid with a dominant hypoconid imbricated toward the protoconid and without entoconid.

Hoplictis baihu n. sp.

Figures 2a–f, 4a–c, 5a–c, Table 1

Derivation of name. Named in honour of the holy beast Baihu (Bái Hǔ in Chinese), a white tiger from traditional Chinese culture, which is considered to be the symbol of the West, in accordance of the western part of China where the new species was found and in relation to its hypercarnivorous felid-like m1.

Holotype. V24986, partial left hemimandible with c and p2 alveolus, and complete p3–m2.

Referred material. V25014, partial left hemimandible with p2, broken p3, p4 and a broken m1.

Type locality. Tieersihabahe, Xinjiang, China: Halamagai Fm., late Shanwangian or early Tunggurian, MN5–6.

Diagnosis. Small *Hoplictis* with short p2, m1 protoconid higher than paraconid, with reduced metaconid, and weak cingulid, and much reduced m2.

Differential diagnosis. Differs from *Hoplictis florancei*, *Hoplictis noueli*, *Hoplictis anatolicus*, *Hoplictis helbingi* and *Hoplictis grangerensis* by its smaller dimensions. It differs from *Hoplictis florancei*, *Hoplictis noueli* and *Hoplictis anatolicus* in the shorter p2, the lesser development of the p4 distal accessory cuspid, and in the weaker m1 cingulid. It differs from *Hoplictis florancei* in the presence of m1 metaconid. It differs from *Hoplictis anatolicus* in the slender p2 and p3, in the reduced m1

Table 1 Measurements (in mm) of mustelid teeth from the Ulungur River area

	p2	L	W	W/L			
V24986 (alveolus)	4.42		2.38				
V25014	5.32		2.72	0.51			
V24988 (alveolus)	10.10		5.52				
	p3	L	W	W/L			
V24986	5.46		3.22	0.59			
V25014	5.38						
V24988 (alveolus)	11.42		6.18				
	p4	L	W	W/L	Lp4/Lm1		
V24986	7.12		3.72	0.52	0.65		
V25014	7.52		3.52	0.47	0.54		
V24988 (alveolus)	13.88		7.46		0.68		
	m1	L	PL	AW	TrL	PW	TrH
V24986	11.02		4.42	4.48	8.58	3.72	7.02
V24988 (alveolus)	20.28			6.62			
	m2	L	W	W/L	Lm2/Lm1		
V24986	2.62		2.58	0.98	0.24		
V24988 (alveolus)	7.00		5.12		0.35		
	mandible	height p2	width p2	height m1	width m1	w/h p2	w/h m1
V24986		12.68	8.12	13.48	6.82	0.64	0.51
V24988		23.82	10.82	27.32	10.78	0.45	0.39

Abbreviations: EL, external length; IL, internal length; L, length; W, width; PL, paraconid length; AW, anterior (trigonid) width; PW, posterior (talonid) width; TrL, trigonid length; TrH, trigonid height.

metaconid, in the relatively broader m1 talonid, and in the much more reduced m2. Additionally, it differs from *Hoplictis helbingi* and *Hoplictis grangerensis* in the shorter m1 paraconid, in the presence of m1 metaconid, in the relatively broader m1 talonid and in the reduced m2.

Description. V24986 is a fragmentary left hemimandible with p3–m2 (Fig. 2a–c). The mandible is deep and massively built. The depth of the horizontal ramus is nearly uniform in the preserved part. The symphysis is elongated, its medial surface is rugose, and the attachment of the fibrocartilage pad is more conspicuous in the dorsal area of the symphysis. The distal part of the symphysis reaches the middle part of the p3. Three mental foramina are present in the anterior part of horizontal ramus. The anterior one is the smallest and is located at the caudal edge of the root of the canine. The middle one is the largest and is located at the boundary between the p2 and the p3. The caudal one is located at the distal part of the p3. The masseteric fossa is deep and its rostral edge reaches the boundary between the m1 and the m2. The alveoli for i1–i3 and canine are present (Fig. 2c). The canine, relatively large (measurements at the base 6.22×4.52 mm) and the p2 are broken at the most basal level of the crown. The p1 is absent (Fig. 2c). The p2 is double-rooted and oriented slightly distolingually. The larger distal root indicates that the tooth is distally broadened. The p3 is high and sharp. Buccally, the mesial cristid is nearly straight whereas the distal cristid is slightly concave. The widest part of the tooth lies in the posterior area. No accessory cuspids are present, but there is a small bulge in the base of the distal cristid. The p4 is mesiodistally enlarged in relation to the other premolars, and widened distally as is the cases in the p2–3. It has a similar height to that of the p3 and both teeth are probably higher than the m1 paraconid. A tiny mesial cingulid cusp is present at the mesial corner of the p4. A distinct distal accessory cuspid is also present and is located buccally at

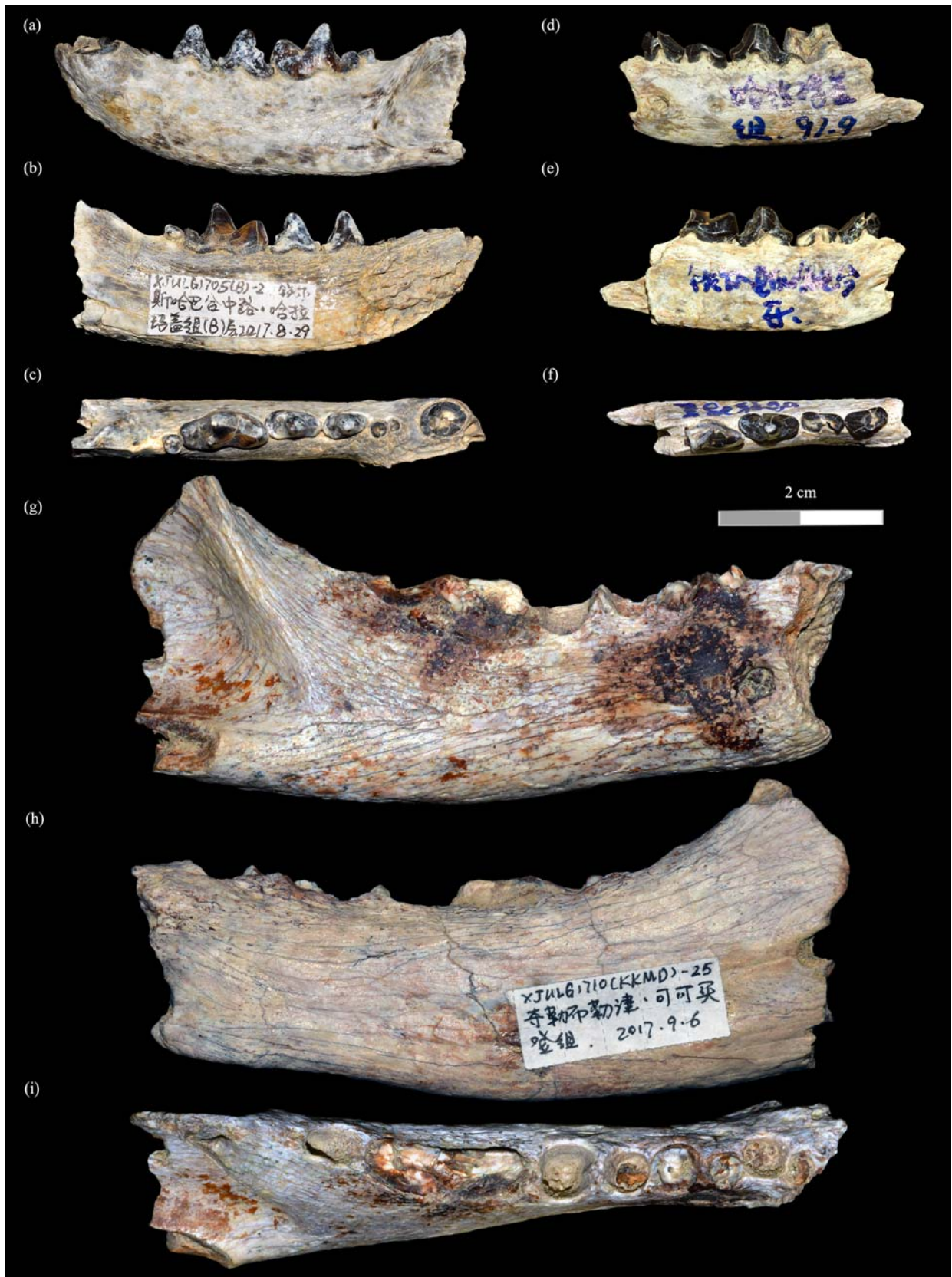


Fig. 2. New fossil material of *Hoplictis* from the Halamagai and Kekemaideng Formations (middle Miocene, China). (a–c) *Hoplictis baihu* n. sp., left hemimandible, V24986 (holotype) from Halamagai. (a) buccal view, (b) lingual view, (c) occlusal view; (d–f) *Hoplictis baihu* n. sp., partial left hemimandible, V25014 from Halamagai. (d) buccal view, (e) lingual view, (f) occlusal view; (g–i) *Hoplictis* cf. *helbingi*, partial right hemimandible, V24988 from Duolebulejin (Kekemaideng Fm.). (g) buccal view, (h) lingual view, (i) occlusal view.

the distal cristid of the main cuspid. The distal cingulid forms a short shelf. The m1 is relatively high, and its protoconid is manifestly higher than the paraconid and the main cuspids of the p3 and the p4. The width across the trigonid is distinctly greater than that across the talonid. The paraconid is rather elongated and slightly lingually turned. The lingual wall between the paraconid and the protoconid is concave. The protoconid leans slightly distally, with the distal slope of the protoconid rather steep. There is a large wear facet in the occlusal area of both paraconid and protoconid. The metaconid is very small, worn, and confined at the distolingual slope of the protoconid. The talonid is relatively short. The hypoconid is low and is located buccally on the talonid with its tip imbricated towards the protoconid (Fig. 2a–c). The hypoconulid is indistinct and the entoconid is absent. The m2 is much reduced being a tiny button-like tooth; its length and width are similar and no cuspid can be identified in the crown.

V25014 is a horizontal ramus of a left hemimandible with p2–4 and the mesial part of the m1 (Fig. 2d–f). The presence or absence of the p1 cannot be determined on the available material. However, the presence of a concavity with a subcircular edge in the place in which should be a p1 (Fig. 2f), might suggest that there was one and it was lost, being filled with mandibular bone while the mustelid was alive. The mandibular corpus is slightly smaller than that of V24986 but similar in overall morphology. Two mental foramina are present in the buccal side of the mandible. The mesial one is larger and located at the mesial part of the p2, whereas the distal one is smaller and located at the distal part of the p3. The symphysis is less rugose than that of V24986, and the distal part of the symphysis is less extended, only reaching the boundary between the p2 and the p3. The p2 is relatively elongated in relation to the p3. Neither accessory cuspids nor cingulids are present. The cuspid is broken at its apex. This cuspid is located at the mesial part of the tooth. The distal area of the premolar is widened. The p3 is broken and less broad than that of V24986. The p4 is morphologically close to that of V24986, but it is narrower distally and has a more centrally located distal accessory cuspid. Only the lingual part of the m1 paraconid and protoconid are preserved.

Hoplictis helbingi (Viret, 1951)

1892 *Aelurogale intermedia* Depéret, A.M.L., t.V, pl. I, fig. 3.

1951 *Ischyriactis helbingi* Viret, p. 52, pl. II, fig. 12a–c, 13a–b.

1972 *Ischyriactis (Hoplictis) helbingi* Crusafont-Pairó, p. 254, pl. I, fig. 1a–b.

Lectotype. Designated herein, a right m1 (1293) figured by Viret (1951, pl. II, fig. 12a–c) from La Grive, France (MN7–8).

Other localities. Castell de Barberà, Vallès-Penedès Basin, Spain (MN9) (Crusafont-Pairó 1972).

Diagnosis. Large *Hoplictis* with long P4 with reduced protocone; p4 alveolus distally widened; long and slender m1, without metaconid, compressed talonid in length and

width, and marked lingual entocristid; oval m2 alveolus.

Hoplictis cf. *helbingi*

Figures 2g–i, 4j–k, Table 1

Material. V24988, edentulous right hemimandible.

Locality. Kekemaideng, Xinjiang, China: Duolebulejin, Fm., c. late Tunggurian, MN7–8.

Description. Large hemimandible (Fig. 2g–i) with a relatively deep horizontal ramus, which gets deeper distally, and more massive than V24986. The depth behind the m1 is significantly greater than that behind the p2. The mesial part of the mandible is missing including part of the symphysis, the canine and p1. The distolingual area of the symphysis extends posteriorly to the middle part of the p2. There is only one large mental foramen present between p2 and p3. The masseteric fossa is deep and extends to the m2. All teeth are missing, except for a small portion of the m1, but the alveoli of p2–4 and m2 are preserved (Fig. 2i). Judging from the alveoli, p2–p4 are massive. In all three premolars, the distal root is larger than the mesial one, suggesting that these teeth are distally widened. We cannot assert the presence or absence of the p1, but judging from the preserved area near the mesial part of p2, it might be lost. The p2 is mesiobuccally and distolingually rotated, whereas the p3 and the p4 are nearly parallel to the sagittal plane. The m1 is broken at the most basal area of the crown. The mesial root is similar in size to the distal one. The overall morphology of the m1 judging from the alveolus indicates that it is an elongated and slender molar (Fig. 2i). The lingual wall is concave and the buccal one is convex. The m1 preserves the most distal area of the protoconid. The talonid is not buccolingually enlarged. The m2 is represented by a single oval alveolus.

5 Comparison and Discussion

The systematic position of *Hoplictis* has been controversial and intricate due to the scarcity of material and partly because of its similarities with *Ischyriactis* Helbing, 1930. Initially, the first remains of *Hoplictis* from Pontlevoy-Thenay, early middle Miocene (MN5) were described as a mutation of *Trochictis zibethoides*, sp. mut. *florancei* Mayet, 1908, and similarly a hemimandible from Artenay, late early Miocene (MN4) was described as a mutation of *Trochictis zibethoides*, sp. mut. *noueli* Mayet, 1908. This author, Mayet (1908), considered the small differences found between these new forms and the large *Trochictis zibethoides* (Blainville, 1842) from Sansan, middle Miocene (MN6)—defined initially as *Viverra zibethoides* Blainville, 1842—were not enough to create new species. However, Helbing (1930) established the monospecific genus *Ischyriactis* for *Trochictis zibethoides* from Sansan and placed in this new genus the latter material from Pontlevoy-Thenay and Artenay. Later, Ginsburg (1961) erected the genus *Hoplictis* as a subgenus of *Ischyriactis* recognizing *Ischyriactis (Hoplictis) noueli*, *Ischyriactis (Hoplictis) florancei*, and *Ischyriactis (Hoplictis) helbingi*; he subsequently raised it to generic status (Ginsburg and Morales 1992; Ginsburg 1999, 2002; Baskin 2005). The latter assignment to generic level is

followed herein.

There is a significant convergence in the dentitions of the large mustelids of Central Europe and Turkey during the early and middle Miocene, which is reflected in the complex systematic history described above. The dentition of the earlier species of *Hoplictis* (*H. noueli*, *H. florancei*, and *H. anatolicus*) from the early-middle Miocene (MN4–6) of Eurasia can easily be mistaken for those of the European *Ischyriactis* spp., particularly *I. zibethoides*, in the MN5–6, and also *Laphictis mustelinus* throughout MN4–8 (Viret, 1933; Helbing 1936; Villalta Comella and Crusafont Pairó 1943; Petter 1963; Roth 1989) and those of *Iberictis* spp., (Ginsburg and Morales 1992; Valenciano et al., 2018) from the early Miocene (MN4) of Western

Europe. However, *Hoplictis* possesses a longer P4 with a reduced protocone; more reduced M1 with a smaller metacone and a smaller lingual platform (excepting *H. anatolicus*, in which the lingual platform is not reduced); a somewhat higher m1 with a residual or even absent metaconid, and a slenderer and shorter talonid, as well as the existence of a dominant hypoconid imbricated toward the protoconid than those of these mustelids.

The dental morphology of *Hoplictis baihu* n. sp. from Tiersihabahe, Halamagai Fm., fits very well with the generic diagnosis despite its remarkably smaller size in comparison with all previously described species of this genus (Figs. 3 and 4). *Hoplictis baihu* shares with *H. noueli* and *H. florancei*, a primitive m1 talonid within the

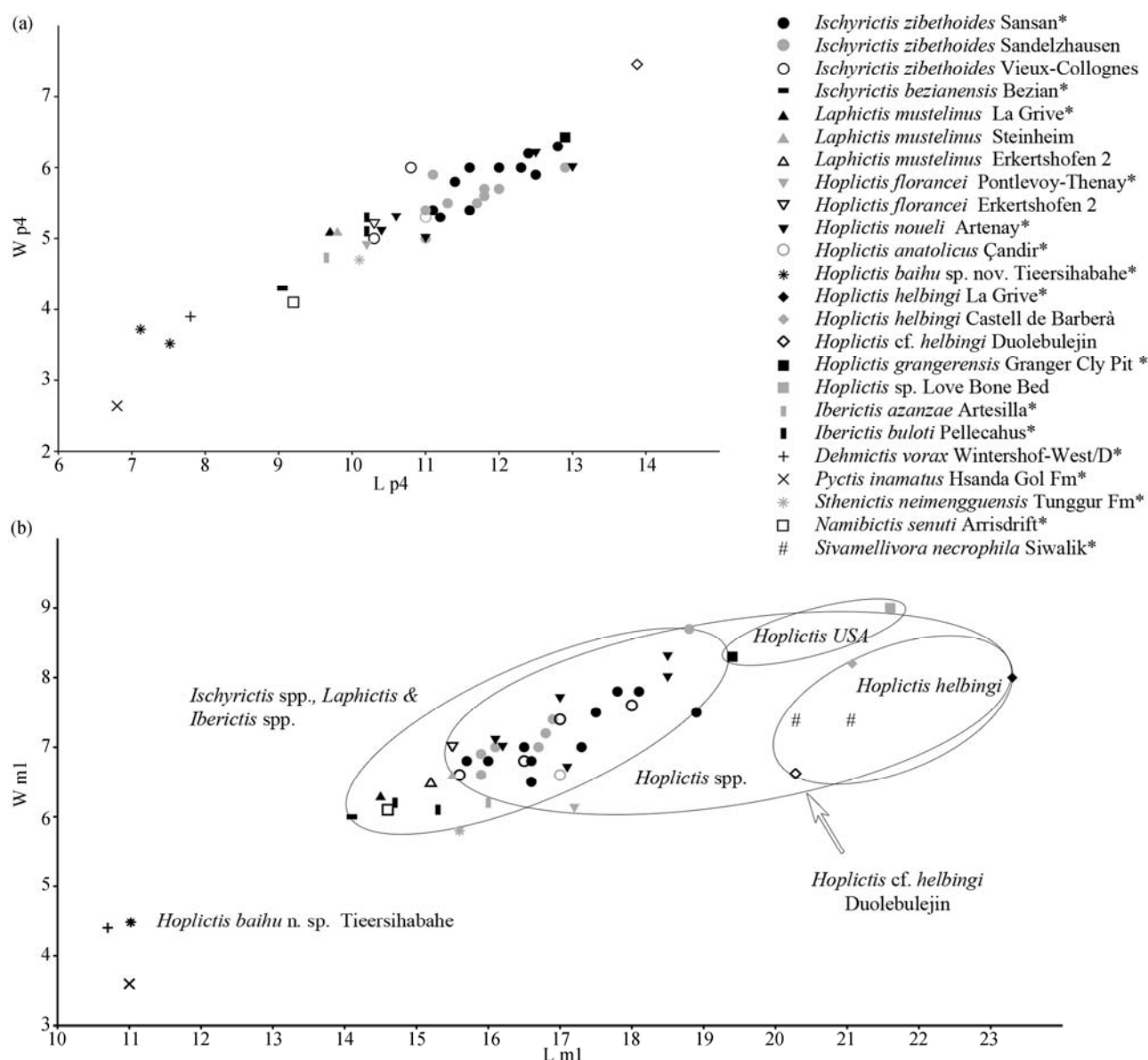


Fig. 3. Measurements (in mm) of the lower dentition of *Hoplictis* spp., *Ischyriactis* spp., *Iberictis* spp., *Laphictis mustelinus*, *Sivamellivora necrophila*, *Pycotis inamatus*, *Dehmictis vorax* depicted using bivariate plots of bucco-lingual width (W) vs mesio-distal length (L). (a) p4; (b) m1. * means the type locality of each species.

Sources: Mayet, 1908; Pilgrim, 1932; Viret, 1933; Helbing, 1936; Dehm, 1950; Viret, 1951; Mein, 1958; Bryant, 1968; Crusafont-Pairó, 1972; Edwards, 1976; Schmidt-Kittler, 1976; Roth, 1989; Ginsburg and Morales, 1992; Morales et al., 1998; Babbitt, 1999; Baskin, 2005; Nagel et al., 2009; Tseng et al., 2009; and Peigné, 2012.

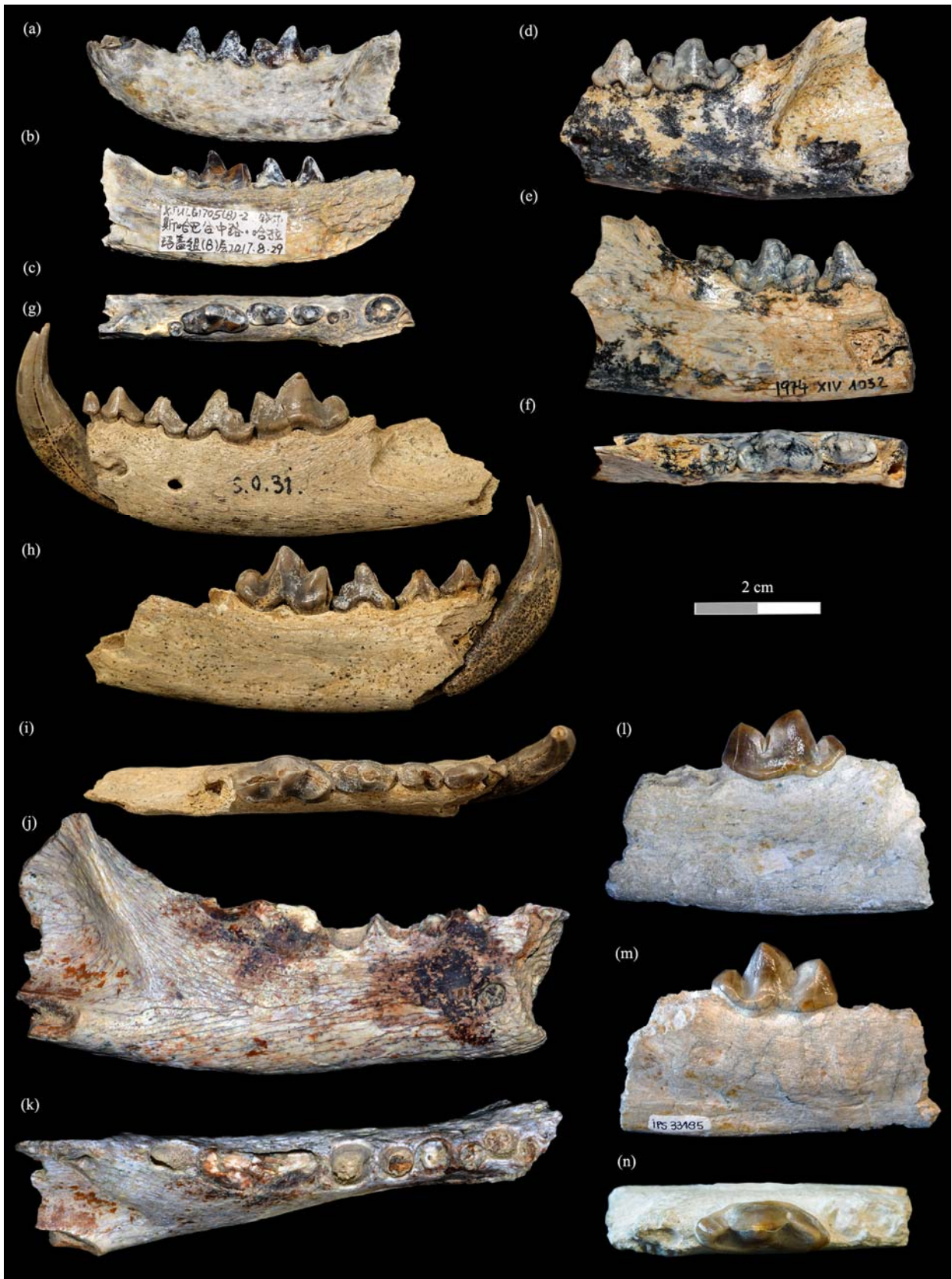


Fig. 4. Mandibles of species of *Hoplictis* considered in this manuscript.

(a–c) *Hoplictis baihu* n. sp., left hemimandible, V24986 (holotype) from Tiejersihabahe (Halamagai Fm.). (a) buccal view, (b) lingual view, (c) occlusal view; (d–f) *Hoplictis florancei* (type species), partial left hemimandible BSPG 1974- XIV- 1032 from Erkertshofen 2, MN4. (d) buccal view, (e) lingual view, (f) occlusal view; (g–i) *Hoplictis noueli*, partial left hemimandible NMB SO31 from Artenay, MN4. (g) buccal view, (h), lingual view, (i) occlusal view; (j–k) *Hoplictis* aff. *helbingi*, partial right hemimandible, V24988 from Duolebulejin (Kekemaideng Fm.). (j) buccal view, (k) occlusal view; (l–n) *Hoplictis helbingi*, partial left hemimandible IPS33185 from Castell de Barberà, MN9. (l) buccal view, (m) lingual view, (n) occlusal view.

group, which consists of a lesser buccolingual reduction of the talonid compared to those of the more derived taxa, *H. helbingi* and *H. grangerensis*, from the middle-late Miocene (Figs. 3 and 4). Likewise, other *Hoplictis* from MN4–6 such as *H. noueli* and *H. anatolicus* and the Halamagai mustelid still retain the m1 metaconid, which is lost in *H. florancei*, *H. helbingi* and *H. grangerensis*. The presence or absence of the metaconid in the sample of *H. noueli* from Artenay is variable, being lost in some specimens housed at MNHN (J. Morales pers. comm.), which reflects the trend towards the loss of the m1 metaconid even in the early species of the genus. The Halamagai mustelid differs from *H. florancei* and *H. noueli* (Fig. 4d–i) in having a shorter p2, a lesser development of the p4 distal accessory cuspid, and a weaker m1 cingulid. It also differs from *H. anatolicus* in having a slenderer p2 and p3, a further reduced m1 metaconid and a relatively broader m1 talonid, as well as a much more reduced m2. Additionally, the more derived later forms of *Hoplictis* (*H. helbingi* see Fig. 4l–n and *H. grangerensis*) are larger and slenderer, with the m1 paraconid higher than that of the Chinese one. A direct comparison with *Hoplictis? petteri* (Crusafont-Pairó, 1972) from Can Llobateres I, Vallès-Penedès Basin, Spain, early Vallesian, MN9, is not possible because it is known exclusively from a very large and robust P4. Consequently, because of the above, we erect *Hoplictis baihu* n. sp., which represents not only the first record of *Hoplictis* in Asia and also the smallest species of the genus. Among the earlier species, *H. baihu* would seem to be primitive, closer to *H. florancei* and *H. noueli* than to *H. anatolicus*, but also it possesses some derived features such as a very reduced m2. However, based on the available remains, it is not possible to obtain a deeper understanding of the evolutionary affinities of this taxon within this genus.

Compared with Eurasiatic gulonines (wolverines, martens and relatives), *H. baihu* is smaller than *Sthenictis neimenguensis* from the middle Miocene of the Tunggur Fm., Inner Mongolia, China (Tseng et al., 2009), and is similar in size to some Central European mustelids from early and middle Miocene (Fig. 3), such as *Dehmictis vorax* from the early Miocene, MN3, of Wintershof-West, Germany (Dehm 1950), and some primitive martens from middle Miocene of Europe (see Ginsburg 1999, Peigné 2012) (Fig. 5). The overall morphology of these ancient gulonines is very different from those of *H. baihu*. Among other features, they possess longer and slenderer lower premolars, smaller accessory cuspid in the p4; an m1 with a greater development of the metaconid, a longer, wider and more basined talonid and a more developed m2 than those of the Halamagai Fm., *Hoplictis*. Additionally, *D. vorax* and *Martes sansaniensis* have an enlarged entocristid unlike *H. baihu* (Fig. 5d–g). *Sthenictis neimenguensis*, *D. vorax* and *M. sansaniensis* have in common the presence of a relatively unreduced talonid basin, which becomes more trenchant in other hypercarnivorous mustelids such as the Holarctic *Hoplictis* spp., the Asiatic *Pycotis inamatus* Babbitt, 1999, and the African *Namibictis senuti*.

Pycotis inamatus from Hsanda Gol Fm., late Oligocene

of Mongolia (Babbitt 1999), is older but more evolved than *H. baihu*, which shares a similar size and an analogous morphology of the lower molars, including a reduction of the m2. However, *H. baihu* differs in having wider p3 and p4, the occurrence of a distal accessory cuspid in p4, and in the presence of a more primitive m1. In this sense, the m1 of *H. baihu* shows a metaconid, lower paraconid and hypoconid, and a lesser basined m1 talonid than those of *P. inamatus*. Although there is a strong resemblance in size and shape between the new Chinese form and *P. inamatus*, the highly derived state of the Mongolian mustelid, and the great temporal gap between the two makes the inclusion of this new taxon in *Pycotis* unlikely. Interestingly, the remarkable convergence in the dentition of these two forms can be understood by the possession of a comparable hypercarnivorous diet in these Asiatic taxa.

Namibictis senuti represents an additional hypercarnivorous form exclusively known from mandibular remains (Morales et al., 1998, 2003). Morales et al. (1998) described it from fossils of the late early Miocene from Arrisdrift, Namibia; it is a large mustelid, which is close in morphology to *Hoplictis* spp., (Figs. 4 and 5n–p). Like the former mustelids, it has a high p4, a residual m1 metaconid and a modified m1 talonid, being reduced in length and width. However, it possesses a taller distal accessory cuspid in the p4, and a more derived m1 talonid, the hypoconid of which is extremely beveled into the lingual wall, representing the main difference between the African mustelid and *Hoplictis*.

The absence of dentition in the hemimandible V24988 (Figs. 2g–i and 4j–k), assigned herein to *Hoplictis* cf. *helbingi* from Duolebulejin (Kekemaiden Fm.), makes taxonomic attribution difficult. The presence of the enlarged p2, p3, a reduced m2 and the absence of the m3 exclude it from the Ursidae (bears including hemicyonines). The m2 alveolus, albeit slightly oval in V24988, is not as elongated and double-rooted as in the Ailuridae (red pandas and relatives). The presence of a p2, absence of diastema between canine and lower premolars, and the more developed alveolus of m2 than those of the Felidae (cats and relatives) exclude it from this family. The occurrence of a relatively slender p2 and p3, and relatively enlarged distal root in m1 in comparison with the Hyaenidae (hyaenas) and extinct hyaena-like Percrocutidae prevent its attribution to either of these families. In this sense, the only family of carnivores to which V24988 can be assigned is to the Mustelidae, albeit a diverse group, because of the enlargement and robusticity of the alveoli of the premolars and the reduction of the post-carnassial molars. The large dimensions of the hemimandible V24988, means that its inclusion in the European Miocene mustelids is unlikely, notably *Iberictis* Ginsburg and Morales, 1992, *Ischyriictis*, and *Laphictis* Viret, 1933, and understandably not in *Hoplictis baihu* either (Fig. 3). Nevertheless, its size is comparable to the mandibles of some giant mustelids found in Eurasia and North America (*Eomellivora* Zdanksy, 1924, *Hoplictis* and *Plesiogulo* Zdanksy, 1924), although both *Eomellivora* and the gulonine *Plesiogulo* appear in China exclusively during the late Miocene

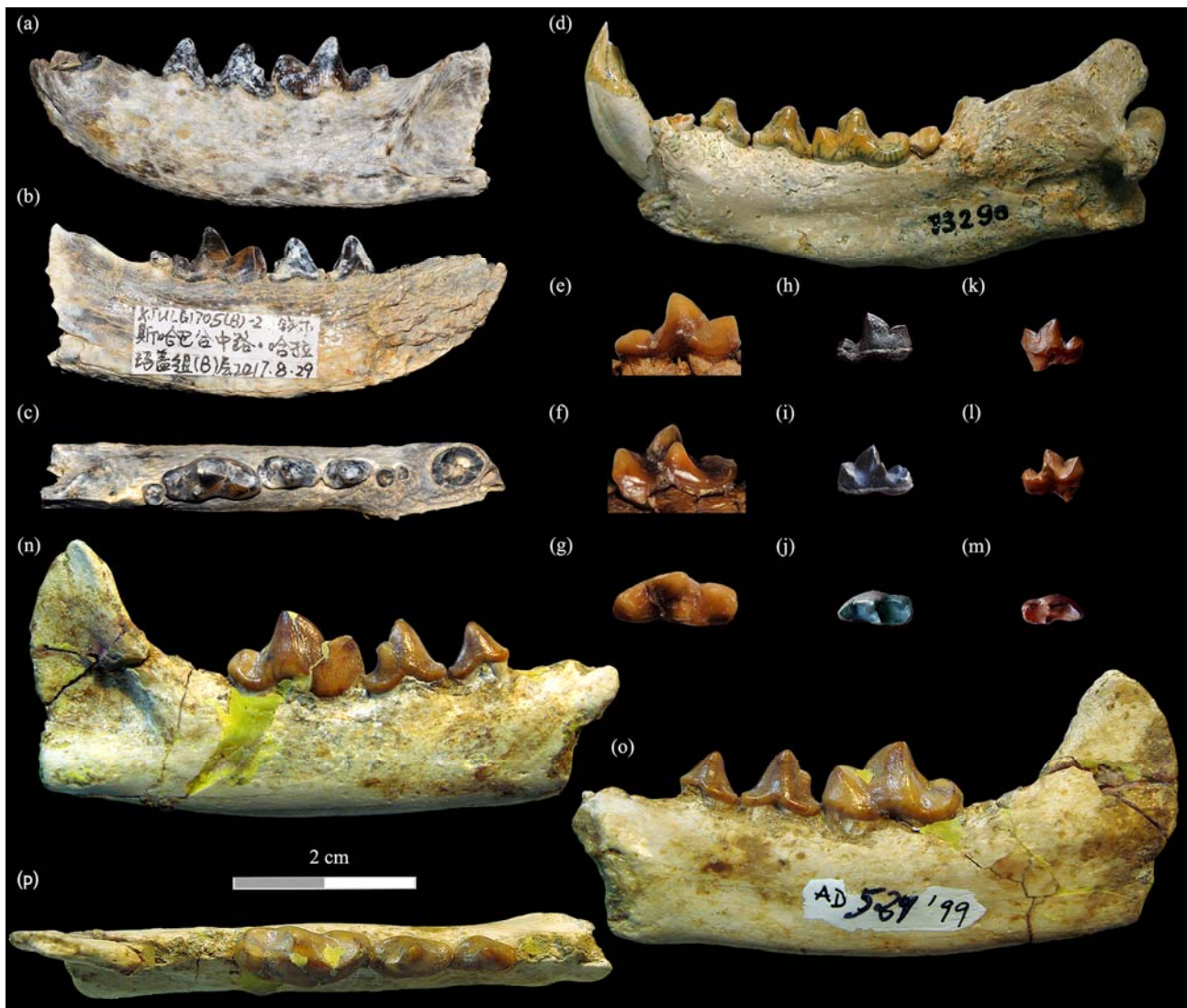


Fig. 5. *Hoplictis baihu* n. sp. and main comparative lower dentitions of middle Miocene small- to medium-sized mustelids from Europe and Africa considered in this work. (a–c), *Hoplictis baihu* n. sp., left hemimandible, V24986 (holotype) from Tiersihabahe (Halamagai Fm.).

(a) buccal view, (b) lingual view, (c) occlusal view; (d) *Dehmictis vorax*, right hemimandible, BSPG 1937-II-13290 from Wintershof-West, Germany, lingual view; (e–g) *Martes sansaniensis*, right m1, MNHN Sa962 from Sansan, France, MN6. (e) buccal view, (f) lingual view, (g) occlusal view; (h–j) *Martes munki*, cast of right m1 housed at MNCN, from La Grive MN7–8. (h) buccal view, (i) lingual view, (j) occlusal view; (k–m) *Martes burdigaliensis*, left m1, cast of the holotype housed at MNCN, from Vieux-Collonges, France MN5. (k) buccal view, (l) lingual view, (m) occlusal view; (n–p) *Namibictis senuti*, right hemimandible, AD 529'99 from Arrisdrift, Namibia, middle Miocene. (n) buccal view, (o) lingual view, (p) occlusal view.

(MN11–13) (Zdansky 1924; Teilhard de Chardin 1945; Kurtén 1970; Valenciano et al., 2015, 2018). Among these large mustelids, the mustelid from Duolebulejin might be related with the mellivorines *Eomellivora* and *Hoplictis* owing to the possession of a rotated p2 in the lower tooth row, big alveoli for the p3 and p4, enlarged and slender m1, and a slightly oval m2 alveolus.

Thus, only two large mustelid candidates within *Hoplictis* lived in Europe and North America at the same time as the Duolebulejin mustelid—*H. helbingi* and *H. grangerensis*, respectively. *Hoplictis helbingi* is a poorly known large mustelid found in Western Europe, the only described material of which consists of a P4 and m1 from La Grive, MN7–8 (Viret 1951) and a fragmentary mandible with a complete m1 and both p4 and m2 alveoli

from Castell de Barberà, early late Miocene, MN9 (Crusafont-Pairó 1972) (Fig. 4l–n). *Hoplictis helbingi* is characterized by possession of a felid-like m1, which is long and slender with a reduced talonid. The first remains from La Grive were interpreted by Depéret (1892) to be an m1 of *Aelurogale intermedia* Filhol, 1872, a saber-tooth Feliformia in the family Nimravidae, a species that is currently assigned to *Nimravus intermedius* (Piveteau, 1931). Viret (1951) realised that this carnivoran from La Grive was not a Feliformia and placed it within the Mustelidae. The fragmented hemimandible of *H. helbingi* from Castell de Barberà (Fig. 4l–n) possesses alveoli for the p4 and m2 and the dimensions and morphology of which are practically identical to those of V24988 (Figs. 2g–i, and 4j–k). Even though the ranges of variation of the

teeth of *H. helbingi* and *H. grangerensis* are incompletely known, the size of the alveoli of the Chinese hemimandible corresponds better within the range of variability of *H. helbingi* than that of the North American *H. grangerensis* (Fig. 3), in which the m1 is more robust. The m1 of *H. grangerensis* described by Edwards (1976) is slenderer than the corresponding tooth in the holotype; the m1 is broken and worn, so it is not useful for comparison. Hence, we attribute the edentulous hemimandible V24988 to *Hoplictis* cf. *helbingi*, presumably representing the first possible record of *Hoplictis helbingi* outside Western Europe. However, more material is necessary in order to clarify the designation of this specimen.

Sivamellivora Kretzoi, 1942 was created based on a complete m1 (GSI No. 243: holotype) and a few lower premolars described as *Mellivora* (?) *necrophila* Pilgrim, 1932 from the Lower Siwaliks (India), Chinji formation ca. 14–11.2 Ma (Patnaik, 2013). Later, it was assigned to *Ischyriactis* (*Hoplictis*) *necrophila* by Schmidt-Kittler (1976) and finally determined as *Hoplictis necrophila* by Petter (1987) (Bonis et al., 2009). Recently Bonis et al. (2009: p 46) stated that *Hoplictis* and *Sivamellivora* are synonyms with priority over the Siwalik one. In any case, if this proposal is valid, it would not affect the whole genus, but rather the most derived forms such as *Hoplictis helbingi* and *H. grangerensis*, which are closer in size and morphology to the Siwaliks species (Fig. 3). However, the premolars of *S. necrophila* show a primitive pattern, which is what led Kretzoi (1942) to create a distinctive genus separating it from similar forms. Thus, more material of *S. necrophila* is needed to evaluate that hypothesis.

A third species of a very large *Hoplictis* was described from Can Llobateres I, Vallès-Penedès Basin, Spain, early Vallesian, MN9, as *Hoplictis petteri* (Crusafont-Pairó, 1972), represented by a large and robust P4. However, based on the only two available P4 of *Hoplictis* (*H. helbingi* and *H. anatolicus* see Viret, 1951 and Schmidt-

Kittler, 1976, respectively), the attribution of this fossil to the genus is doubtful. Its morphology is closer to the early late Miocene, MN9, *Eomellivora* (= *Hadriactis*) *fricki* from Austria (Pia 1939; Zapfe 1948; Valenciano et al., 2017). The tooth from Can Llobateres I is close morphologically and has similar dimensions to the P4 of *E. fricki* (NHMW 2016/0065/0001) (Valenciano et al., 2017). Therefore, we propose to reattribute it to *E. fricki* (= *Hoplictis petteri*), expanding its paleobiogeographic distribution from Austria to the Iberian Peninsula.

5.1 Palaeobiogeographical implications

The earliest specimens of *Hoplictis* are recorded in Western and Central Europe during the late early Miocene (MN4) (Fig. 6) with *H. noueli* from Artenay and *H. florancei* from Erkertshofen 2 (Mayet, 1908; Roth 1989). Later, *Hoplictis* taxa dispersed eastwards to Turkey in the early middle Miocene (MN5–6) with *H. anatolicus* and to Northwest of China in the late Shanwangian–early Tunggurian or MN5–6 with *H. baihu*. The phylogenetic relationships of *H. baihu* n. sp. are as yet uncertain, but based on its primitive traits and some shared features with the European *H. noueli* and *H. florancei*, it could indicate a possible Western or Central European affinity.

The occurrence for the first time of *Hoplictis* in Asia is coherent with the dispersion event registered previously from Europe to North America via Asia (Qiu 2003; Baskin 1998, 2005). This event has been proven recently with amphicyonids from the Halamagai Fm. (Jiangzuo et al., 2018) and supports a Palaearctic Neogene faunal exchange of carnivorans between Europe and Asia during the early middle Miocene.

At the end of the middle Miocene the largest species of the genus appeared. *Hoplictis helbingi* has been recorded in Western Europe throughout the middle Miocene and early late Miocene (c. MN7–9) and the genus subsequently migrated towards North America during the early late Miocene (Fig. 6). The presence of *H. cf. helbingi* in China could suggest that *Hoplictis* migrated from

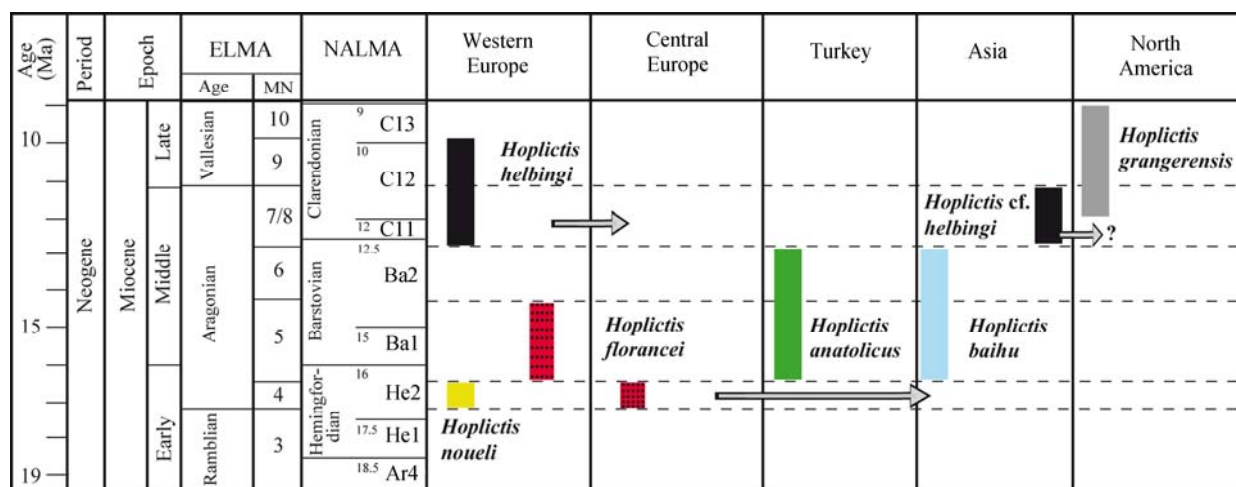


Fig. 6. Chronostratigraphic position of species of *Hoplictis*. The arrows indicate dispersion events.

Chronostratigraphical and biochronological correlations of NALMA based on a Tedford et al. (2004), Albright et al. (2008), and Hilgen et al. (2012); European Mammal Neogene Units (MN) based on Hilgen et al. (2012). Stratigraphic ranges of the taxa based on Mayet (1908), Viret (1951), Bryant, (1968), Crusafont-Pairó (1972), Edwards (1976), Schmidt-Kittler (1976), Roth (1989), Gürbüz (1992), Baskin (2005) and this manuscript. Abbreviations: Ar4, Arikarean 4; ELMA, European land mammal ages; NALMA, North American land mammal ages (units defined by immigrant taxa).

Europe to North America, through Northwest of China during the late Tunggurian, equivalent to MN7–8 in Europe, where *H. grangerensis* evolved in the North American continent in the late Clarendonian. Nevertheless, the absence of dentition in the described mandible of *H. cf. helbingi* makes it impossible to verify such a hypothesis, nor to make a direct comparison between *H. helbingi* and *H. grangerensis*. Nonetheless, the occurrence in Asia of these two species of *Hoplictis*, emphasizes the importance of the study of the mustelids and other carnivores of the middle Miocene of Northwest China, in order to increase our understanding of these faunas.

6 Conclusions

We describe a new species of *Hoplictis* (*Hoplictis baihu* n. sp.) from Tieersihabahe (Halamagai Fm.), and the presence of a second species of the same genus from Duolebulejin (Kekemaideng Fm.), provisionally attributed to *H. cf. helbingi*, from the middle Miocene of Halamagai and Kekemaideng Fms., in Ulungur River area, Xinjiang, North-Western China. These new fossil mustelids represent the first undoubted remains of the family reported in the Halamagai Fm. and the first record of Carnivora in the Kekemaiden Fm. Similarly, they denote the first occurrence of *Hoplictis* in East Asia, thereby greatly expanding the known distribution and diversity of the genus.

Hoplictis baihu is the smallest recognised species of *Hoplictis*. It is coeval with *H. florancei* and *H. anatolicus*, but is different enough to warrant erection of a distinct species. The large edentulous mandible from Duolebulejin (Kekemaiden Fm.) is attributed to *H. cf. helbingi*, which is related to the large-sized lineage of *Hoplictis* from the late middle Miocene, and might represent the first record of *H. helbingi* outside Western Europe.

The occurrence in Asia of these two species of *Hoplictis* supports a Palaearctic Neogene dispersal event of carnivorans between Europe and Asia during the late Shanwangian–early Tunggurian corresponding to MN5–6 in Europe, as well as another dispersion event from Europe to North America, via Northwest China during the late Tunggurian, equivalent to MN7–8 in Europe.

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