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Authors

Jiangzuo, Qigao

Wang, Xiaoming

Law, Chris J

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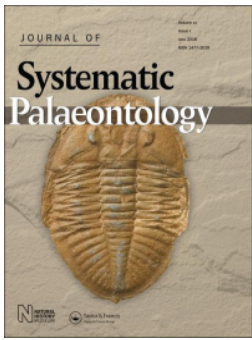
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Presence of *Cernictis* and *Lutravus* (Ictonychinae, Mustelidae, Carnivora) in eastern Asia and the dispersal of Ictonychinae during the Late Miocene

Qigao Jiangzuo[a,b]*, Xiaoming Wang[a,c] (iD), Chris J. Law[d,e], Denise Su[f], Yi Jia[g], Shijie Li[a], Jiao Fu[a], Zhenyu Kuang[h], Jiayong Cao[h], Bin Zou[i], Sukuan Hou[a], Shiqi Wang[a]*, Tao Deng[a]* (iD) and Xueping Ji[j]*

[a]Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, 10044, China; [b]State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, Nanjing 210008, China; [c]Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Blvd, Los Angeles, CA, 90007, USA; [d]University of Texas, Austin, TX, 78712, USA; [e]University of Washington, WA, 98195, USA; [f]Institute of Human Origins and School of Human Evolution and Social Change, Arizona State University, Tempe, AZ, 85287, USA; [g]Hezheng Paleozoological Museum, Linxia, 731200, China; [h]Zhaotong Institute of Cultural Relics Protection and Archaeology, Zhaotong, 657000, China; [i]Zhaoyang Museum, Zhaotong, 657000, China; [j]Kunming Natural History Museum of Zoology, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, 650201, China

Cernictis and *Lutravus* are two early members of Ictonychinae (Mustelidae) from North America, but their origin and phylogenetic position are unclear. In this study, we describe a rich Late Miocene assemblage of mustelids from Baode in northern China and from Shuitangba, Zhaotong and Shihuiba, Lufeng, in southern China. We recognize *Cernictis baskini* sp. nov. from Baode, *Cernictis lufengensis* from Shihuiba and Shuitangba, *Lutravus dianensis* sp. nov. from Shihuiba, and *Shansictis xinzhouensis* gen. et sp. nov. from Baode. Our systematic phylogenetic analyses of this group using total-evidence tip-dating place both *Lutravus* and *Shansictis* within Lyncodontini, with the former in a more basal position, and *Cernictis* as a basal member of Ictonychini. Even though the within-genera relationships of the Late Miocene Ictonychinae are still not fully understood, the divergence of the two tribes is likely to have occurred in the Late Miocene of eastern Asia, with the subfamily undergoing rapid intercontinental dispersals after its initial diversification.

http://zoobank.org/urn:lsid:zoobank.org:pub:5F10058A-42CC-4C47-BA90-43B114ACD1A4

Keywords: Neogene; China; Lyncodontini; Ictonychini; total evidence; tip dating

Introduction

Mustelidae is the largest family in the Order Carnivora, with more than 60 species, and it is globally distributed (Ewer, 1973; Law et al., 2018; Pocook, 1921; Sato et al., 2012). Ictonychinae is one of the eight major lineages of modern Mustelidae, now mainly found in South America and Africa, with only one species, *Vormela peregusna*, known from Eurasia and none from North America (Larivière, 2002; Sato et al., 2012; Yensen and Tarifa, 2003a, 2003b). During the Plio–Pleistocene, however, Ictonychinae flourished in the northern Hemisphere, with at least eight genera in Eurasia and North America: *Baranogale*, *Vormela*, *Pannonictis*, *Martellictis*, *Enhydrictis*, *Eirictis*, *Trigonictis* and *Sminthosinis* (Bartolini Lucenti, 2018; Bjork, 1970; Colombero et al., 2012; García et al., 2008; García and Howell, 2008; Jiangzuo et al., 2019; Kormos, 1931; Kowalski, 1959; Liu and Qiu, 2009; Peters and Vos,

2012; Pilgrim, 1932; Qiu et al., 2004; Ray et al., 1981; Rook, 1995; Rook et al., 2018; Spassov, 2001; Tedford et al., 1991). Most of these ictonychine mustelids were moderate to large in body size and occupied an important niche after the extinction of larger Late Miocene or earliest Pliocene mustelids, e.g. *Eomellivora*, *Plesiogulo* and *Simocyon* (Harrison, 1981; Koufos, 1982; Salesa et al., 2022; Valenciano et al., 2015; Wolsan and Semenov, 1994, 1996).

In contrast to the rich Plio–Pleistocene fossil record, the origin and early diversification of ictonychine mustelids remain unclear. This is mainly due to the paucity of Late Miocene mustelids. The earliest definite ictonychine mustelids come from eastern Asia and North America, both in the Late Miocene. In Baode, Shanxi Province, a mustelid partial cranium was first designated as Mustelidae gen. indet. sp. nov. (Zdansky, 1927). Zdansky (1927) did not connect this form with modern or fossil ictonychine mustelids. Kormos (1931) was the

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*Corresponding authors. Emails: jiangzuo@ivpp.ac.cn; wangshiqi@ivpp.ac.cn; dengtao@ivpp.ac.cn; jxpchina@foxmail.com

first to recognize the close relationship between the latter and *Pannonictis* from Europe, and most later authors generally accepted it as an ictonychine mustelid (Jiangzuo et al., 2019).

In North America, two genera, *Lutravus* and *Cernictis*, were related to ictonychine mustelids. *Lutravus* was first described as an otter from the Thousand Creek beds (Furlong, 1932), late early Hemphillian (Janis et al., 1998; Tedford et al., 2004). Due to the large P4 inner lobe and the morphology of the M1, Furlong (1932) regarded it as an early member of Lutrinae (as reflected by his choice of the Latin name) and did not compare it with any other mustelids. Gazin (1934) described two North American Pliocene species which he assigned to *Lutravus*, and compared *Lutravus* with modern *Galictis* and the Plio–Pleistocene *Pannonictis* from Europe, raising the idea that *Lutravus* might alternatively be related to Lyncodontini (called Grisoninae at that time). Reig (1956) explicitly assigned *Lutravus* to Lyncodontini, but gave no explanation for this. Baskin (1998) also followed this assignment and mentioned the presence of anterior grooves on the upper canine as characteristic of Lyncodontini.

Cernictis is a poorly known genus, with its type species, *C. hesperus*, only known from mandibular fragments with p4 and m1 (Hall, 1935). Reig (1957) connected this genus to *Eira* and assigned it to Galictini. While *Eira* has been removed from this group based on molecular phylogenetic analyses (Law et al., 2018; Sato et al., 2012), *Cernictis* was still assigned to Lyncodontini by Baskin (2011). The Late Miocene fossil record of Ictonychinae is thus rare and incomplete,

and the early diversification and dispersal history of the subfamily are unclear.

In this study, we present new material of Late Miocene fossil mustelids from three localities in China, including the Baode fauna in northern China and two hominoid sites in Southern China: Shihuiba, Lufeng; and Shuitangba, Zhaotong (Fig. 1). These mustelids show key similarities to Ictonychinae, offering valuable insights into the early evolutionary history of the subfamily.

Material and methods

Institutional abbreviations

AMNH FM, fossil mammal collection of the American Museum of Natural History, New York, USA; **AMNH F:AM**, Frick collection (fossil mammals), Division of Paleontology, AMNH, New York, USA; **AMNH M**, mammal collection of the American Museum of Natural History, New York, USA; **CCEC**, Centre de Conservation et d'Etude des Collections, Lyon, France; **HM(V)**, Hezheng Paleozoological Museum, Hezheng, China; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, USA; **PMU**, Lagrelius Collection, Paleontological Museum Uppsala, Uppsala, Sweden; **UCBL**, Université Claude Bernard Lyon 1, Lyon, France; **UCMP**, University of California Museum of Paleontology, Berkeley, USA; **USNM**, Smithsonian National Museum of Natural History, Washington, DC, USA; **UWPI**, Institut
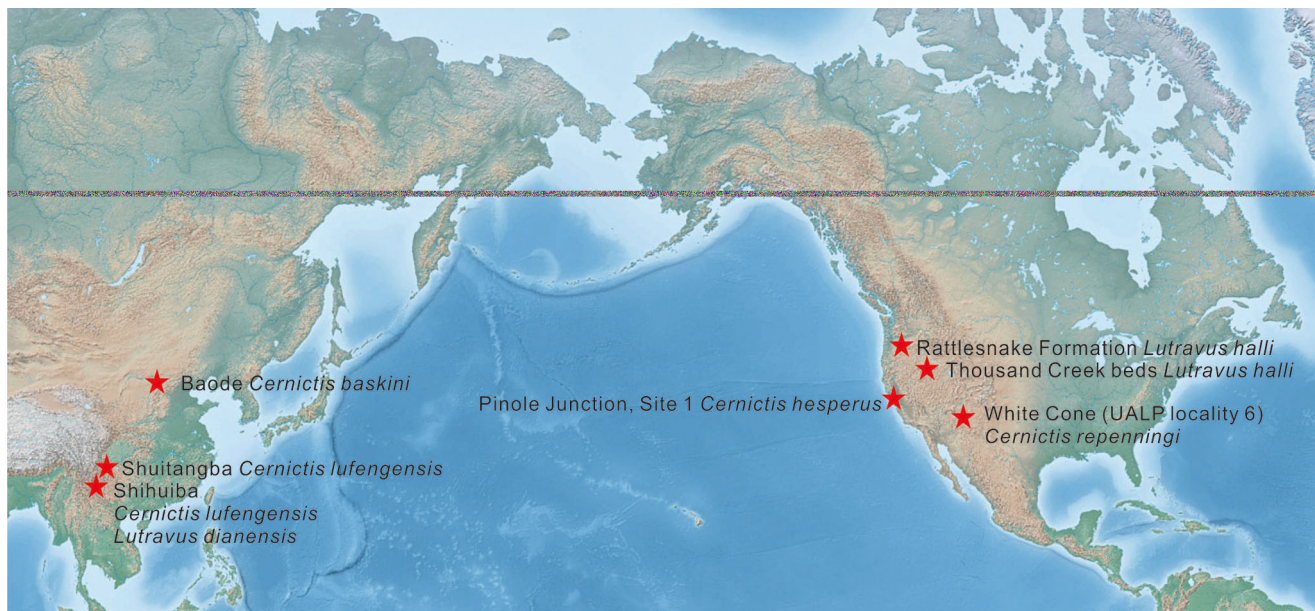

Figure 1. Localities of Late Miocene Ictonychinae investigated in this study.

für Paläontologie der Universität Wien, Vienna, Austria; **ZICRPA**, Zhaotong Institute of Cultural Relics Protection and Archaeology, Zhaotong, China.

Other abbreviations

Hh, Hemphillian; **M/m**, upper/lower molar; **MN**, units of the Neogene land mammals of Europe; **P/p**, upper/lower premolar.

Material

The newly described material in this study is housed at the IVPP, AMNH and ZICRPA. Materials of modern species of Ictonychinae studied for comparison and/or for coding the character matrix are from AMNH. Materials of fossil *Cernictis* are from UCMP, *Lutravus* from the UCMP and LACM, *Trigonictis* and *Sminthosinis* from USNM, *Eirictis* from HM and IVPP, *Enhydrictis* from UWPI, and *Martellictis* and *Baranogale* from CECC. The measured features are shown in Figure 2, with measurements reported in Tables 1 and 2.

Phylogenetic analyses

This analysis includes most ictonychine genera, as well as most Late Miocene and extant species belonging to
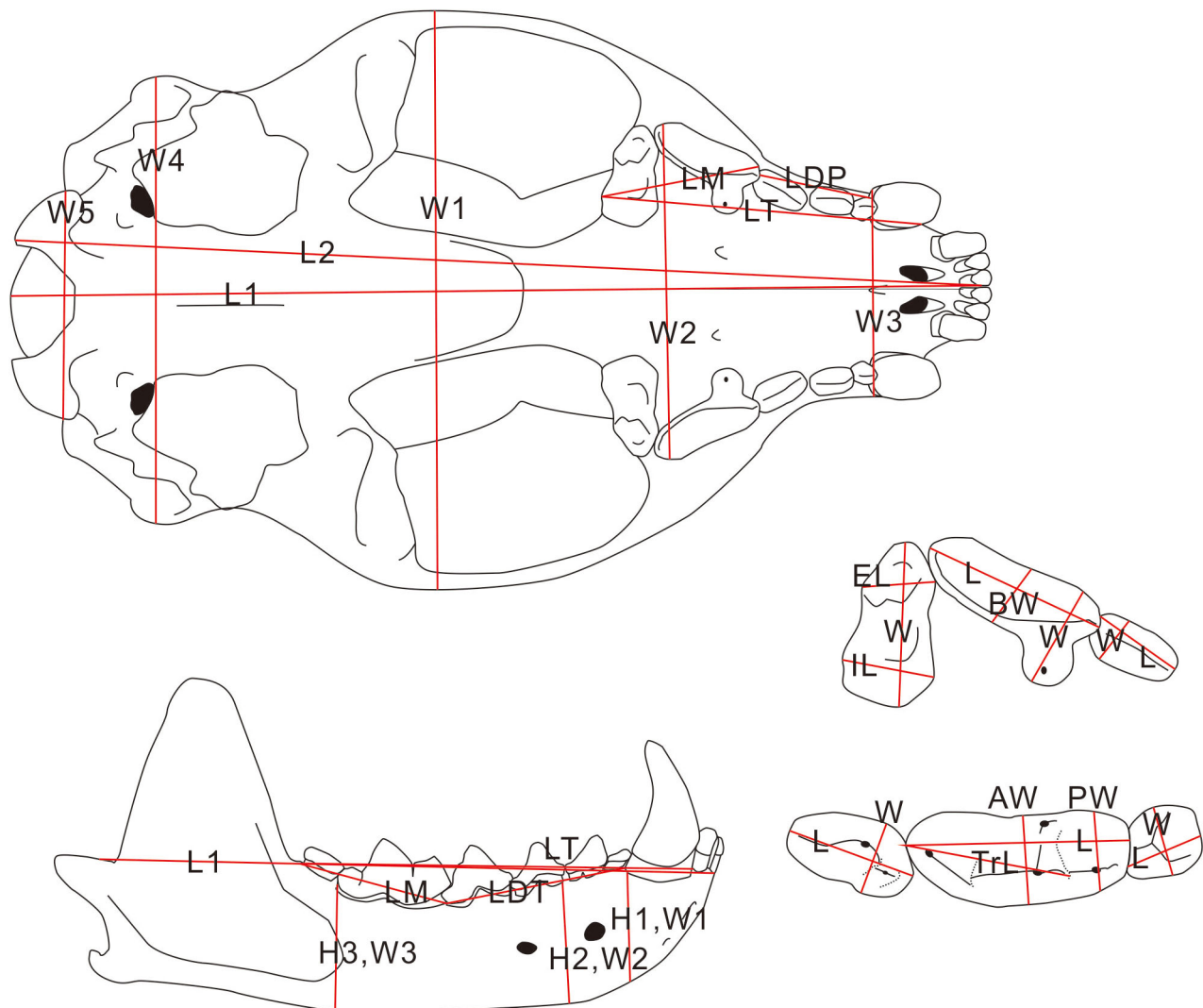
Figure 2. Craniodental measurements of Mustelidae used in this study. **Abbreviations: AW**, trigonid width; **BW**, P4 blade width across the apex of the paracone; **EL**, external length; **H1–3**, **W1–3**, mandibular height and width behind c, p2 and m1; **IL**, internal length; **L**, length; **L1**, cranial or mandibular total length; **L2**, condylobasal length; **LDP**, diastema distance C–P4 or c–m1; **LM**, P4-M1 length or m1–m2 length; **LT**, C–M1 or c–m1 length; **M/m**, upper/lower molar; **PW**, talonid width; **TrL**, trigonid length of the m1; **W1**, (in cranium) cranial zygomatic width; **W2**, (in cranium) palate width at the widest part of the tooth row; **W3**, (in cranium) rostrum width across the canine; **W4**, mastoid width; **W5**, condyle width.

Table 1. Cranial and upper dental measurements (mm). The blank represents the measurement is not applicable to the specimens.

Specimen number	Locality	Taxon	CL	CW	CH	P1L	P1W	P2L	P2W	P2H	P3L	P3W	P3H	P4L	P4W	P4BW	P4H
AMNH22342	Baode	*Cernictis baskini*	5.32	4.48		1.82	1.62				6.28	3.62	4.88				
AMNH22342	Baode	*Cernictis baskini*	5.32	4.58		1.52	1.82	4.38	2.68	4.12	6.28	3.72		10.02	6.28	4.14	6.02
AMNH22339	Baode	*Cernictis baskini*	5.02	4.12	11.78						6.28	3.38	5.00				
ZT2010-0317	Shuitangba	*Cernictis lufengensis*									6.28	2.84	4.13	8.74	5.78	3.39	4.53
ZT-2015-0194	Shuitangba	*Cernictis lufengensis*												9.45	5.10	3.84	
V27053	Shihuiba	*Cernictis lufengensis*									7.48	2.70	3.81	9.86		3.69	5.47
LACM CIT63-478	Thousand Creek, Humboldt Co.	*Lutravus halli*						5.74	3.65	5.69	7.43	4.47	5.88	11.48	8.31	5.64	6.92
LACM CIT63-478	Thousand Creek, Humboldt Co.	*Lutravus halli*	7.46	5.88	15.55			5.71	3.71	5.29				11.45	8.23	5.57	6.99
IVPP V27033	Shihuiba	*Lutravus dianensis*															
IVPP V27034	Shihuiba	*Lutravus dianensis*															
IVPP V27035	Shihuiba	*Lutravus dianensis*												11.33	8.45	5.47	7.55
IVPP V27036	Shihuiba	*Lutravus dianensis*												12.37	9.86		
			M1EL	M1IL	M1W	L1	LT	LM	LDP	W4	W2	W3				
AMNH22342	Baode	*Cernictis baskini*	5.02	3.92	9.48												
AMNH22342	Baode	*Cernictis baskini*	5.42	4.02	8.94												
AMNH22339	Baode	*Cernictis baskini*															
ZT2010-0317	Shuitangba	*Cernictis lufengensis*						13.92	9.60								
ZT-2015-0194	Shuitangba	*Cernictis lufengensis*	5.63	5.14	10.17												
V27053	Shihuiba	*Cernictis lufengensis*															
LACM CIT63-478	Thousand Creek, Humboldt Co.	*Lutravus halli*	6.52	6.78	10.42	85.78	29.12	13.42	10.20	45.00	32.48	20.92					
LACM CIT63-478	Thousand Creek, Humboldt Co.	*Lutravus halli*	6.44	6.98	10.04	38.68	28.54	13.32	10.38		36.76	25.95					
IVPP V27033	Shihuiba	*Lutravus dianensis*	6.60	6.77	11.37	38.92		17.73	13.82								
IVPP V27034	Shihuiba	*Lutravus dianensis*	7.07	7.55	11.10			18.21	14.13		8.37	4.91					
IVPP V27035	Shihuiba	*Lutravus dianensis*															
IVPP V27036	Shihuiba	*Lutravus dianensis*				4.13	3.87	6.90	4.12	4.95	7.36	4.27	6.00				

Table 2. Mandibular and lower dental measurements (mm). The blank represents the measurement is not applicable to the specimens.

Specimen number	Locality	Taxon	cL	cW	cH	p1L	p1W	p2L	p2W	p2H	p3L	p3W	p3H	p4L	p4W	p4H	m1L	m1AW	m1TrL	m1PW
UCMP22968	Pinole Junction	*Cernictis hesperus*												8.68	4.01	6.34	11.23	5.01	8.38	4.72
AMNH22342	Baode	*Cernictis baskini*	5.52	5.04				4.00	3.02	3.62	5.38	3.12	4.50	6.42	3.52	5.32	10.02	5.00	7.22	4.42
AMNH22342	Baode	*Cernictis baskini*						4.38	2.82	4.08	4.92	3.12		6.52	3.52					
AMNH22339	Baode	*Cernictis baskini*	5.82	4.42	10.68			4.00	2.48	3.42	5.02	2.82	4.50	6.68	3.44	5.12	9.78	4.58	6.88	4.02
AMNH22339	Baode	*Cernictis baskini*	6.32	4.12	10.22			3.52	2.44	3.68	5.12	2.78	4.52	6.72	3.32	5.32	10.00	4.48	7.12	
V6885.1	Shihuiba	*Cernictis lufengensis*									3.64	2.12		4.62	2.64		7.24	3.04	4.52	3.10
V6885.2	Shihuiba	*Cernictis lufengensis*															7.52	3.04	5.20	3.04
V27054	Shihuiba	*Cernictis lufengensis*									4.16	2.26	3.40	4.85	2.55	3.33	7.69	3.43	5.09	3.21
V27055	Shihuiba	*Cernictis lufengensis*									3.80	2.16	2.83	4.70	2.35	3.19	7.44	3.17	5.25	2.99
V27056	Shihuiba	*Cernictis lufengensis*									4.60	2.52		6.62			9.17	4.12	5.82	3.53
V27057	Shihuiba	*Cernictis lufengensis*															8.28	3.23	5.46	3.07
ZT2015-0321	Shuitangba	*Cernictis lufengensis*									5.10	2.40	3.92	5.88	2.84	4.35	8.27	3.74	5.67	3.36
ZT2015-0151	Shuitangba	*Cernictis lufengensis*												6.82	3.46	5.28	10.80	4.81	7.21	5.04
ZT2007-02-017	Shuitangba	*Cernictis lufengensis*						3.76	1.87	2.15				5.55	2.85		8.50	3.65	5.77	3.77
ZT2010-03-277	Shuitangba	*Cernictis lufengensis*									4.22	2.46					8.19	3.81	5.68	3.77
ZT2009-03-355	Shuitangba	*Cernictis lufengensis*									4.81	2.14	3.81				8.20	3.58	5.90	3.82
ZT2007-02-062	Shuitangba	*Cernictis lufengensis*									3.62	1.80	2.74				7.18	3.09	8.42	2.92
ZT2007-01-295	Shuitangba	*Cernictis lufengensis*						4.13	2.47								9.17	3.82	6.58	3.92
LACM CIT63-643	Thousand Creek, Humboldt Co.	*Lutravus halli*												8.26	4.81	6.98	14.09	6.02	10.31	5.87
UCMP22463	Rattlesnake F. V3045	*Lutravus halli*												8.37	4.37	6.34	13.87	5.84	10.11	5.45
IVPP V27029	Shuitangba	*Lutravus dianensis*	8.34	6.67				5.81	3.81		7.07	4.03		8.80	4.40	6.70	13.30	5.67	9.47	5.40
IVPP V27030	Shuitangba	*Lutravus dianensis*						6.23	4.23		6.80	4.47		8.60	4.94	5.67	14.03	6.47	9.57	5.91
IVPP V27031	Shuitangba	*Lutravus dianensis*	7.58	6.78	~53	4.28	3.41													
IVPP V27032	Shuitangba	*Lutravus dianensis*						5.37	3.86	3.53	6.20	3.90		7.53	3.98	6.04	12.68	5.54	8.22	5.82
V6887	Shuitangba	*Lutravus dianensis*												8.20	4.28					
(alternate headers)			m1L	m2W	L1	LT	LM	LDP	H1	W1	H2	W2	H3	W3						
UCMP22968	Pinole Junction	*Cernictis hesperus*	4.22	3.58									11.67	5.40						
AMNH22342	Baode	*Cernictis baskini*				33.82	13.38	14.92	10.62	6.42	11.28	5.96	11.58	6.02						
AMNH22342	Baode	*Cernictis baskini*											10.48	5.64						
AMNH22339	Baode	*Cernictis baskini*				34.00	12.62	16.48	8.56	5.82	10.62	5.78	10.30	5.72						
AMNH22339	Baode	*Cernictis baskini*				34.78	13.42	15.88			10.18	5.80	10.12	6.02						
V6885.1	Shihuiba	*Cernictis lufengensis*																		
V6885.2	Shihuiba	*Cernictis lufengensis*																		
V27054	Shihuiba	*Cernictis lufengensis*									7.14	3.96	7.97	3.52						
V27055	Shihuiba	*Cernictis lufengensis*									6.14	3.98	6.50	3.49						
V27056	Shihuiba	*Cernictis lufengensis*									7.85	4.18	8.57	4.70						
V27057	Shihuiba	*Cernictis lufengensis*																		
ZT2015-0321	Shuitangba	*Cernictis lufengensis*				27.77	10.68	14.36	6.79	4.36	7.51	4.36	8.54	4.08						
ZT2015-0151	Shuitangba	*Cernictis lufengensis*				34.89	13.48	16.08	8.66	6.19	9.30	4.81	11.21	4.99						
ZT2007-02-017	Shuitangba	*Cernictis lufengensis*					10.88	15.20			7.03	4.28	8.08	3.74						
ZT2010-03-277	Shuitangba	*Cernictis lufengensis*				28.81	10.76	14.60	6.61	4.79	7.28	4.55	7.42	4.07						
ZT2009-03-355	Shuitangba	*Cernictis lufengensis*					12.07	13.79			6.99	4.28	7.95	4.56						

(Continued)

Table 2. (*Continued*).

Specimen number	Locality	Taxon	cL	cW	cH	p1L	p1W	p2L	p2W	p2H	p3L	p3W	p3H	p4L	p4W	p4H	m1L	m1AW	m1TrL	m1PW
ZT2007-02-062	Shuitangba	*Cernictis lufengensis*				23.38	10.01	10.36	4.98	3.24	5.68	3.18		5.65	2.97					
ZT2007-01-295	Shuitangba	*Cernictis lufengensis*																		
LACM CIT63-643	Thousand Creek, Humboldt Co.	*Lutravus halli*																		
UCMP22463	Rattlesnake F. V3045	*Lutravus halli*												14.80	8.43		15.16	6.82		
IVPP V27029	Shuitangba	*Lutravus dianensis*	7.06	5.27		49.83	20.19	22.54												
IVPP V27030	Shuitangba	*Lutravus dianensis*			~76	47.91	18.47	22.01	16.93					17.45	7.71		18.66	7.27		
IVPP V27031	Shuitangba	*Lutravus dianensis*																		
IVPP V27031	Shuitangba	*Lutravus dianensis*															17.99	8.40		
IVPP V27032	Shuitangba	*Lutravus dianensis*																		
V6887	Shuitangba	*Lutravus dianensis*															16.51	6.50		

these genera. Some earlier records, such as *Trochictis*, which has a controversial subfamily assignment (Morlo et al., 2021), were not included in the analysis as this study is focused on the diversification and dispersal of crown Ictonychinae. We carried out a total-evidence Bayesian inference (BI) phylogenetic analysis with tip-dating methods (Ronquist et al., 2012a). For genetic data, we used the matrix of Law et al. (2018), which includes 46 genes. These genes were concatenated and treated as having independent models (GTR + Gamma). The morphological matrix was expanded from the one used by Jiangzuo et al. (2019), adding more characters to accommodate the variation of Ictonychini and the new fossil species described in this study. A total of 27 species and 58 characters are included in the matrix. The Mk model was used for morphological data (Lewis, 2001). Mrbayes 3.2.7 was used in BI with tip-dating methods (Huelsenbeck and Ronquist, 2001; Ronquist et al., 2012b). A fossilized birth-death model was used in the analysis (Zhang et al., 2016).

Systematic palaeontology

Order **Carnivora** Bowdich, 1821
Family **Mustelidae** Batsch, 1788
Subfamily **Ictonychinae** Pocock, 1921
Type genus **Ictonyx** Kaup, 1835

Included genera. Extant genera *Vormela*, *Ictonyx*, *Poecilogale*, *Galictis* and *Lyncodon* and fossil genera *Baranogale*, *Shansictis*, *Pannonictis*, *Martellictis*, *Enhydrictis*, *Eirictis*, *Trigonictis*, *Sminthosinis* and *Stipanicicia*.

Remarks. The subfamily was erected by Pocock (1921) based on craniodental and external morphology. This subfamily initially included only *Ictonyx* and *Poecilogale*. With our current understanding based on a molecular framework (Law et al., 2018; Sato et al., 2012), morphological synapomorphies of the subfamily have yet to be investigated. While the morphological traits shared by its members make it difficult to define the subfamily, with further work needed to clarify this, Ictonychinae is characterized by having a short rostrum, moderate to well-developed m1 talonid (independently lost in several genera, e.g. *Lyncodon* and *Poecilogale*), mostly with major palatine foramen located in maxilla (except *Cernictis*), M1 mostly without strong middle constriction (in contrast to Mustelinae, but see *Poecilogale*, whose M1 also has a strong middle constriction), and p1 mostly lost (in contrast to Guloninae, but present in *Lutravus*). However, these characters do not unambiguously define the subfamily, and further work is needed.

Tribe **Ictonychini** Pocock, 1921

Included genera. Extant genera *Vormela*, *Ictonyx* and *Poecilogale* and fossil genera *Cernictis* and *Baranogale*.

Remarks. The modern members of the tribe are characterized by having a connected pterygoid process and auditory bulla. This character is easily recognized and unique, but the fossil members of the tribe, *Cernictis* and *Baranogale*, are primitive for these traits and they are not developed as in the extant taxa.

Cernictis Hall, 1935

Type species. *Cernictis hesperus* Hall, 1935.

Included species. *Cernictis repenningi* Baskin, 2011, *Cernictis lufengensis* (Qi, 1983), *Cernictis baskini* sp. nov., and ?*Cernictis adroveri* (Petter, 1964).

Emended diagnosis. Small-sized mustelid (modern *Martes* size). Cranium low, with nearly straight dorsal profile. Postorbital process of frontal weak, and postorbital constriction elongated. Braincase expanded. P1 present and p1 absent. P2 and P3 surrounded by cingulum. P4 with conical protocone and inner lobe not expanded. M1 antero-posteriorly shortened with distinct metacone and inner lobe not expanded. p4 with posterior accessory cuspid present. m1 with distinct metaconid, with its posterior border forming a 'V'-shaped valley with entoconid ridge, and talonid wide.

Differential diagnosis. Differs from *Baranogale* in having more robust mandible, wider rostrum, P1 present, wider M1 inner lobe and wider m1 talonid. Differs from *Vormela* by having more marked postorbital constriction, less robust cranium, longer rostrum, pterygoid not connected with bulla, less reduced anterior premolars, P4 with larger and more anteriorly located inner lobe with conical protocone, M1 with larger metacone, m1 with larger metaconid. Differs from *Martes* by having shorter and higher rostrum, M1 without enlarged inner lobe, loss of p1, and more robust m1.

Remarks. *Cernictis* was established from scare material, with only p4 and m1 known (Hall, 1935). The recognition of *Cernictis baskini* sp. nov. from Baode provides the first diagnostic craniomandibular traits for this genus.

Cernictis baskini sp. nov.
(Fig. 3)

2011 *Cernictis* sp. Baskin: 3.

Holotype. AMNH F:AM22342, nearly complete skull from Majialianggou (old spelling Ma chia lien ko), Baode, Shanxi Province of Northern China.

Assigned material. AMNH F:AM22339, a complete mandible and associated upper canine and P3, from Jijiamaogou (old spelling Chi chia mao ko), Baode, Shanxi Province of northern China.

Etymology. In honour of Jon A. Baskin, who made a great contribution to the study of Musteloidea and who first recognized the Baode material as *Cernictis* (Baskin, 2011).

Diagnosis. Medium-sized *Cernictis*. Cranium low, with nearly straight dorsal profile. Postorbital process of frontal weak, and postorbital constriction elongated. Braincase expanded. The mandibular corpus is relative deep and robust. P4 with a narrow protocone. M1 antero-posteriorly shortened, with weak middle constriction, metacone distinct and metaconule absent. p2 and especially p3 with distinct anterior and posterior cingulid cuspids. p3 with very weak and indistinct posterior accessory cuspid, and p4 with distinct posterior accessor cuspid. m1 with large metaconid.

Differential diagnosis. Differs from *C. hesperus* and *C. repenningi* by having larger m1 metaconid and smaller size. Differs from *C. repenningi* by having smaller m1 talonid. Differs from *C. lufengensis* by having slightly larger size, better developed p3 and p4 accessory cuspids, and narrower P4 protocone.

Description

AMNH F:AM22342 (Fig. 3A–C) is a nearly complete skull, with the cranium lacking the zygomatic arch and occipital shield and the mandible lacking the ascending rami (Fig. 3E–J). The mandible of AMNH F:AM22339 (Fig. 3K–P) is complete.

The cranium is generally wide and flat. The dorsal profile is only slightly curved. The rostrum is short. The postorbital process is very small but distinct. The postorbital constriction is not strong, but this part is rather elongated before the braincase. The braincase is expanded, much wider than the rostrum. The temporal ridges unite into a very weak sagittal crest at the point slightly distal to the postorbital process of the frontal. The anterior border of the orbit forms a weak ridge, located at the level of P3. The infraorbital foramen is relatively large and anteriorly inclined in lateral view. Ventrally, the anterior palatine fissure is rounded and located medial to the canine. The major posterior palatine foramen is small and located in the anterior part of the P4. The palatine distal to the toothrow is narrow and extends posterior to the M1. The auditory bulla is largely triangular in shape, with a short bony external auditory meatus. The posterior opening of the internal carotid canal is located in the middle of the bulla. The medial border of the bullas from both sides tapers mesially. The hypoglossal foramen is separated from the posterior lacerated foramen.

Figure 3. *Cernictis baskini* sp. nov. Holotype: AMNH F:AM22342, from Majialianggou, Baode. **A–D,** cranium, ventral, dorsal, lateral and anterior views; **E–G,** left mandible, lateral, medial and occlusal views; **H–J,** right mandible, lateral, medial and occlusal views. **K–M,** AMNH F:AM22339, left mandible from Jijiamaogou, Baode, lateral, occlusal and medial views; **N–P,** AMNH F:AM22339, right mandible from Jijiamaogou, Baode, lateral, medial and occlusal views.

The horizontal ramus of the mandible has a uniform depth. There are two distinct mental foramina in AMNH F:AM22339, located at the level of the p2/p3, and p4. On the left side of AMNH F:AM22342, the anterior foramen is subdivided into several smaller foramina, with the posterior one located at the level of the p3/p4. The whole ascending ramus is bent anteriorly, with the anterior border of the coronoid process slightly inclined anteriorly (taking the toothrow as the horizontal). The coronoid process is slender. The mandibular condyle is short and weak.

The incisor row is straight. The I2 is slightly larger than the I1, and the I3 is larger still. The canine has a rounded cross section and there is no anterior groove. The P1 is small and button-like. The P2 has a convex medial border and weak cingula are present in its anterior and postero-lingual sides. The P3 has a stronger medial convexity, and the cingulum surrounds the tooth. The P4 is slender, with a slightly concave buccal border, a distinct parastyle, and a narrow protocone. Distinct cingula are present from parastyle to protocone, and from protocone distally to the whole medial border of the tooth. The M1 is small and shortened antero-posteriorly. The metacone is smaller than the paracone but still distinct. The inner lobe is not expanded. The protoconule is poorly separated and the metaconule is absent. The protocone is in the anterior part of the inner lobe and is moderate in size.

The lower incisors and p1 are not preserved. The lower canine is curved, with a rugous surface. The p2 and p3 are distinctly inclined anteriorly. There is no accessory cuspid on the p2, and in the p3 the anterior and posterior cingulid cuspids are weakly defined. The posterior accessory cuspid in p3 is very weak but present in both AMNH F:AM22342 and AMNH F:AM22339. The p4 has clearly defined anterior and posterior cingulid cuspids and a distinct posterior accessory cuspid. The m1 is stout, with a large metaconid nearly the same size as the protoconid. The talonid is slightly narrower than the trigonid. The entoconid is weak and ridge-like. In medial view, the posterior border of the metaconid and the entoconid of the m1 form a deep 'V'-shaped valley. The hypoconulid is present in AMNH F:AM22339 but not in AMNH F:AM22342. The m2 has well marked protoconid and metaconid, the metaconid being stronger.

Cernictis lufengensis (Qi, 1983)
(Figs 4–6)

1983 *Proputorius lufengensis* Qi: 11.

Holotype. IVPP V6885.1, a partial mandible from Shihuiba, Lufeng, Yunnan Province of southern China.

Assigned material. From Shihuiba: IVPP V6885.2, partial mandible with m1; new material includes IVPP V27054-V27057, three mandibular fragments; IVPP V27058, isolated m1; IVPP V27053, maxillary fragments with broken P3 and P4. From Shuitangba, Zhaotong, Yunnan Province of southern China: ZT2010-0317, maxillary fragment with P3–P4; ZT2015-0194, maxillary fragment with P4–M1; ZT2015-0321, partial mandible with p3–m1; ZT2015-0151, partial mandible with p4 and m1; ZT2007-02-017, nearly complete mandible with p2 and m1 without symphysis; ZT2010-03-277, partial mandible with p3–m1; ZT2009-03-355, partial mandible with p3–m1; ZT2007-02-062, partial mandible with p3 and m1; ZT2007-01-295, associated lower dentition, with c–m1, and dp3 and dp4; ZT2007-02-082 partial mandible with dp3 and dp4.

Diagnosis. Small-sized *Cernictis* with pronounced sexual dimorphism; mandibular corpus relatively shallow; P4 with slightly expanded inner lobe; p2 and p3 without distinct anterior and posterior cingulid cuspid; m1 with moderately sized metaconid.

Differential diagnosis. Differs from other species of the genus by being smaller in size and having weakly developed p3 and p4 accessory cuspids.

Description

There are two maxillae from Shuitangba and one from Shihuiba, all poorly preserved. The infraorbital foramen, preserved in all three specimens, is large, and located above the paracone of the P4. Judging from the alveolus, the P1, while not preserved in these specimens, would have been present and small. The P3 is well preserved in ZT2010-0317 (Fig. 5E). It has a clear medial convexity and is surrounded by the cingulum. The P3 of V27053 (Fig. 5A, B) is incompletely preserved and the development of medial convexity is unclear. The P4 of ZT2010-0317 has a large and slightly expanded inner lobe, with distinct mesial and distal cingula. However, in ZT2015-0194 (Fig. 5C, D) the inner lobe is clearly smaller, more anteriorly located, and not expanded, suggesting the presence of variation in the protocone. The M1 of ZT2015-0194 is antero-posteriorly shortened. The metacone is only slightly smaller than the paracone, and the inner lobe is not expanded.

The most complete mandible is ZT2007-02-017 (Fig. 4D–F), lacking only the symphysial region. The horizontal ramus is uniform in depth, and, in general, the ramus is shallow. The coronoid process has a triangular shape and is not anteriorly bent as in *C. baskini*. The mandibular condyle is also lower than that in *C. baskini*. Two large mandibular foramina are located below the p2 and p3, with a tiny additional one between them at
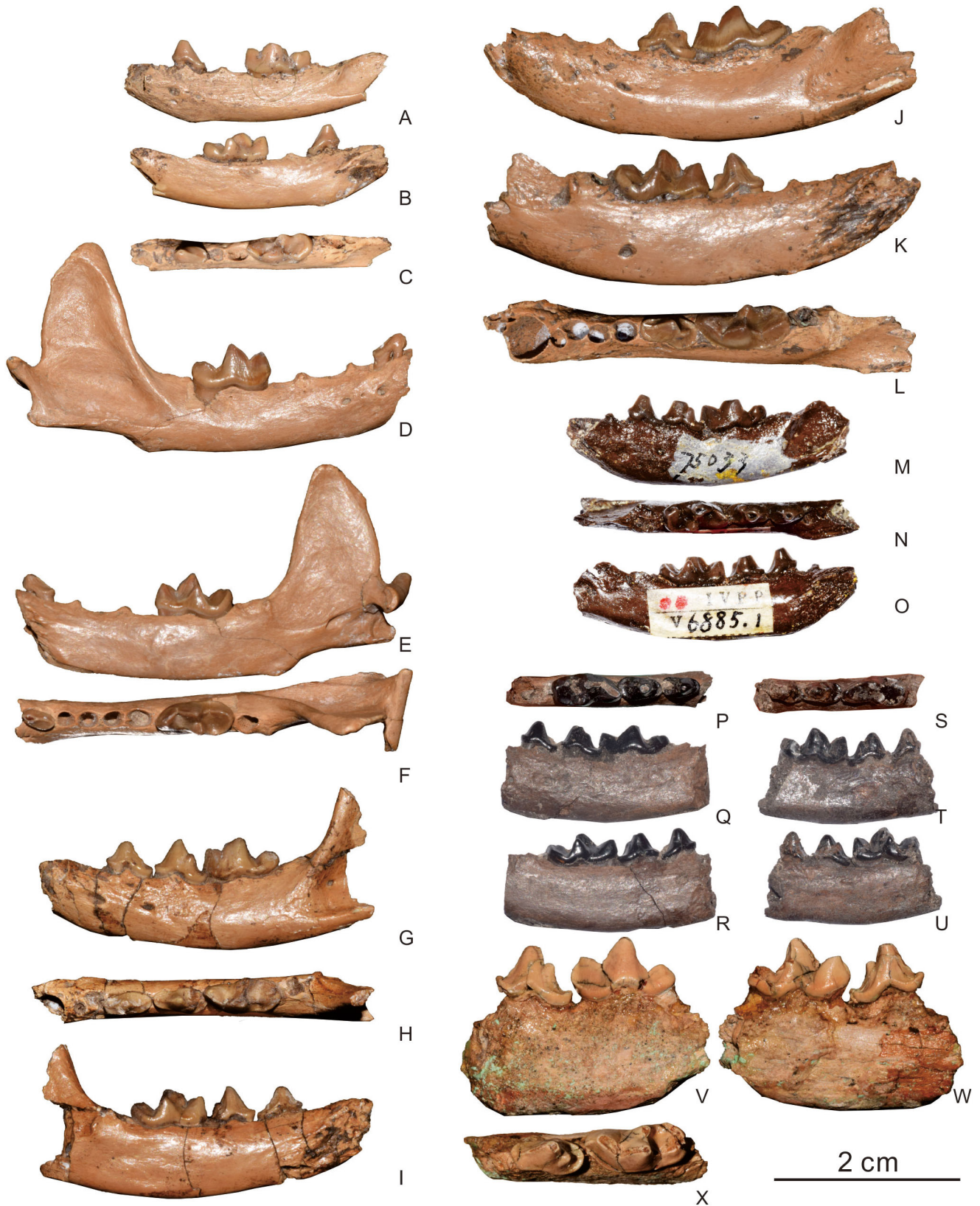
Figure 4. Mandibles of *Cernictis lufengensis* (A–L from Shuitangba, E–G from Shihuiba) and *Cernictis hesperus* (H). **A–C,** ZT2007-02-062, lateral, medial, and occlusal views; **D–F,** ZT2007-02-017, lateral, medial, and occlusal views; **G–I,** ZT2015-0321, lateral, occlusal, and medial views; **J–L,** ZT2015-0151, lateral, medial, and occlusal views; **M–O,** IVPP v6885.1, lateral, occlusal, and medial views; **P–R,** IVPP V27054, occlusal, medial, and lateral views; **S–U,** IVPP V27055, occlusal, medial, and lateral views; **V–X,** UCMP22968, lateral, medial, and occlusal views.
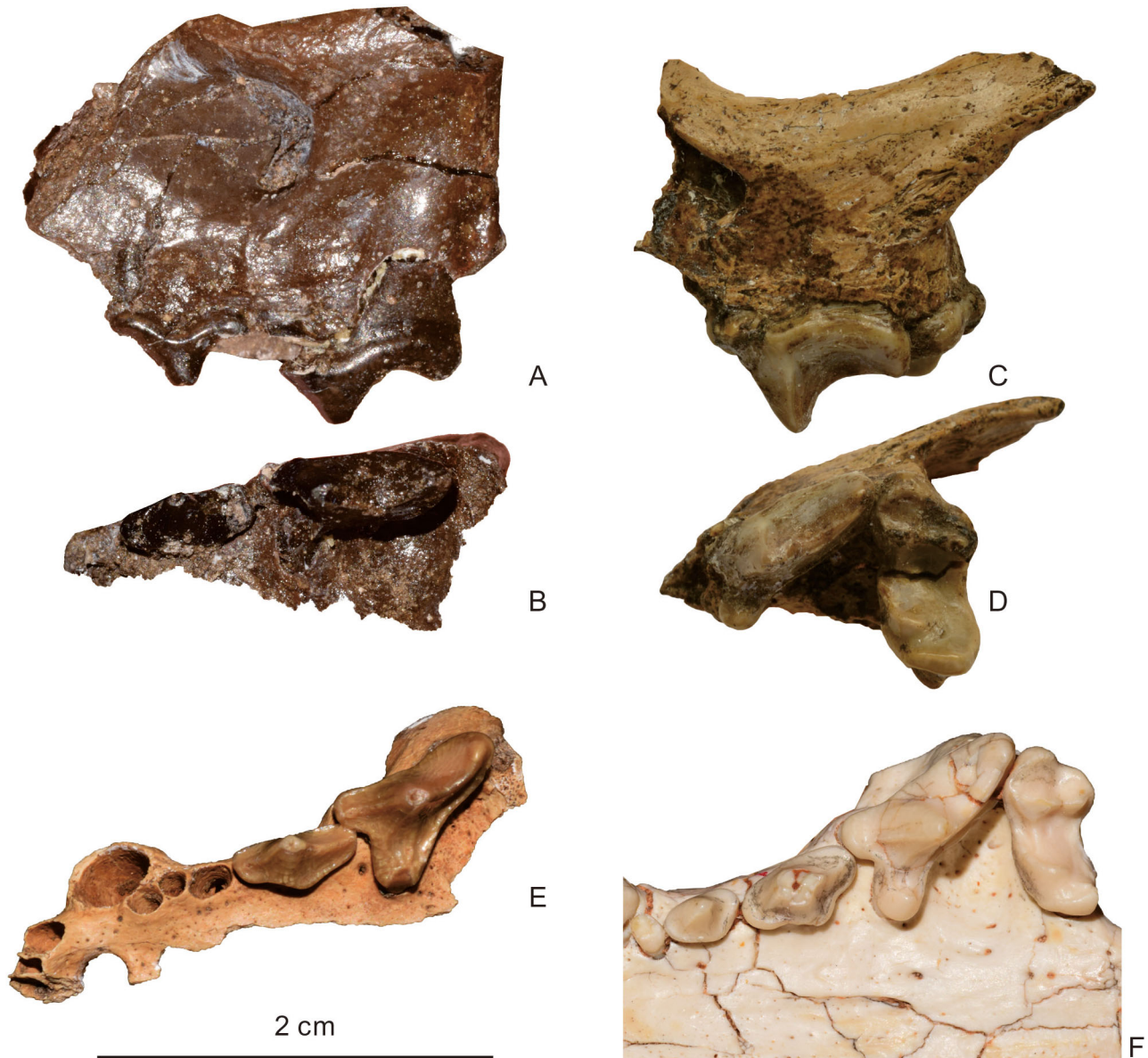
Figure 5. Maxillae of *Cernictis lufengensis* (A, B from Shihuiba, C, D from Shuitangba) and *Cernictis baskini* (D, Baode). **A, B,** IVPP V27053, lateral and occlusal views; **C, D,** ZT-2015-0194, lateral and occlusal views; **E,** ZT2007-02-317, occlusal view; **F,** AMNH F:AM22342, occlusal view.

the level of the p2 distal root. A weak subangular lobe is present slightly distal to the anterior border of the masseteric fossa. This lobe is not seen in any other specimens. ZT2015-0151 (Fig. 4J–L) represents the largest-sized mandible recovered from Shuitangba. It has a deeper mandibular corpus than the other mandibles, in absolute size and also relative to the length of m1. The ramus in this specimen is slightly deeper posteriorly. In contrast, in the smallest individual, ZT2007-02-062 (Fig. 4A–C), the mandibular ramus is rather shallow and becomes shallower posteriorly. In most

mandibles, there are two mental foramina, with slight variations in position.

The lower canine has two distinct posterior ridges and a medial ridge. It is unclear whether the two distal ridges are only an abnormal variant (normally only posterior ridges). The p2 is very low and strongly inclined anteriorly. The p3 is higher-crowned and is weakly (ZT2009-03-355) or moderately (ZT2007-02-062) inclined anteriorly. In most p3s, there is no distinct cingulid cusp, but this is distinct in IVPP V27055 (Fig. 4S–U) and weak in ZT2009-03-355. The p4 has a

Figure 6. Humerus of *Cernictis lufengensis*, ZT2009-03-614, from Shuitangba, Zhaotong. **A**, lateral view; **B**, ventral (posterior) view; **C**, medial view; **D**, dorsal (anterior) view.

distinct posterior accessory cuspid, but the anterior and posterior cingulid cuspids are always weak or absent. The m1 has a moderately-sized metaconid, located distal to the protocone. The anterior margin of the talonid has an antero-buccal to postero-lingual orientation. The m2 is not preserved in any specimen. The dp3 has a sharp main cusp, with the anterior cingulid cusp either developed (ZT2007-02-082) or absent (ZT2007-01-295). There is a postero-lingual ridge present. The dp4 has a reduced metaconid and a very short talonid.

A complete humerus (Fig. 6, Length: 58.58 mm, distal Width: 15.76 mm) from Shuitangba is assigned to *C. lufengensis*, as it is the only small mustelid discovered so far. The great tubercle and lesser tubercles are both weak. The bone shaft is rather curved in lateral view. The epicondylar foramen is present. The curved humerus is reminiscent of that of Lutrinae, and suggests a potential semiaquatic behaviour.

Tribe **Lyncodontini** Pocock, 1921

Included genera. Extant genera *Galictis* and *Lyncodon* and fossil genera *Shansictis*, *Pannonictis*, *Martellictis*, *Enhydrictis*, *Eirictis*, *Trigonictis*, *Sminthosinis* and *Stipanicicia*.

Remarks. This tribe is characterized by having a distinct anterior groove in the upper canine. This character is highly distinctive among Mustelidae. Most members of the tribe have an enlarged and basined P4 inner lobe (independently lost in *Eirictis*), and p4 has no posterior accessory cuspid.

Lutravus Furlong, 1932

Type species. *Lutravus halli* Furlong, 1932.

Assigned species. *Lutravus dianensis* sp. nov.

Emended diagnosis. Medium-sized mustelid (modern *Lutrogale* size). P1/p1 present. P3, p3, and p4 surrounded by cingulum. P4 with wide protocone, and weak and shelf-like hypocone and expanded inner lobe. Enlarged

M1, with distinct metacone, and inner lobe slightly expanded. p4 with no posterior accessory cuspid. m1 robust, with strong paraconid, and distinct metaconid. m2 enlarged, with distinct protoconid and metaconid.

Differential diagnosis. Differs from *Pannonictis*, *Trigonictis* and other Plio–Pleistocene Lyncodontini in having less differentiated P4 protocone and hypocone, and presence of p1. Differs from *Shansictis xinzhouensis* gen. et sp. nov. in having more robust dentition and mandible, more enlarged M1. Differs from *Martes* by being larger in size, having more robust dentition, the absence of p4 posterior accessory cuspid, and more enlarged m2. Differs from Lutrinae by having anterior groove in the upper canine, P4 inner lobe smaller, M1 more transversely elongated, m1 with smaller talonid.

Lutravus dianensis sp. nov.
(Fig. 7)

1983 *Lutra* sp. Qi: 14.

Holotype. IVPP V27033, associated P4 and M1, and IVPP V27035, a P3, possibly associated with holotype, from Shihuiba, Lufeng, Yunnan Province of southern China.

Paratype. IVPP V27030, a largely complete mandible from Shihuiba, Lufeng, Yunnan Province of southern China.

Assigned material. IVPP V6887, a mandibular fragment with p4 and m1; IVPP V27034, an isolated M1; IVPP V27036, a maxillary fragment with I3 and P1–P4; IVPP V27029, a partial mandibular fragment with c–m2; IVPP V27031 a partial mandibular fragment with p2–m1. All from Shihuiba, Lufeng, Yunnan Province of southern China.

Etymology. Dian is the abbreviated name for Yunnan Province in Chinese.

Diagnosis. Large Ictonychinae; mandible very robust and deep, with deep masseteric fossa; premolars very robust, with surrounding cingula; P4 robust, with small parastyle and expanded inner lobe, distinct protocone, and weak hypocone shelf; M1 enlarged, with distinct metacone and metaconule, and inner lobe slightly enlarged; p3 shortened; m1 robust, with stout paraconid.

Differential diagnosis. Differs from *Lutravus halli* by having P4 with parastyle, and M1 with smaller metacone, p3 shorter and wider, m1 with more massive paraconid.

Occurrence. Shihuiba, Lufeng, southern China; Baodean stage.

Description
In the partial maxilla IVPP V27036 (Fig. 7A), the I3 has a distinct medial cingulum. The P1 is small and pointed. The P2 and P3 have surrounding cingula. The P4 is robust with a slightly concave buccal border. There is a small but distinct parastyle. A distinct antero-medial crest is present from the apex of the paracone to the anterior border of the inner lobe. The inner lobe is expanded, with a weakly separated protocone and a weak hypocone shelf extending to the posterior 1/3 of the tooth. The M1 is enlarged and wide antero-posteriorly. The metacone is distinct but clearly smaller than the paracone. The postprotocrista is weak and turns buccally. There is a small metaconule present medial to the metacone, not connected with the postprotocrista. The inner lobe is slightly expanded.

IVPP V27030 (Fig. 7F–H) is well preserved, lacking only the dorsal part of the coronoid process and the anterior-most part of the symphysis. The horizontal ramus is rather deep and has a uniform depth from the canine to the m1. Two mental foramina of equal size are located at the level of the p2 and p3/p4. The masseteric fossa is deep and has a clearly defined border. The anterior border of the coronoid process is posteriorly inclined.

The lower canine is robust, with a rugous surface. The p1 is present. The p2 and p3 have concave lingual contours. Like the upper premolars, the lower premolars are also surrounded by cingulids, especially on the anterior and posterior sides. There is no posterior accessory cuspid in the p4. The m1 is robust and has an especially massive paracone. The metaconid is moderate in size. The talonid is nearly the same width as the trigonid. The entoconid is ridge-like and weak. The m2 is antero-posteriorly elongated, with distinct paraconid and hypoconid and strong protoconid and metaconid.

Shansictis xinzhouensis gen. et sp. nov.
(Figs 8, 9)

1927 Mustelide gen. indet., sp. nov. Zdansky: 17, Taf. I, fig. 26; Taf. II, fig. 1, 3.
1931 *Pannonictis* sp. Kormos: 172.
1967 Mustelidae gen. ind. sp. Ficcarelli and Torre: 139.
2008 *Pannonictis pachygnatha* García et al.: fig. 2.

Holotype. PMU M3802 (cranium) and PMU M3803 (mandible), a partial cranium and associated mandible from Baode Couty, Xinzhou City, Shanxi Province of northern China. This is the only known material of this species.

Etymology. Species and genus names from Xinzhou City, Shanxi Province, where the specimens were discovered.

Figure 7. *Lutravus dianensis* sp. nov. (A, B, F–O, all from Shihuiba, Lufeng) and *Lutravus halli* (C–E, P–U). **A,** IVPP V27036, occlusal view; **B,** IVPP V27033 and IVPP V27035, occlusal view; **C–E,** LACM CIT63-478, Thousand Creek, Humboldt County, ventral, lateral and anterior views; **F–H,** IVPP V27030, lateral, medial and ventral views; **I, J,** IVPP V6887, lateral and ventral views; **K–L,** IVPP V27031, lateral and ventral views; **M–O,** IVPP V27029, lateral, medial and ventral views; **P–R,** LACM CIT63-643, Thousand Creek, Humboldt County, lateral, medial and ventral views; **S–U,** UCMP22463, Rattlesnake Formation V3045, lateral, medial and ventral views.
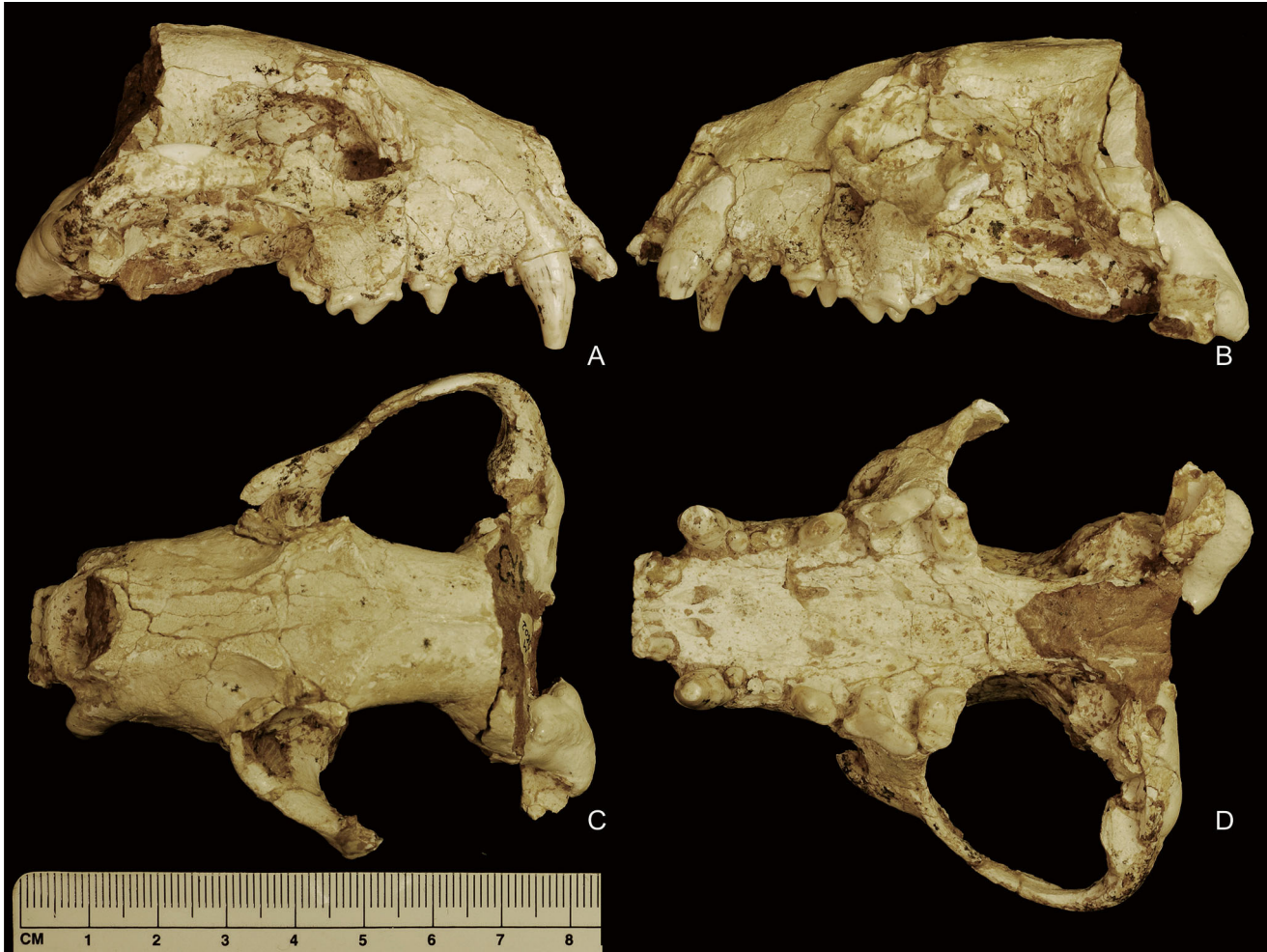
Figure 8. *Shansictis xinzhouensis* PMU M 3802, partial cranium from Baode. **A–B**, lateral view; **C**, dorsal view; **D**, ventral view.

Diagnosis. Large Ictonychinae; rostrum relatively long; preorbital fossa present; postorbital constriction elongated but not strong; mandible moderately deep, with deep masseteric fossa; canine robust; P1 and p1 both present; premolars not robust and without surrounding cingula; P4 with distinct parastyle, enlarged inner lobe, distinct paracone, and weak hypocone shelf; M1 not enlarged, with slightly expanded inner lobe; m2 rounded, without clear cusps.

Differential diagnosis. Differs from *Lutravus* in having less robust mandible and dentition, premolars without surrounding cingula, and smaller M1 and m2. Differs from *Pannonictis* and *Trigonictis* in having a longer rostrum, presence of p1, premolars without surrounding cingula, P4 with protocone and hypocone not distinguished, and M1 inner lobe less expanded.

Description

The partial cranium (PMU M3802) has a slightly elongated rostrum. The postorbital process of the frontal is weak. The postorbital constriction is moderately developed and elongated. The zygomatic arch is very wide. The temporal ridges from both sides quickly unite into a weak sagittal crest. There is a shallow preorbital depression developed in the maxilla. The major palatine foramen is located medial to the P3. The bony choana seems to be quite elongated, but as this part is not prepared, this trait cannot be clearly observed.

The mandible (PMU M3803) has a uniform height in the horizontal ramus. There are two mental foramina on both sides; on the left the two are equal in size, located below the p2 and p3/p4, but on the right side the two foramina are both located below the p3, and the ventral one is larger. The anterior border of the masseteric fossa is clearly defined. The coronoid process is symmetrical antero-posteriorly.

The upper incisor row is straight, with the I3 distinctly larger than the I1 and I2. The upper canine is robust. The premolars have no surrounding cingula. The P4 is slender, with a moderately sized basined inner

lobe. The protocone is developed, and the hypoconid is very weak and ridge-like. The M1 has a slightly widened inner lobe, and the metacone is slightly smaller than the paracone. The p1 is present. The p2–p4 has no accessory cuspid. The m2 is small, with a very weak protoconid, and a very weak traverse ridge.

Discussion

Comparison

The specimens of small mustelids from Baode, Shuitangba, and Shihuiba clearly represent a lineage close to the North American *Cernictis* (Baskin, 2011; Hall, 1935). They have no p1, which distinguishes them from *Martes*, *Trochictis*, *Sinictis*, *Circamustela* and *Aragonictis* of the Middle and Late Miocene (Petter, 1964; Valenciano et al., 2020, 2022; Zdansky, 1924b). They further differ from the three latter genera, which have a more hyper-carnivorous dentition, in having more robust cheek teeth and m1 with larger metaconid and wider talonid (Valenciano et al., 2020, 2022; Zdansky, 1924b). They also differ from *Baranogale* in having P1, a wider M1 inner lobe, and an m1 talonid. Therefore, the small mustelids from Baode, Shuitangba, and Shihuiba all differ from the known Eurasian taxa. They also differ from the small mephitid *Neoyunnanotherium* from the same locality in having a very different dental structure, with clearly developed cusps in the molars (Deshmukh and Valenciano, 2022).

Among the North American mustelids, *Cernictis* is poorly known, with the type species, *C. hesperus*, known only from mandibular fragments with p4 and m1. However, the mandible from Baode resembles *C. hesperus* in the dentition. They both have distinct anterior and posterior cingulid cuspids and a posterior accessory cuspid in the p4, as well as a m1 with a wide talonid and a posterior border that forms a 'V'-shaped valley with the entoconid. These shared traits link the Baode mustelid to the North American *Cernictis*. The major difference with the Baode mandible is the smaller m1 metaconid in *C. hesperus*. The specimens from Shuitangba and Shihuiba do not have distinct anterior and posterior cingulid cuspids in the p4 but otherwise have a similar p4 and m1. The upper dentition from Shuitangba is morphologically close to that in the Baode material. The P4 has an anteriorly located inner lobe, with a distinct protocone and a rudimentary hypocone shelf. The M1 is antero-posteriorly short and the inner lobe is not expanded, nor is there a distinct middle constriction. These shared traits between the Shuitangba and Baode materials link them together. Based on these shared characters, the Asian material is assigned to

Figure 9. *Shansictis xinzhouensis* PMU M 3803, mandible from Baode. **A**, left lateral view; **B**, ventral view; **C**, right lateral view.

Cernictis. In general, the specimens from Shuitangba and Shihuiba are smaller, have a more slender mandible (Fig. 10), and a larger m1 metaconid than the Baode species, and therefore represent a different species.

The larger mustelid from Shihuiba is much stouter in mandible and dentition than the smaller one discussed above. It is very close to *Lutravus* from North America in morphology. The dentition of the Shihuiba large mustelid closely resembles that of *L. halli*. The premolars are robust and surrounded by cingula; the P4 is stout

with an enlarged inner lobe, in which a ridge-like protocone and a weaker hypocone shelf are present. The inner lobe extends along the medial wall of the paracone-metacone to the posterior 1/3 of the tooth. The M1 is enlarged, with the inner lobe wider than the outer one, and with a small metaconule. The m1 has a massive paracone and the talonid is similar in width to the trigonid. These shared traits are not seen in other mustelids and the Shihuiba mustelid is therefore assigned to *Lutravus*. The Shihuiba *Lutravus* differs from *L. halli* in having a P4 with a distinct parastyle (in the latter species, the parastyle is absent and a very weak cingulum is present in its location) and more rugous premolar surfaces, a deeper mandible, a M1 with a smaller

metacone, a shorter and wider p3, and a m1 with a more massive paraconid (Fig. 10). *Lutravus* differs from *Pannonictis* and *Trigonictis* in having generally more robust premolars, unseparated P4 protocone-hypocone, a more massive m1 paraconid, and a more elongated m2. It differs from *Eirictis* in having an enlarged P4 inner lobe. It differs from *Shansictis* ('Mustelidae indet. sp. nov.' of Zdansky, 1927) from Baode in having a more robust dentition, a P4 with a larger inner lobe, a larger m1, and premolars with surrounding cingula. The latter has long been linked to *Pannonictis* by many authors (Kormos, 1931; Schreuder, 1937), but it in fact shows clear differences from *Pannonictis* in having a p1, more slender premolars without distinct surrounding cingula,
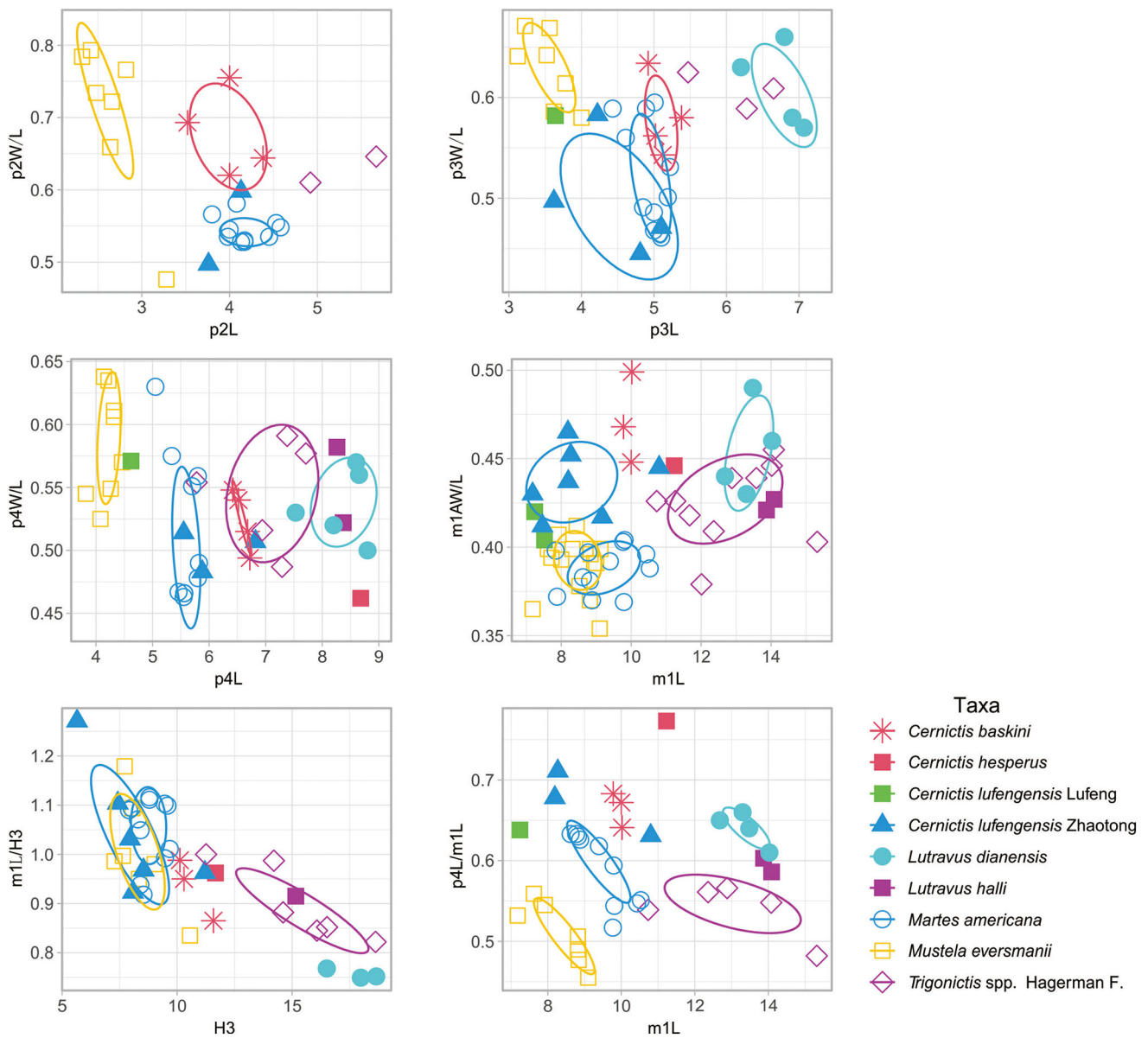

Figure 10. Metric comparison of Late Miocene Ictonychinae and some related taxa.

and a P4 with unseparated protocone and hypocone. It is also much older than *Pannonictis* (Plio–Pleistocene). Our phylogeny (Fig. 11) supports its placement as a basal Lyncodontini, and it is here erected as the new genus and species *Shansictis xinzhouensis*.

Phylogenetic analyses

Our total-evidence BI phylogeny (Fig. 11) supports a deep divergence of the two tribes of Ictonychinae in the Late Miocene. The topology of the extant species is not different from that inferred purely on molecular data (Koepfli et al., 2008; Law et al., 2018; Sato et al., 2012). The four species of *Cernictis* are recovered as basal to crown Ictonychini, not forming a monophyletic group. However,

considering the poor preservation of the type species, *C. hesperus*, the inferred relationship between these species may not be reliable, which is also reflected by the relatively low posterior probabilities at these nodes. The possibility that these species represent a monophyletic group cannot be excluded. Despite these difficulties, we still assign them to *Cernictis*. The Plio–Pleistocene *Baranogale* is recovered as a sister group to *Vormela*. *Lutravus* is placed as basal to crown Lyncodontini and several Plio–Pleistocene genera, e.g. *Eirictis*, *Pannonictis*, *Sminthosinis* and *Trigonictis*. Again, as with *Cernictis*, the two species of *Lutravus* are not recovered as sister taxa even though they differ by only one trait in the matrix. *Shansictis xinzhouensis* is supported as sister to the clade of *Martellictis* + *Enhydrictis*, though also with low support.

Figure 11. Total-evidence tip-dating tree of Ictonychinae, with posterior probabilities marked at nodes.

The relatively weak support for the relationships between the Late Miocene Ictonychinae is probably a result of two factors. The first is the generally limited preservation of these species, with some only known from jaw fragments. The second is the unspecialized nature of these Late Miocene species, which lack clear autapomorphies. Nevertheless, the dichotomy of the two tribes receives relatively good support. We examined the 47 most frequently sampled topologies and found that *Lutravus* and *Shansictis* are always located within Lyncodontini, whereas in most cases all *Cernictis* are located within Ictonychini. In some cases (20/47), *C. repenningi* and sometimes also *C. hesperus* are located as basal to Lyncodontini, but the more completely known Asiatic *Cernictis* are always basal to Ictonychini. In summary, the interrelationships of the Miocene Ictonychinae within *Cernictis* and *Lutravus* require further study, pending the description of new and more complete material; however, based on the present evidence, the diversification of the two tribes is supported by our phylogeny.

The divergence times inferred in this analysis (Supplemental material Fig. S1) are generally younger than those inferred purely based on molecular phylogenies (Law et al., 2018). This is likely to be correlated with including more fossil taxa in this study, which helps to better constrain the evolutionary chronological framework. We propose that using a total-evidence tip-dating method can result in more reliable estimates of divergence time.

Early dispersal of Ictonychinae

Even though the intrageneric relationships of the Late Miocene Ictonychinae are not completely clear, our results suggest that intercontinental dispersals in this subfamily occurred by the Late Miocene, as *Lutravus* and *Cernictis* had wide distributions in both eastern Asia and North America. In North America, *Lutravus* appeared in Hh2 (6.5–7.5 Ma), and *Cernictis* slightly later in Hh3 (5.8–6.5 Ma) (Tedford et al., 2004), broadly contemporaneous with their counterpart species in eastern Asia (6–7 Ma, and 5.7–7 Ma, respectively) (Dong and Qi, 2013; Kaakinen et al., 2013).

In North America, the fossil record is generally better and more complete, and no Ictonychinae are known from an earlier age (Baskin, 1998, 2011). In the Old World, some Early and Middle Miocene species have been proposed as related to Ictonychinae, e.g. *Trochictis* (Baskin, 2011; Reig, 1957), although some other authors assign this genus to Guloninae (Ginsburg, 1999). During the Late Miocene, there were high levels of faunal exchange between Eurasia and North America, but this was highly asymmetrical, with dispersals from Eurasia to North

America much more common than those in the opposite direction (Jiangzuo and Wang, 2022; Qiu, 2003). Therefore, we propose that both *Lutravus* and *Cernictis* are likely to have originated in Eurasia and dispersed to North America together with many other carnivores, e.g. *Amphimachairodus*, *Pristifelis*, several Agriotheriini, *Pekania*, *Plesiogulo*, *Eomellivora* and *Simocyon* (Harrison, 1981; Jiangzuo and Flynn, 2020; Jiangzuo et al., 2022, 2023; Jiangzuo and Wang, 2022; Samuels and Cavin, 2013; Savage, 1941; Stock and Hall, 1933; Thorpe, 1921; Wang et al., 2012; Zdansky, 1924a).

Conclusions

Our systematic study reveals a high diversity of Ictonychinae in the Late Miocene of eastern Asia, including the identification of new species such as *Cernictis baskini* from Baode, *Lutravus dianensis* from Shihuiba, and the new genus and species *Shansictis xinzhouensis* from Baode. Additionally, we assign the species *Cernictis lufengensis* from Shuitangba and Shihuiba, Yunnan, to Ictonychinae. *Cernictis* is an early member of Ictonychini, whereas *Lutravus* and *Shansictis* are early members of Lyncodontini. Even though the phylogenetic relationships of species within these genera are still not fully clear, the dichotomy of the two tribes in the Late Miocene is supported by our phylogeny. Both *Cernictis* and *Lutravus* are likely to have originated in Eurasia and dispersed to North America shortly after their appearance.

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No potential conflict of interest was reported by the author(s).

ORCID

Xiaoming Wang ⓘ http://orcid.org/0000-0003-1610-3840
Tao Deng ⓘ http://orcid.org/0000-0003-0069-5474

References

Bartolini Lucenti, S. (2018). Revising the species '*Mustela*' *ardea* Gervais, 1848–1852 (Mammalia, Mustelidae): *Martellictis* gen. nov. and the systematics of the fossil 'Galictinae' of Eurasia. *Comptes Rendus Palevol*, *17*, 522–535. https://doi.org/10.1016/j.crpv.2018.02.003

Baskin, J. A. (1998). 9 Mustelidae. In C. M. Janis, K. M. Scott, & L. L. Jacobs (Eds.), *Evolution of Tertiary mammals of North America: Terrestrial carnivores, ungulates, and ungulatelike mammals* (pp. 152–173). Cambridge University Press.

Baskin, J. A. (2011). A new species of *Cernictis* (Mammalia, Carnivora, Mustelidae) from the Late Miocene Bidahochi Formation of Arizona, USA. *Palaeontologia Electronica*, *14*, 1–7.

Batsch, A. J. G. C. (1788). *Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien, für akademische Vorlesungen entworfen und mit den nöthigsten Abbildungen versehen Erster Theil.* Academischen Buchhandlung.

Bjork, P. R. (1970). The Carnivora of the Hagerman local fauna (late Pliocene) of southwestern Idaho. *Transactions of the American Philosophical Society*, *60*, 3–54. https://doi.org/10.2307/1006119

Bowdich, T. E. (1821). *An analysis of the natural classification of Mammalia, for use of students and travelers*. J. Smith.

Colombero, S., Pavia, M., & Rook, L. (2012). *Pannonictis nestii* (Galictinae, Mustelidae), a new element in the vertebrate association of the human site of Pirro Nord (Italy, Early Pleistocene). *Geodiversitas*, *34*, 665–681. https://doi.org/10.5252/g2012n3a11

Deshmukh, U., & Valenciano, A. (2022). *Neoyunnanotherium* nom. nov., a replacement name for the genus *Yunnanotherium* Qi (2014 (Carnivora, Mephitidae) non Han, 1986 (Tragulidae). *Zootaxa*, *5222*, 298–300. https://doi.org/10.11646/zootaxa.5222.3.7

Dong, W., & Qi, G.-Q. (2013). Hominoid-producing localities and biostratigraphy in Yunnan. In X. M. Wang, L. J. Flynn, & M. Fortelius (Eds.), *Fossil mammals of Asia* (pp. 293–313). Columbia University Press.

Ewer, R. F. (1973). *The carnivores*. Cornell University Press.

Ficcarelli, G., & Torre, D. (1967). Il mustelide *Enhydrictis galictoides* del Pleistocene della Sardegna. *Palaeontographia Italica*, *33*, 139–160.

Furlong, E. L. (1932). A new genus of otter from the Pliocene of the northern Great Basin province. *Carnegie Institution of Washington Publication*, *418*, 93–103.

García, N., Arsuaga, J. L., Castro, J. M. B. D., Carbonell, E., Rosas, A., & Huguet, R. (2008). The Epivillafranchian carnivore *Pannonictis* (Mammalia, Mustelidae) from Sima del Elefante (Sierra de Atapuerca, Spain) and a revision of the Eurasian occurrences from a taxonomic perspective. *Quaternary International*, *179*, 42–52. https://doi.org/10.1016/j.quaint.2007.09.031

García, N., & Howell, F. C. (2008). New discovery of a large mustelid – *Pannonictis* cf. *nestii* – (Carnivora: Mammalia) from the Early Pleistocene locality of Sima del Elefante (Sierra de Atapuerca, Spain). *Palaeontographica Abteilung a –Stuttgart*, *284*, 1–16. https://doi.org/10.1127/pala/284/2008/1

Gazin, C. L. (1934). Upper Pliocene mustelids from the Snake River basin of Idaho. *Journal of Mammalogy*, *15*, 137–149. https://doi.org/10.2307/1373984

Ginsburg, L. (1999). Order Carnivora. In G. E. Rossner, & K. Heissig (Eds.), *The Miocene land mammals of Europe* (pp. 109–148). Pfeil.

Hall, E. R. (1935). A new mustelid genus from the Pliocene of California. *Journal of Mammalogy*, *16*, 137–138. https://doi.org/10.2307/1374362

Harrison, J. A. (1981). *A review of the extinct wolverine, Plesiogulo (Carnivora, Mustelidae) from North America*. Smithsonian Institution Press. https://doi.org/10.5479/si.00810266.46.1

Huelsenbeck, J. P., & Ronquist, F. (2001). MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, *17*, 754–755. https://doi.org/10.1093/bioinformatics/17.8.754

Janis, C. M., Scott, K. M., Jacobs, L. L. (1998). *Evolution of Tertiary mammals of North America: Terrestrial carnivores, ungulates, and ungulatelike mammals*. Cambridge University Press.

Jiangzuo, Q., & Flynn, J. J. (2020). A new species of *Agriotherium* from North America, and implications for understanding transformations in the metaconid–entoconid complex of bears. *Journal of Mammalian Evolution*, *27*, 775–787. https://doi.org/10.1007/s10914-019-09480-x

Jiangzuo, Q., Flynn, J. J., Wang, S., Hou, S., & Deng, T. (2023). New fossil giant panda relatives (Ailuropodinae, Ursidae): A basal lineage of gigantic Mio–Pliocene cursorial carnivores. *American Museum Novitates*, *2023*, 1–71. https://doi.org/10.1206/3996.1

Jiangzuo, Q., Li, S., & Deng, T. (2022). Parallelism and lineage replacement of the Late Miocene scimitar toothed cats from the Old and New World. *iScience*, *25*, 105637. https://doi.org/10.1016/j.isci.2022.105637

Jiangzuo, Q., Liu, J., Jin, C., Song, Y., Liu, S., Lü, S., Wang, Y., & Liu, J. (2019). Discovery of *Enhydrictis* (Mustelidae, Carnivora, Mammalia) cranium in Puwan, Dalian, Northeast China demonstrates repeated intracontinental migration during the Pleistocene. *Quaternary International*, *513*, 18–29. https://doi.org/10.1016/j.quaint.2019.01.024

Jiangzuo, Q. G., & Wang, S. Q. (2022). Northeastern Asia humidification at the end of the Miocene drives the boost of mammalian dispersals from the Old to New World. *Journal of Palaeogeography*, *12*, 50–68. https://doi.org/10.1016/j.jop.2022.09.002

Kaakinen, A. N. U., Passey, B. H., Zhang, Z.-Q., Liu, L.-P., Pesonen, L. J., & Fortelius, M. (2013). Stratigraphy and paleoecology of the classical dragon bone localities of Baode County, Shanxi Province. In X. Wang, L. J. Flynn, & M. Fortelius (Eds.), *Fossil mammals of Asia* (pp. 203–217). Columbia University Press.

Kaup, J. J. (1835). *Das Thierreich in Seinen Hauptformen Systematisch Beschrieben*. Diehl.

Koepfli, K. P., Deere, K. A., Slater, G. J., Begg, C., Begg, K., Grassman, L., Lucherini, M., Veron, G., & Wayne, R. K. (2008). Multigene phylogeny of the Mustelidae: Resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. *BMC Biol*, *6*, 10. https://doi.org/10.1186/1741-7007-6-10

Kormos, T. (1931). *Pannonictis pliocaenica* n. g. n. sp., a new giant mustelid from the Late Pliocene of Hungary. *Annalibus Instituti Regii Hungarici Geologici*, *29*, 1–16.

Koufos, G. D. (1982). *Plesiogulo crassa* from the upper Miocene (lower Turolian) of northern Greece. *Annales Zoologici Fennici*, *19*(3), 193–197.

Kowalski, K. (1959). *Baranogale helbingi* Kormos and other Mustelidae from the bone breccia in Podlesice near Kroczyce (Poland). *Acta Palaeontologica Polonica*, *4*, 61–69.

Larivière, S. (2002). *Ictonyx striatus*. *Mammalian Species*, *698*, 1–5. https://doi.org/10.1644/1545-1410(2002)698<0001:IS>2.0.CO;2

Law, C. J., Slater, G. J., & Mehta, R. S. (2018). Lineage diversity and size disparity in Musteloidea: Testing patterns of adaptive radiation using molecular and fossil-based methods. *Systematic Biology*, *67*, 127–144. https://doi.org/10.1093/sysbio/syx047

Lewis, P. O. (2001). A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology*, *50*, 913–925. https://doi.org/10.1080/106351501753462876

Liu, J. Y., & Qiu, Z. X. (2009). Carnivora. In C. Z. Jin & J. Y. Liu (Eds.), *Paleolithic site – the Renzidong Cave, Fanchang, Anhui Province* (pp. 220–282). Science Press.

Morlo, M., Le Maitre, A., Bastl, K., Engel, T., Lutz, H., Lischewsky, B., Berg, A.v., & Nagel, D. (2021). First record of the mustelid *Trochictis* (Carnivora, Mammalia) from the early Late Miocene (MN 9/10) of Germany and a re-appraisal of the genus Trochictis. *Historical Biology*,

33, 1183–1195. https://doi.org/10.1080/08912963.2019.1683172

Peters, N., Vos, J. d. (2012). A villafranchian mustelid, *Pannonictis ardea* (Gervais, 1859) (Carnivora, Mustelidae) from Langenboom (Noord-Brabant, The Netherlands). *Cainozoic Research*, *9*, 9–14.

Petter, G. (1964). Deux Mustélidés nouveaux du Pontien d'Espagne orientale. *Bulletin du Muséum national d'histoire naturelle (Sér. 2)*, **36**, 270–278.

Pilgrim, G. E. (1932). The genera *Trochictis*, *Enhydrictis* and *Trocharion*, with remarks on the taxonomy of the Mustelidae. *Proceedings of the Zoological Society of London*, *4*, 845–867. https://doi.org/10.1111/j.1096-3642.1932.tb01566.x

Pocock, R. I. (1921). On the external characters and classification of the Mustelidae. *Proceedings of the Zoological Society of London*, *91*, 803–837. https://doi.org/10.1111/j.1096-3642.1921.tb03292.x

Qi, G. (1983). Description of Carnivora fossils from Lufeng. *Acta Anthropologica Sinica*, *2*, 11–20.

Qiu, Z. X. (2003). Dispersals of Neogene carnivorans between Asia and North America. *Bulletin of the American Museum of Natural History*, *109*, 18–31.

Qiu, Z. X., Deng, T., & Wang, B. Y. (2004). *Early Pleistocene mammalian fauna from Longdan, Dongxiang, Gansu, China*. Science Press.

Ray, C. E., Anderson, E., Webb, D. S. (1981). The Blancan carnivore *Trigonictis* (Mammalia: Mustelidae) in the eastern USA. *Brimleyana*, *5*, 1–36.

Reig, O. A. (1956). Note préliminaire sur un nouveau genre de mustélidés fossiles du Pléistocene de la République Argéntine. *Mammalia*, *20*, 223–230. https://doi.org/10.1515/mamm.1956.20.3.223

Reig, O. A. (1957). Un mustélido del género *Galictis* del Eocuartario de la provincia de Buenos Aires. *Ameghiniana*, *1*, 33–47.

Ronquist, F., Klopfstein, S., Vilhelmsen, L., Schulmeister, S., Murray, D. L., & Rasnitsyn, A. P. (2012a). A total-evidence approach to dating with fossils, applied to the early radiation of the hymenoptera. *Systematic Biology*, *61*, 973–999. https://doi.org/10.1093/sysbio/sys058

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Hohna, S., Larget, B., Liu, L., Suchard, M. A., & Huelsenbeck, J. P. (2012b). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, *61*, 539–542. https://doi.org/10.1093/sysbio/sys029

Rook, L. (1995). *Pannonictis nestii* (Carnivora, Mammalia) from the late Villafranchian of Pietrafitta (Umbria, Italy). Preliminary note. *Ecologae Geologicae Helvetiae*, *88*, 853–864.

Rook, L., Bartolini Lucenti, S., Tuveri, C., & Arca, M. (2018). Mustelids (Carnivora, Mammalia) from Monte Tuttavista fissure fillings (Early and Middle Pleistocene; Orosei, Sardinia): Taxonomy and evolution of the insular Sardinian Galictini. *Quaternary Science Reviews*, *197*, 209–223. https://doi.org/10.1016/j.quascirev.2018.08.022

Salesa, M. J., Peigné, S., Antón, M., & Morales, J. (2022). Chapter 2 – Evolution of the family Ailuridae: Origins and Old-World fossil record. In A. R. Glatston (Ed.), *Red panda* (2nd ed.) (pp. 15–29). Academic Press.

Samuels, J. X., & Cavin, J. (2013). The earliest known fisher (Mustelidae), a new species from the Rattlesnake Formation of Oregon. *Journal of Vertebrate Paleontology*,

33, 448–454. https://doi.org/10.1080/02724634.2013. 722155

Sato, J. J., Wolsan, M., Prevosti, F. J., D'Elia, G., Begg, C., Begg, K., Hosoda, T., Campbell, K. L., & Suzuki, H. (2012). Evolutionary and biogeographic history of weasel-like carnivorans (Musteloidea). *Molecular Phylogenetics and Evolution*, *63*, 745–757. https://doi.org/ 10.1016/j.ympev.2012.02.025

Savage, D. E. (1941). Two new middle Pliocene carnivores from Oklahoma with notes on the Optima fauna. *The American Midland Naturalist*, *25*, 692–710. https://doi.org/ 10.2307/2420725

Schreuder, A. (1937). A note on the Carnivora of the Tegelen Clay, with some remarks on the Grisoninae. *Archives Néerlandaises de Zoologie*, *2*, 73–94. https://doi.org/10. 1163/187530137X00023

Spassov, N. (2001). *Zorillas* (Carnivora, Mustelidae, Ictonychini) from the Villafranchian of Bulgaria with a description of a new species of Baranogale Kormos, 1934. *Geodiversitas*, *23*, 87–104.

Stock, C., & Hall, E. R. (1933). The Asiatic genus *Eomellivora* in the Pliocene of California. *Journal of Mammalogy*, *14*, 63–65. https://doi.org/10.2307/1374038

Tedford, R. H., Albright III, L. B., BarnoskyA. D., Ferrusquia-Villafranca, I., Hunt Jr, R. M., Storer, J. E., Swisher III, C. C., Voorhies, M. R., Webb, S. D., & Whistler, D. P. (2004). Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene epochs). In M. O. Woodburne (Ed.), *Late Cretaceous and Cenozoic mammals of North America: Biostratigraphy and geochronology* (pp. 169–231). Columbia University Press.

Tedford, R. H., Flynn, L .J., Qiu, Z., Opdyke, N. D., & Downs, W. R. (1991). Yushe Basin, China: Paleomagnetically calibrated mammalian biostratigraphic standard for the Late Neogene of Eastern Asia. *Journal of Vertebrate Paleontology*, *11*, 519–526. https://doi.org/10. 1080/02724634.1991.10011420

Thorpe, M. R. (1921). Two new fossil Carnivora. *American Journal of Science*, *1*, 477–483. https://doi.org/10.2475/ajs. s5-1.6.477

Valenciano, A., Abella, J., Sanisidro, O., Hartstone-Rose, A., Álvarez-Sierra, M. Á., & Morales, J. (2015). Complete description of the skull and mandible of the giant mustelid *Eomellivora piveteaui* Ozansoy, 1965 (Mammalia, Carnivora, Mustelidae), from Batallones (MN10), late Miocene (Madrid, Spain). *Journal of*

Vertebrate Paleontology, *35*, e934570. https://doi.org/10. 1080/02724634.2014.934570

Valenciano, A., Morales, J., Azanza, B., & Demiguel, D. (2022). *Aragonictis araid*, gen. et sp. nov., a small-sized hypercarnivore (Carnivora, Mustelidae) from the upper middle Miocene of the Iberian Peninsula (Spain). *Journal of Vertebrate Paleontology*, *41*, 1–11. https://doi.org/10. 1080/02724634.2021.2005615

Valenciano, A., Pérez-Ramos, A., Abella, J., & Morales, J. (2020). A new hypercarnivorous mustelid (Mammalia, Carnivora, Mustelidae) from Batallones, late Miocene (MN10), Torrejón de Velasco, Madrid, Spain. *Geodiversitas*, *42*, 103–121. https://doi.org/10.5252/ geodiversitas2020v42a8

Wang, X., Tseng, Z., & Takeuchi, G. (2012). Zoogeography, molecular divergence, and the fossil record–the case of an extinct fisher, *Pekania palaeosinensis* (Mustelidae, Mammalia), from the late Miocene Baogeda Ula Formation, Nei Mongol. *Vertebrata PalAsiatica*, *50*, 293–307.

Wolsan, M., & Semenov, Y. (1994). Dental evolution in the late Miocene genus *Eomellivora* (Carnivora, Mustelidae) and its biostratigraphic implications, Neogene and Quaternary Mammals of the Palearctic. Conference in honour of professor Kazimierz Kowalski (pp. 17–21).

Wolsan, M., & Semenov, Y. A. (1996). A revision of the late Miocene mustelid carnivoran *Eomellivora*. *Acta zoologica cracoviensia*, *39*, 593–604.

Yensen, E., & Tarifa, T. (2003a). *Galictis cuja*. *Mammalian Species*, *728*, 1–8. https://doi.org/10.1644/728

Yensen, E., & Tarifa, T. (2003b). *Galictis vittata*. *Mammalian Species*, *727*, 1–8. https://doi.org/10.1644/727

Zdansky, O. (1924a). *Jungtertiare Carnivoren Chinas*. Geological Survey of China.

Zdansky, O. (1924b). Jungtertiäre Carnivoren Chinas. *Palaeontologia Sinica*, *ser. C2*, 1–149.

Zdansky, O. (1927). Weitere Bemerkungen uber fossile Carnivoren aus china. *Palaeontologica Sinica*, *Series C4*, 1–28.

Zhang, C., Stadler, T., Klopfstein, S., Heath, T. A., & Ronquist, F. (2016). Total-evidence dating under the fossilized birth-death process. *Systematic Biology*, *65*, 228–249. https://doi.org/10.1093/sysbio/syv080

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