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# *Sonidolestes wendusui*, a new genus of Erinaceinae (Eulipotyphla, Mammalia) from the Lower Miocene of Inner Mongolia, China

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## ABSTRACT

A new erinaceine, *Sonidolestes wendusui* gen. et sp. nov., from the Early Miocene of Inner Mongolia in China, is described here. The tooth morphology of this new taxon is quite unique. Especially, the enlarged p4 has a regressed paraconid and lacks the metaconid and the paralophid, unlike any known member of the Erinaceinae. *Sonidolestes wendusui* probably feeds on snails or coleopteran insects. The new erinaceine demonstrates the experimentation of members of the Asian Erinaceinae with different food and ecological niches.

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Erinaceinae; Early Miocene;  
Inner Mongolia; durophagy

## Introduction

China has a rich and continuous fossil record of erinaceids, which can be traced back to *Eochenus* from the Middle Eocene of Jilin (Wang and Li 1990). Although the members of Galericinae and Brachyericinae also exist in China, the Erinaceinae occupied the dominant position as it appeared in the Early Oligocene. This is in sharp contrast to western Eurasia, where the Galericinae hold the dominant position throughout the Neogene (e.g. Van den Hoek Ostende 2001; Van den Hoek Ostende et al. 2016; Furió et al. 2018).

So far, a total of four fossil genera belonging to the Erinaceinae have been reported. In 1926, Teilhard de Chardin was the first to report *Palaeosceptor rectus* from Saint-Jacques in Inner Mongolia (Teilhard de Chardin 1926; McKenna and Holton 1967; Sulimski 1970). *Amphechinus kansuensis* and *Amphechinus minimus* were named and described by Bohlin (1942) from Oligocene of Gansu based on dentaries, and he also recorded *Palaeosceptor* cf. *P. rectus*. Zhai (1978) reported *P. cf. P. rectus* and ?*Amphechinus* sp. in Feiyue Station of Xinjiang, and the latter was classified as *Palaeosceptor gigas* (Qiu and Tong, 2015). Huang (1984) reported three species of Erinaceinae from the Lower Oligocene of Ulanatal in Inner Mongolia, which include *Palaeosceptor acridens*. Qiu (1996) named *Mioechinus? gobiensis* from Middle Miocene Tunggur Formation in Inner Mongolia. Shortly afterwards, Bi named *Amphechinus bohlini* from the Lower Miocene in Xinjiang (Bi 2000). *Oligoechinus lanzhouensis* was named from the Upper Oligocene in Gansu (Li et al. 2019). In all, over nearly a hundred years, a total of four genera and eight species of fossil Erinaceinae and some finds in open nomenclature have been reported from Inner Mongolia, Gansu, and Xinjiang in northern China (Figure 1; Table 1). All of them are mainly represented by mandibular fragments or isolated teeth.

Like other small mammals of the same period, such as Lagomorpha, although the same genus can be found in the faunas from the North Aral of Kazakhstan (Lopatin 2004, 2006), in fact, the Erinaceinae members of China are closer to the taxon from the Valley of Lakes of Mongolia (Ziegler et al. 2007). Both them have

a lot of the same species. Here, a new genus and species of subfamily Erinaceinae from the Lower Miocene of Inner Mongolia is described. The material comprises an articulated partial skull and mandibles. In addition, there are four isolated teeth that had been detached before fossilisation and were preserved between the skull and the mandibles.

## Geological setting

The central region of Inner Mongolia where Sonid Left Banner is found is located in the continental accretionary margin between the North China Plate and the Siberian Plate. Controlled by the late Mesozoic-Cenozoic large strike-slip faults, this region was a subsidence area during the Late Cenozoic, where continental sediments of varying thickness were deposited. The sedimentary layer is not thick, and the section is also very discontinuous, but it is rich in vertebrate fossils and contains several micromammal faunas (Qiu and Li 2016).

The discovery of vertebrate fossils in Sonid Left Banner began with the Central Asiatic Expedition of the American Museum of Natural History, when a fauna represented by *Platybelodon* was discovered at several sites in the Tunggur Tableland south of Saihan Gobi (Osborn 1929; Spock 1929). These sites subsequently became the classic Late Tertiary sites in East Asia. Later, the Sino-Soviet Palaeontological Expedition also carried out excavations and research in Sonid Left Banner (Chow and Rozhdestvensky 1960). Since 1986, the Institute of Vertebrate Palaeontology and Paleoanthropology of the Chinese Academy of Sciences has continuously been involved in studies in Sonid Left Banner (Qiu et al. 1988). In addition to the localities with large vertebrates, so far, seven Neogene small mammal localities have been reported from Sonid Left Banner. There are the Early Miocene localities of lower Auerban, Gashunyin Adege, and upper Auerban, the Middle Miocene sites of Moergen, Tamuqin and the Late Miocene localities Balunhalagen and Bilutu (Figure 1) (Qiu and Wang 1999; Qiu et al. 2006, 2013; Wang et al. 2009, 2019; Qiu and Li 2016).



**Figure 1.** Geographic distribution of fossil genus of Erinaceinae from Oligocene and Miocene of China. 1. Halajin Hushu; 2. Aoerban, Balunhalagen, Bilutu, Gashunyin Adege; 3. Moergen, Tamqin; 4. Tairum Nur; 5. Amuwusu; 6. Saint-Jacques; 7. Qianlishan; 8. Ulantatal; 9. Xiagou, Quantougou, Shajingyi; 10. Feiyue Station; 11. Ulungur River; 12. Keziletuogayi.

The material used in this study was collected from Layer C of IM 201905, which is about 5 km southwest from the Aoerban locality (Qiu and Li 2016; Wang et al. 2019). The mammalian fossil assemblage in this layer has not yet been fully studied. In addition to the reported *Synexallerix junggarensis* (Li and Li, 2022), the insectivores of the fossil assemblage also include a small Brachyericinae, one or two Erinaceinae, a Uropsilinae, and two or three Soricidae. The rodent fauna consists mainly of Tachyoryctoidinae, including *Tachyoryctoides* and *Ayakozomys*, as well as Distylomyidae, Sciuridae, Zapodidae, and Cricetidae; the lagomorphs include *Sinologomys* and *Desmatolagus*. In addition, there are some remains of Artiodactyla, Perissodactyla and Carnivora. A similar assemblage was reported in the lower Aoerban locality and other early Miocene assemblages in eastern Asia (Meng et al. 2006; Qiu and Li 2016).

## Materials and methods

The material was collected in 2019 with other materials from the same locality, and is housed in Institute of Vertebrate Palaeontology and Palaeoanthropology (IVPP), Chinese Academy of Sciences, Beijing. The cavities of the skull and mandibles are filled to varying degrees with denser metallic minerals, which could not be displayed or reconstructed by CT scans, so traditional photography was used. The isolated teeth were scanned by the 225 Micro CT at Key Laboratory of Vertebrate Evolution and Human Origins of the Chinese Academy of Sciences. The CT models of teeth were reconstructed with VGSTUDIO MAX 3.4.

The anatomical terminology of the Erinaceidae follows Butler (1948) and Rich (1981). Upper teeth are indicated by capital letters, lower teeth by lower-case letters. The measurement method of skull and mandibles follows Yang et al. (2007). The measurement method of teeth follows Engesser (1980) and Ziegler et al. (2007). All measurements are given in mm.

The abbreviations are used in this study: (IVPP) Institute of Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences, China; (V) collection of vertebrates in IVPP; (LMS/A) Chinese land mammal stage/age system; (IM) IVPP field locality in Inner Mongolia.

## Systematic palaeontology

Order Eulipotyphla Waddell, Okada, and Hasegawa, 1999

Family Erinaceidae Fischer, 1814

Subfamily Erinaceinae Fischer, 1814

Genus *Sonidolestes* gen. nov.

### Type species

*Sonidolestes wendusui* gen. et sp. nov.

### Diagnosis

Small erinaceid. The posterior end of the nasal exceeds the anterior margin of the orbit; the lacrimal foramen is located in the orbit and can be seen from lateral view; the optic foramen is located slightly anteriorly above the suboptic foramen, and the sphenorbital foramen is located on the posterior ventral side of the suboptic foramen, close to the orbitonasal foramen; The palatine vacuity (palatine fissures) is not developed; the palatine is not significantly expanded behind the transverse crest, with a vestigial posterior nasal spine; the mandibular mental foramen is located slightly anterior below the anterior root of the p4. The dental formula is 3-1-3-3/2-1-2-3; I2, I3, C, and P2 all have double roots; P4 has a bulbous paracone; M1 and M2 have conical metaconules; i1 is chisel-like; p4 is massive, with a bulbous protoconid, tiny paraconid, and absent metaconid, paracristid and protocristid.

### Etymology

Sonid-, named after Sonid Left Banner, the region where the holotype was found; and -lestes, from ancient Greek *lēistēs*, thief, bandit.

### Comparisons

The new genus *Sonidolestes* differs from all Erinaceinae genera with a known p4 in having a very bulbous protoconid, a tiny paraconid and lack the metaconid. It differs from all Erinaceinae genera except *Scymnerix* in with very undeveloped palatine vacuity (Lopatin 2003). It differs from most Erinaceinae genera with a known I2 in having two completely separate roots (only *Amphexichinus horncloudi* and *Scymnerix* have two fused roots) (Rich and Rasmussen 1973; Lopatin 2003). It differs from all fossil Erinaceinae genera

**Table 1.** Geographic and stratigraphic positions of fossil genera of Erinaceinae from Oligocene and Miocene of China.

<i>Palaeosaptor</i>		
<i>Palaeosaptor acridens</i> Matthew et Granger, 1924		
Ulantatal, Alxa Left Banner, Inner Mongolia	Ulantatal Formation, Lower Oligocene	Huang 1984
<i>Palaeosaptor</i> cf. <i>P. acridens</i>		
Dingdanggou, Subei, Gansu	Paoniuyan Formation, Upper Oligocene	Wang et al. 2003; Wang et al. 2008
Keziletuogayi, Burqin, Xinjiang	Keziletuogayi Formation, Lower Oligocene	Ye et al. 2005
<i>Palaeosaptor rectus</i> Matthew et Granger, 1924		
Saint-Jacques, Hanggin Banner, Inner Mongolia	Ulanbulag Formation, Lower Oligocene	Teihard de Chardin, 1926; McKenna and Holton 1967; Sulimski 1970
<i>Palaeosaptor</i> cf. <i>P. rectus</i>		
Qianlishan, Hanggin Banner, Inner Mongolia	Yikebulage Formation, Upper Oligocene	Wang et al. 1981
Xiagou, Lanzhou, Gansu	Lower red member, Upper Oligocene	Qiu et al. 1997; Qiu 2000
Yindirte, Subei, Gansu	Paoniuyan Formation, Upper Oligocene	Bohlin 1942; Wang et al. 2008
Feiyue Station, Hami, Xinjiang	Taoshuyuanzi Formation, Oligocene	Zhai, 1978
Ulungur River, Fuyun, Xinjiang	Tiersihabahe Formation, Upper Oligocene; Suosuoquan Formation, Lower Miocene	Ye et al. 2001; Meng et al. 2006
<i>Palaeosaptor gigas</i> (Lopatin, 2002)		
Feiyue Station, Hami, Xinjiang	Taoshuyuanzi Formation, Oligocene	Zhai, 1978
<i>Ampechinus</i>		
<i>Ampechinus kansuensis</i> (Bohlin, 1942)		
Yindirte, Subei, Gansu	Paoniuyan Formation, Upper Oligocene	Bohlin 1942; Wang et al. 2003; Wang et al. 2008
Ulungur River, Fuyun, Xinjiang	Tiersihabahe Formation, Upper Oligocene	Meng et al. 2006
<i>Ampechinus minimus</i> (Bohlin, 1942)		
Yindirte, Subei, Gansu	Paoniuyan Formation, Upper Oligocene	Bohlin 1942; Wang et al. 2003; Wang et al. 2008
Ulungur River, Fuyun, Xinjiang	Tiersihabahe Formation, Upper Oligocene	Meng et al. 2006
<i>Ampechinus</i> cf. <i>A. minimus</i>		
Ulungur River, Fuyun, Xinjiang	Suosuoquan Formation, Lower Miocene	Meng et al. 2006
<i>Ampechinus bohlini</i> Bi, 2000		
Ulungur River, Fuyun, Xinjiang	Suosuoquan Formation, Lower Miocene	Bi 2000
<i>Ampechinus</i> cf. <i>A. bohlini</i>		
Ulungur River, Fuyun, Xinjiang	Suosuoquan Formation, Lower Miocene	Meng et al. 2006
<i>Ampechinus</i> aff. <i>A. taatsingolensis</i> Ziegler et al., 2007		
lower Auerban, Sonid Left Banner, Inner Mongolia	Auerban Formation, Lower Miocene	Li 2021
Gashunyin Adege, Sonid Left Banner, Inner Mongolia	Gashunyin Adege Bed, Lower Miocene	Li 2021
<i>Mioechinus</i>		
<i>'Mioechinus' gobiensis</i> Qiu, 1996		
Moergen, Sonid Left Banner, Inner Mongolia	Tunggur Formation, Middle Miocene	Qiu 1996
Tamqin, Sonid Right Banner, Inner Mongolia	Tunggur Formation, Middle Miocene	Qiu et al. 2013
Amuwusu, Sonid Right Banner, Inner Mongolia	Amuwusu Bed, Upper Miocene	Qiu et al. 2013
Auerban, Sonid Left Banner, Inner Mongolia	Auerban Formation, Lower Miocene	Li 2021
Gashunyin Adege, Sonid Left Banner, Inner Mongolia	Gashunyin Adege Bed, Lower Miocene	Li 2021
Halajin Hushu, Abag Banner, Inner Mongolia	Halajin Hushu Bed, Upper Miocene	Qiu et al. 2021
Quantougou, Lanzhou, Gansu	Xianshuihe Formation, Middle Miocene	Qiu 2000
<i>'Mioechinus'</i> cf. <i>'M. gobiensis</i>		
Tairum Nur, Sonid Right Banner, Inner Mongolia	Tunggur Formation, Middle Miocene	Qiu et al. 2013
Balunhalagen, Sonid Left Banner, Inner Mongolia	Balunhalagen Bed, Middle Miocene	Qiu et al. 2013
Bilutu, Sonid Left Banner, Inner Mongolia	Bilutu Bed, Upper Miocene	Qiu et al. 2013
Ulungur River, Fuyun, Xinjiang	Halamagai Formation, Middle Miocene	Bi, 1999; Ye et al. 2001
<i>Oligoechinus</i>		
<i>Oligoechinus lanzhouensis</i> Li et al., 2019		
Shajingyi, Lanzhou, Gansu	Ganjiatan Formation, Oligocene	Li et al. 2019

except *Untermannerix* in with the lacrimal foramen in located inside the orbit and can be visible in lateral view (Rich 1981).

*Sonidolestes wendusui* gen. et sp. nov.

#### Holotype

IVPP V 31355, an incomplete skull, mandibles and associated, isolated teeth belonging to the same individual (Figure 2).

IVPP V 31355-1, an incomplete skull with both P4-M3, the root of right I1, the roots of right I3.

IVPP V 31355-2, both mandibles, with left i1, p4, m2; right m1-m3 (Figure 3);

IVPP V 31355-3, left I2 (Figure 4a); IVPP V 31355-4, left P2 (Figure 4b); IVPP V 31355-5, left c (Figure 4c); IVPP V 31355-6, left m1 (Figure 4d).

#### Diagnosis

As for genus.

#### Etymology

Wendusui, named after Mr. Wendusu, the late former curator of Sonid Left Banner Museum, in recognition of his great contribution to the study of vertebrate fossils at Sonid Left Banner.

#### Type locality and horizon

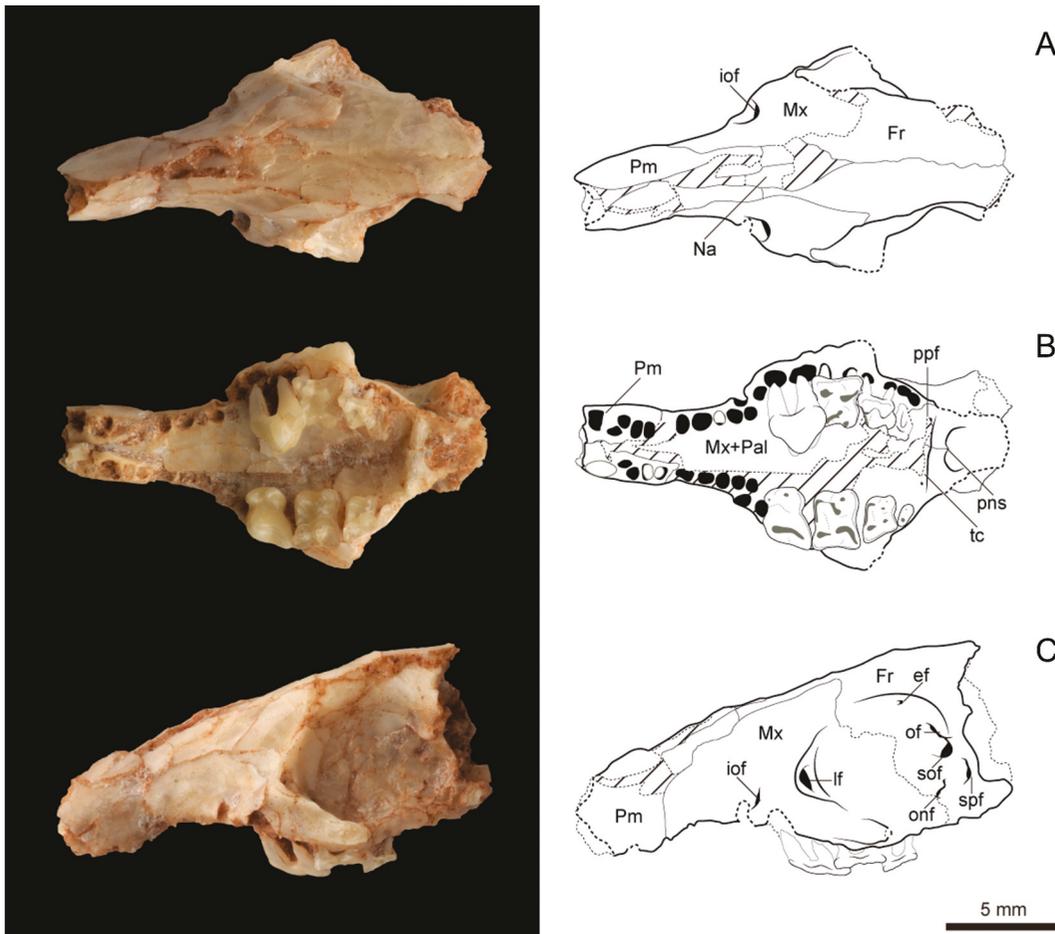
IM 201905, Bayan Nur Town, Sonid Left Banner, Xilin Gol League, Inner Mongolia, China; Aoerban Formation? Lower Miocene or Xiejian to Shanwangian LMS/A.

#### Measurement: (in mm)

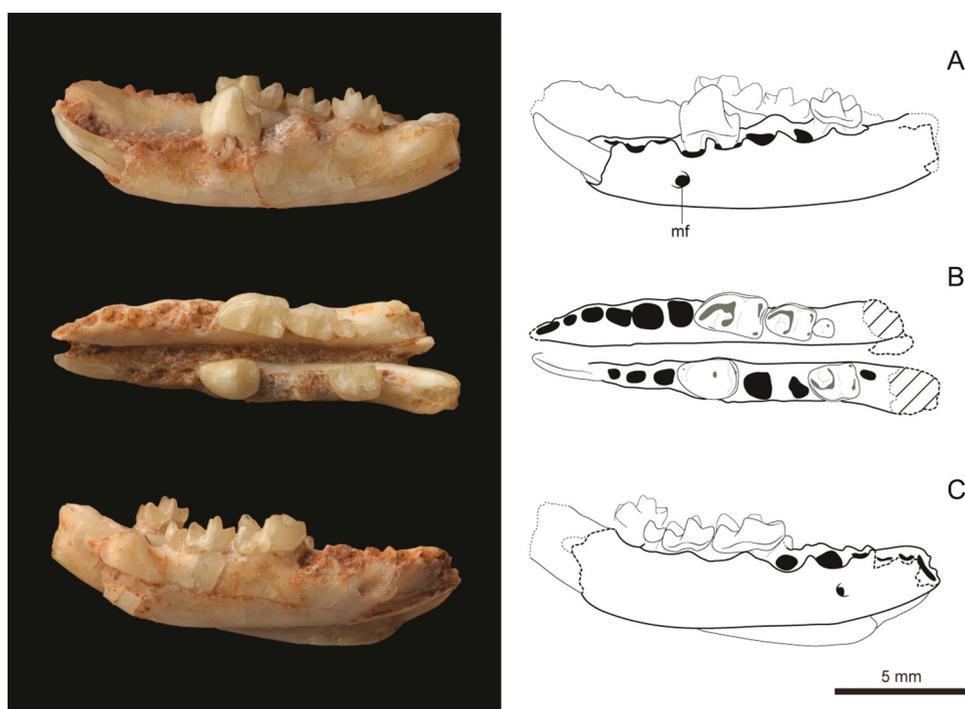
Greatest remaining length, 18.78; greatest remaining width, 9.63; greatest width of the premaxilla, 3.13; smallest interorbital width, 4.26; median palatal length, 15.62; greatest palatal width, 7.70; horizontal ramus height (below the trigonid of m1), left-2.95, right-2.77. The measurements for the dentition are given in Table 2.

#### Description

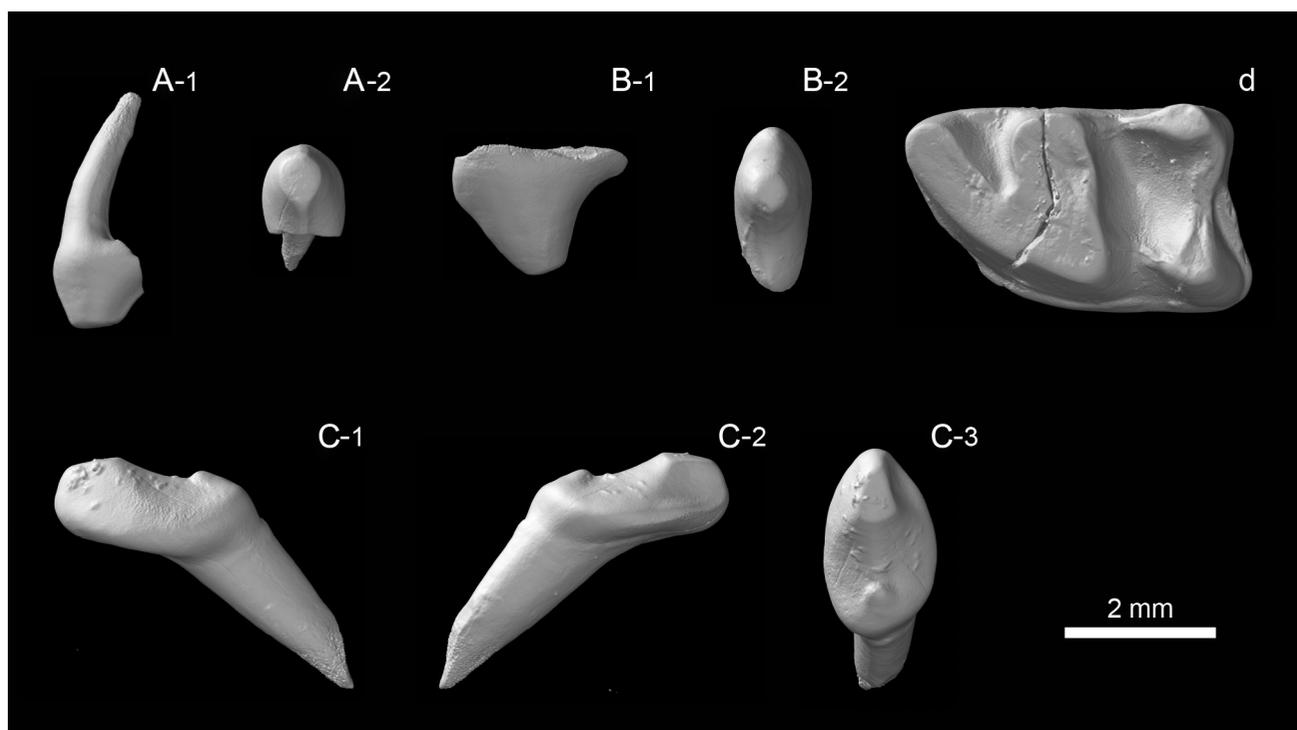
Only the front half of the skull is preserved, and the parietal-squamosal and more posterior parts are missing. The rostrum



**Figure 2.** The skull of *Sonidolestes wendusui* (IVPP V 31355-1) from Inner Mongolia in (A) dorsal, (B) ventral and (C) left lateral views. Abbreviations: **ef**, ethmoid foramen; **Fr**, frontal; **iof**, infraorbital foramen; **lf**, lacrimal foramen; **Mx**, maxilla; **Na**, nasal; **of**, orbit foramen; **onf**, orbitonasal foramen; **Pal**, palatine; **Pm**, premaxilla; **pns**, posterior nasal spine; **ppf**, posterior palatine foramen; **sof**, suboptic foramen; **spf**, sphenorbital foramen; **tc**, transverse crest.



**Figure 3.** The mandibles of *Sonidolestes wendusui* (IVPP V 31355–2) from Inner Mongolia in (A) left lateral, (B) dorsal and (C) right lateral views. Abbreviations: mf, mental foramen.



**Figure 4.** The teeth of *Sonidolestes wendusui* from Inner Mongolia. (A) left I2, IVPP V 31355–3 in labial view and occlusal views; (B) left P2, IVPP V 31355–4 in labial view and occlusal views; (C) left c, IVPP V 31355–5 in labial, mesial and occlusal views; (D) left m1, IVPP V 31355–6 in occlusal views.

**Table 2.** Tooth measurement of *Sonidolestes wendusui*. (L = length; W = width; li = lingual; bu = buccal; a = anterior; p = posterior; tri = trigonid; tal = talonid).

	I2		P2		P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W	L	W
Left	1.21	1.11	2.26	1.03	li-2.43 bu-4.38	a-3.87 p-4.13	li-	a-3.92 p-4.10	li-1.96 bu-2.62	a-3.24 p-2.66	-	1.49
Right	-	-	-	-	li-2.61 bu-4.32	a-3.93 p-4.29	li-3.04 bu-3.66	a-3.94 p-4.21	li-2.10 bu-2.58	a-3.12 p-2.64	0.82	1.55
	i1		c		p4		m1		m2		m3	
	L	L	W	L	W	L	W	L	W	L	W	
Left	5.79	2.42	1.52	3.90	2.63	4.37	tri-2.60 tal-2.68	3.09	tri-2.23 tal-2.21	-	-	
Right	-	-	-	-	-	4.39	tri-2.78 tal-2.92	3.08	tri-2.39 tal-2.25	1.42	1.25	

was slightly twisted and deformed to the left, and the surface of the bones is partly damaged. All teeth before the P4s were lost, and the left P4-M3 are semi-detached from the alveoli. Both ascending rami of the mandibles are missing.

## Skull

### Dorsal view

The nasals are mostly covered by the premaxillae that are pressed and in contact with each other. The nasal is relatively broad. The front end of the nasal is significantly shorter than the dorsal edge of the premaxilla, making the entire external nostril pear-shaped. The posterior ends of the nasals are broken, but their sutures with the frontals show that they end situated quite posteriorly, past the level of the lacrimal foramen. The premaxilla gradually narrows posteriorly and extends to the level of the infraorbital foramen, where it contacts the frontal bone. The width of the premaxilla-frontal suture is smaller than the width of the nasal bone at the same level. The maxilla extends backward slightly beyond the nasal. The postorbital process is weak. Most parts of the frontal-parietal suture are lacking, but the original suture preserved near the midline shows a rear opening, a phenomenon suggesting the possible presence of a small “preparietal”. In dorsal view, the infraorbital foramen and the anterolateral root of the P3 are exposed in front of it. The posterior end of the nasal and the anterior end of the frontal bone have longitudinal groove-like ornamentation.

### Lateral view

The premaxillary-maxillary suture extends upward and backward with a small curvature. The infraorbital foramen is located above the two labial roots of the P3, and the opening is relatively small, only comparable to the lacrimal foramen. No trace of a separate lacrimal is present. The anterior margin of the orbit is above the posterior root of the P4, and the anterior base of the zygomatic arch is aligned with the M2. The lacrimal foramen is located in the orbit and is visible from lateral view. The antorbital flange is more developed than the posterior lacrimal flange, but there is no developed lacrimal tubercle. There is a small lacrimal fenestra behind the lacrimal foramen, extending in a trough-like shape, parallel to the margin of infraorbital. The maxillary foramen is slightly larger than the lacrimal foramen. The frontomaxillary suture curves anteriorly into the orbit before the blunt postorbital process, but was later obscured by fragmentation of the area. The orbitotemporal region

is a rounded triangle whose left structures are better preserved. There is a small ethmoid foramen with an opening facing forward at the top of the orbitotemporal region. The optic foramen and the suboptic foramen are surrounded by the same flange from the rear, and the optic foramen is slightly forward. The positions of sphenorbital foramen and orbitonasal foramen are ambiguous, the former may be located on the posterior ventral side of the suboptic foramen, and the latter may be located further on the ventral side of the suboptic foramen, and the distance between the two is relatively small. The exposed anterolateral root or alveolar of the P3 is also visible in lateral view.

### Ventral view

Although the deformation of the incisor foramen disappeared due to extrusion, the arc trace marks on the premaxilla indicate that there should be a medium-sized incisor foramen, the length of it extending from the middle part of I1 to the front part of I2. Due to the severe damage to the palate, the palatomaxillary suture could not be determined, and it is impossible to judge whether there is a palatine groove, but there is at least no obvious palatine vacuity. There are two distinct posterior palatine foramina and grooves attached to them at the two posterior corners of the palate. The transverse crest is straight without obvious curvature. The palatine hardly expands behind the transverse crest, with a very faint posterior nasal spine.

There are five alveoli on the premaxilla. The first one, the alveolus of I1, is the largest; it is oval in shape with its maximum length in the direction of the long axis of the skull. The second and third alveoli are not above the central axis of the dentition, the former is closer to the medial and the latter is just the opposite, creating an oblique orientation. Together the two are interpreted as accommodating the I2. The fourth alveolus is about the same width as the fifth, the latter is longer, and both accommodate the roots of I3. The maxilla has seven alveoli anterior to P4. The first two alveoli are the largest and have the same width, but the second alveolus is longer than the first. They correspond to the C. The width of the third and fourth alveoli are the same, the latter is also longer than the former, and are consistent with the alveoli of P2. The three alveoli at the posterior end are arranged in a triangle, the anterolateral being the largest and the posterolateral one the smallest, which fits the alveoli of P3. The left M3 completely fell out of its alveolus, lying on the palatine. The M3 has two fused alveola.

## Mandible

The horizontal ramus of the mandible is low and steady. The maximum height is located below m1 to m2. The oval-shaped mental foramen is located below the anterior root of the p4. The masseter crest is weak and is located at the junction of the horizontal and ascending ramus.

The alveolus of i1 is oblong. There are three tooth alveoli between the alveoli of i1 and p4. The first one is the smallest, is almost circular and is interpreted as belonging to i2; the second one is the largest and is considered the alveolus of c; the last one is interpreted as the alveolus of p3. The p4 has the largest alveoli, and the anterior and posterior ones are equally large. The alveoli of m1 are slightly smaller than the ones of p4, and the sizes of the two alveoli are also similar. The alveolus of m3 is slightly smaller than the alveolus of p3.

## Dentition

The dental formula of *Sonidolestes wendusui* is 3-1-3-3/2-1-2-3. I1 has a single root while I2-P2 and M3 have double roots. The other upper teeth have three roots; i1-p3, m3 have single root, and the remaining lower teeth are double-rooted.

Based on the residual right alveolus and left root, I1 is strongly downwardly curved, with the root extending posteriorly to the premaxillary-maxillary suture. I2 preserves only the anterior half of the crown and the anterior root. The crown is stout and conical, with a very short blunt crest extending backward. In the occlusal view, the tooth crown is basically symmetrical to the left and right, and the anterior root is curved backward and slightly curved to the left, suggesting that it is the left I2. The crown of the P2 is relatively low (height is smaller than the length), the distal crest is slightly less developed than the mesial one, but still distinguishable; the angle of the left surface is slightly larger in the occlusal view, and the heel is slightly offset to the right. Combined with the analysis of the spacing of the alveoli, it may be consistent with a left P2. Although P3 was not preserved, its medial alveolus was closer to the midline than P4, indicating that it had a developed lingual lobe. The paracone of P4 is the largest cusp and is very bulbous. The protocone is small and slightly protrudes on the anterior side. The paracone extends posterobuccally with a rounded, blunt shearing metacrista and a weaker carnassial notch. The hypocone is about the same size as the protocone, but is low and located more lingually; the two cusps are connected by a low short crest. The parastyle is small but distinct, making an emargination slightly smaller than the posterior emargination on the anterior margin. There is a weak ridge connecting the protocone to the parastyle. The posterior cingulum extends from the hypocone, wraps around the posterolabial border, but tapers out on the buccal flank of the paracone. The M1 is slightly smaller than the P4, and its width is slightly larger than its length. The molar has an obvious posterior emargination and a weak lingual emargination. The protocone is the largest cusp, the other three main cusps are all conical. The metacone is the highest, slightly smaller than the protocone. The parastyle is well developed, but less protruding forward than that of the P4, and an inconspicuous short crest connects it to the paracone. The M1 bears a distinct, conical metaconule. The preprotocrista and postprotocrista are nearly equal in length, forming a trigon basin with a rounded bottom. The distal end of the preprotocrista points to the parastyle, the postprotocrista connects the protocone and the metaconule, and the hypocone connects to the postprotocrista through a low short crest. There are well-developed cingula on the anterior, labial and posterior side, the ectocingulum being the most developed. In addition, there is

lingual cingulum (entocingulum) between the protocone and the hypocone. The anterior margin of the M2 is significantly longer than the posterior margin. Like M1, except for the protocone, its main cusps are all conical. The hypocone is slightly lower than the other main cusps. The parastyle is small and more buccally located than in M1. The metaconule is ridge-like, the postprotocrista significantly weaker than the preprotocrista, and the hypocone does not connect with the postprotocrista. The basin and cingula are similar to the M1, but the precingulum and ectocingulum are more developed. The M2 has a broad posterior margin. The M3 is a small oval molar with large protocone and ridges. The strongly developed paracone is conical in shape and lies behind the preprotocrista. The postcingulum is stronger than the precingulum. The buccal margin of each tooth behind P4 is close, and the lingual margin is clearly separated, forming narrow triangular spaces between the molars.

The i1 is chisel-like, less curved than I1, and significantly larger than all the remaining teeth between it and p4. The only isolated antemolar has an oblong occlusal surface with a narrow anterior end and an inconspicuous crest. It is considered to be a left c based on the curvature of the main cusp. The main cusp of c is round and blunt, the heel has a vestigial cusp, and the cingulid is inconspicuous. The tooth root is directly obliquely backwards. The p4 is very strong, with a length exceeding that of m2 and slightly less than that of m1. It has a very large and swollen protoconid, and the paraconid is tiny and attached to the protoconid by a short, blunt parolophid; there is no trace of the metaconid. The p4 has a large heel with a robust posterior cingulid bearing a posterolingual cuspule. The trigonid of m1 is slightly narrower than the talonid, but significantly longer. The main cusps of the trigonid are all low and connected by blunt crests; the paraconid and metaconid are slightly higher than the protoconid. The entoconid is higher than the hypoconid; both cusps are ridge-like and extend perpendicular to each other. The paracristid, protocristid and postcristid present distinct notches. The postcristid wraps backward to the posterior base of the entoconid. The oblique cristid is poorly developed, the entocristid descends rapidly down the metaconid, touching a very inconspicuous metacristid. The base of the paraconid protrudes posteriorly with an inconspicuous small crest. The bottom of the trigonid basin and talonid basin is round and blunt. With the exception of the lingual side, the cingulids are developed. The structure of m2 and m1 is similar. The paraconid is lower than the metaconid and less developed than in the m1, the protocristid is shorter, and the lingual crest of the trigonid is more obvious. The m3 is strongly reduced, and the length is only equivalent to the talonid of the m2. The paraconid is ridge-like, and both the protoconid and the metaconid are conical. The protocristid is no more than an inconspicuous crest, barely reaching above the level of the trigonid basin.

## Comparison

*Sonidolestes wendusui* is a small erinaceid whose the greatest remaining length shows similarity to the extant gymnures *Neotetracus sinensis* and *Hylomys parvus*, but also the Erinaceinae *Scymnerix tartareus* (see Lopatin 2003). In terms of tooth size alone, the new species is slightly larger than *Amphechinus minimus* (Bohlin, 1942) and close to *A. microdus* (Lopatin, 2004).

The morphological characters of *Sonidolestes wendusui* skull and mandible are a mosaic. In the new species, the posterior ends of the nasal exceed the anterior margin of the orbit and are close to the posterodorsal margin of the maxilla. This state occurs in the two tribes Scymnericini and Erinaceini of the subfamily Erinaceinae (Butler 1948; Corbet 1988; Frost, 1991; Lopatin 2003), and in some members of the Brachyericinae, such as *Brachyerix*, *Mesechinus* and *Synexallerix* (Rich and Rich, 1971; Rich 1981; Li

and Li 2022). In the extant Galericinae (Butler 1948; Corbet 1988; Frost, 1991), the Amphechini *Amphechinus edwardsi* and members of the Brachyericinae such as *Metechinus* (Rich and Rich, 1971; Rich 1981) and *Metexallerix* (Qiu and Gu, 1988), the nasal does not extend posteriorly beyond the anterior margin of the orbit. The state of the frontopremaxillary suture is one of the key diagnostic characters of the subfamilies of Erinaceidae, but this character is not stable in Erinaceinae. *Sonidolestes wendusui*, some members of Galericinae (*Hylomys*, *Proterix*) and some members of Erinaceinae (*Erinaceus*, *Paraechinus*, *Mesechinus*, *Scymnerix*) have a weak contact or slight separation between premaxillary and frontal. The taxa where the two bones are not in contact at all include some members of Galericinae (*Echinosorex*, *Neohylomys*, *Neotetracus*) and some members of Erinaceinae (*Hemiechinus*). The premaxilla and frontal of Brachyericinae and the fossil Erinaceinae *Amphechinus edwardsi* have a larger contact suture. *Sonidolestes wendusui* probably had a 'preparietal', a feature common in extant erinaceids (Frost et al. 1991).

The lacrimal foramen of the new species is located inside the orbit and can be visible in lateral view. The same characteristic is also found in the Galericinae *Echinosorex* (Butler, 1948) and *Proterix* (Gawne, 1968), the Erinaceinae *Untermannerix* (Rich, 1981) and members of the Brachyericinae. The lacrimal foramen of *Amphechinus* and other extant members of Galericinae are also in the orbit, but they are not visible in lateral view because they have a developed flange anterior to the orbital (Butler 1948; Ziegler 2005). Scymnericini and extant members of the Erinaceini have the lacrimal foramen located above the preorbital crest, which is seen as an advanced feature (Lopatin 2006). The distribution of foramina in the orbitotemporal region is consistent with that of the extant Erinaceinae, namely, the optic foramen is slightly anterior to the suboptic foramen, and the distance between the orbitonasal foramen and the sphenorbital foramen is very short. In *Proterix*, *Scymnerix* and Brachyericinae, the distance between the orbitonasal foramen and the sphenorbital foramen is moderate. In the extant Galericinae, except for *Echinosorex*, the orbitonasal foramen and the sphenorbital foramen are far apart, and the optic foramen and suboptic foramen are vertically aligned (Butler 1948; Lopatin 2003). The optic foramen of *Echinosorex* is far in the front.

*Sonidolestes wendusui* has no or very little palatine apertures, as in Galericinae and Brachyericinae, but also in *Scymnerix*. The palatine apertures are very well developed in both extant and extinct Erinaceinae (such as *Amphechinus edwardsi*, *A. horncloudi*, *Mioechinus oeningensis*, *Untermannerix*) (Butler 1948; Rich 1981; Corbet 1988; Frost et al. 1991). The palatine of *Sonidolestes wendusui* has a very limited expansion behind the transverse palatine crest, with a faint posterior nasal spine. In the Galericinae, with the exception of *Echinosorex*, the expansion of the palatine behind the transverse palatine crest is generally limited, and the posterior nasal spine has different degrees of development. Brachyericinae has no posterior nasal spine, and the palatine is significantly posteriorly expanded; *Scymnerix* also has no posterior nasal spine, but the palatine is barely posteriorly expanded.

The location of the mandibular mental foramen of *Sonidolestes wendusui* is located below the anterior root of the p4. The mental foramen of most members of Erinaceinae are located below p4. Only members of Galericinae, with the exception of *Echinosorex*, and the Erinaceinae *Palaeoscaptor acridens* and *Amphechinus kansuensis* have a foramen located below p3. The mental foramen of members of Brachyericinae is located near below the anterior root of the m1.

Most dental characters of *Sonidolestes wendusui* are consistent with the Erinaceinae. Notably, its I2 has two completely separate

roots, while most members of the Erinaceinae have only one dental root. Only the extinct *Amphechinus horncloudi* and *Scymnerix* have two fused roots (Rich and Rasmussen 1973; Lopatin 2003). The main cusps of the P4 and upper molars of *Sonidolestes wendusui* are mostly conical, the tooth crests are relatively short and blunt, and the bottom of the tooth basin is blunt. This special morphological feature of p4 of the new species is different from all members of the Erinaceidae members except for *Proterix* from the Late Oligocene of North America (Gawne 1968) and *Galerix uenayae* from the Early Miocene of Anatolia (Van den Hoek Ostende 1992); all of these have the very bulbous protoconid, tiny paraconid, and lack the metaconid.

## Discussion

### *Palaeoecological and paleoenvironmental note*

The extant Erinaceidae (including Erinaceinae and Galericinae) are generally considered omnivorous opportunists, which is also reflected in their bunodont dentitions. They typically feed on insects, invertebrates, including worms, slugs, terrestrial molluscs, and spiders. They also eat carrion, eggs, and some reptiles, amphibians, and small mammals. In addition to carnivorous food, living hedgehogs and moonrats feed on fruits, acorns, berries, seeds, roots, and fungi (Best 2018). The diet of the extinct Brachyericinae has not been clarified, and different views suggest that they ate hard-shelled prey (McKenna and Holton 1967), or 'mechanically rough food', including plants (Gureev 1979), or largely carnivorous foods (Lopatin 2003; Lopatin and Zazhigin 2003). But in any case, the tooth morphology of the Brachyericinae predicts its powerful cutting ability.

In comparison, the large p4, degenerated M3/m3, underdeveloped crista and blunt tooth basin indentations of *Sonidolestes wendusui* all indicate that its teeth did not have strong cutting ability, but have a considerable degree of crushing ability, i.e. the ability to handle hard-shelled foods. Combined with the large lingual space between P3 and M2, the new taxon may be feeding on animals with hard outer shells like Coleoptera or snails, but soft and juicy insides. The composition of terrestrial molluscs in the Layer C of IM 201905 is the same as that of biozone C in the Valley of Lakes in Mongolia (Stworzewicz 2007), with many *Gastrocopta* sp. and *Vallonia* sp., which the new taxon may have fed on. As hedgehogs are generally omnivores, the crushing adaptation may also have been useful in the consumption of seeds with hard integuments. *Proterix* from the Late Oligocene of North America may have had a similar diet (Matthew 1903; Gawne 1968).

It is generally believed that the dentition characters of the Erinaceinae remain rather stable compared to the skull characters (Butler 1948), which indicates that the prey and feeding methods of the Erinaceinae have not changed much for a long time. *Scymnerix tartareus* of the Late Oligocene of Mongolia is clearly an outlier. Many of its features, especially the large i2, reduced M2, absence of M3, and the presence of the enamel sculpturing on the teeth are more like the Brachyericinae, although the skull features suggest that it is an unequivocal member of the Erinaceinae (Lopatin 2003). The p4 of *Sonidolestes wendusui*, with a degenerated paraconid and a lack of metaconid and paralophid resembles some of the Galericinae. Both phenomena can be explained by parallel evolution. This shows that at least in the early stages of the Erinaceidae crown group, the Erinaceinae had a high morphological plasticity and strong environmental adaptability, allowing it to compete with the Galericinae and the Brachyericinae. Asia was clearly the main battleground for this competition, in which the Brachyericinae would become extinct. Despite the dominance of the Erinaceinae

throughout most of the Cenozoic, in the end, the Galericinae would take over as the most diverse group.

### Paleodiversity and phylogenetic affinities of the Chinese erinaceids

Northern Asia, including Mongolia, Kazakhstan, and northern China, has a rich and continuous record of fossil Erinaceinae, and most taxa are also widely distributed in the region and can be found in more localities. However, with the exception of the Valley of Lakes in Mongolia where, the research is more systematic and concentrated, the research in other areas is relatively scattered and has a large time span (Ziegler et al. 2007).

Lopatin and Zazhigin (2003) argue that the Brachyericinae in Asia have always coexisted with members of the Erinaceinae, and this is also true for most of the Early Miocene fossil localities in Inner Mongolia. The Lower Auerbach locality delivered two members of the Erinaceinae: *Amphechinus* aff. *A. taatsiingolensis* and “*Mioechinus*” *gobiensis*; three members of the Brachyericinae: *Synexallerix junggarensis* and two other smaller undetermined taxa; there is even a member of the Galericinae. The fauna from Gashunyin Aude locality include five members of the Erinaceinae including *A.* aff. *A. taatsiingolensis* and “*M.*” *gobiensis* and a small representative of the Brachyericinae (Li 2021; Li and Li 2022).

The Layer C of the IM 201905 locality is currently known to have two or three members of the Erinaceinae, including *Sonidoletes wendusui*; two Brachyericines: *Synexallerix junggarensis* and another small taxon similar to the Lower Auerbach and the Gashunyin Aude localities. Among these species, *S. junggarensis* is the largest in individual size, followed by the other Brachyericine. Other members of the Erinaceinae are close in size. In tooth morphology, the Brachyericines focuses on cutting ability while our new taxon focuses on crushing ability and the remaining members of the Erinaceinae are in between these two groups. Dietary specialisation and individual sizes appear as recurrent strategies for different lineages of Erinaceidae to avoid direct competition. This holds, of course, particularly true for periods in which erinaceid diversity was at a maximum, such as the Late Oligocene and Early Miocene. Wazir et al. (2022), for instance, described a Late Oligocene erinaceine with a peculiar P4 morphology. Even though its dietary function is a bit of a mystery, it shows that hedgehogs were experimenting with different dental morphologies.

Durophagy or even malacophagy is not uncommon among the Eulipotyphla. The most obvious example is the Dimylidae, a family in western Eurasia which contained some highly adapted species (e.g. Kliepmann et al. 2014; Van den Hoek Ostende and Fejfar 2015; Crespo et al. 2018). This family clearly had its heydays in the Early Miocene (Van den Hoek Ostende et al. 2016; Furió et al. 2018). Judging by the exo-daentodontology of their dentitions, some extinct soricids (i.e. *Amblycoptus*, *Anourosorex*, *Deinsdorfia*, *Dimylosorex*, *Drepanosorex*, *Macroomys* and *Beremendia*) have been suggested to feed on hard-shelled organisms (Reumer 1984; Furió et al. 2010; Zazhigin and Voyta 2019). Notably, *Sonidoletes* and the other two hedgehogs that show massive p4 and shortened molar row, *Proterix* and *Galerix uenayae* are also Late Oligocene/Early Miocene taxa (Gawne 1968; Van den Hoek Ostende 1992). This is a period known for its relatively warm climate (Zachos et al. 2001) which certainly seems to have favoured eulipotyphlan diversity (e.g. Kliepmann et al. 2015; Furió et al. 2018). Of the three erinaceid taxa, only *Galerix uenayae* is found together with a dimylid, but this *Turkodimylus* is a rare element at the fringes of the range of the family (Van den Hoek Ostende 1995).

Finding three unrelated erinaceids with the same durophagous adaptation in different parts of the world is presumably related with the favourable climatic conditions of the Early Miocene. It is, however, unlikely that it is directly related to the availability of food sources, because snails, beetles and hard seeds are present in nearly every ecosystem. We already noted that eulipotyphlan diversity was very high in that time frame. These conditions would have led to increased competition between insectivores and, certainly in the case of the Left Sonid Banner, in particular between erinaceids. Some lineages seem to have avoided this competition by focusing on more challenging resources by developing a crushing mechanism.

The four fossil genera of the Erinaceinae in China all have different degrees of taxonomic issues. The distinction between *Palaeoscaptor* and *Amphechinus* is currently based on lower molar and mandibular features and has not been fundamentally resolved for other key parts. Neither the number of roots and heel status in m3 nor the number of teeth between the larger incisor and p4 is sufficient to fully distinguish species with similar degrees of evolution in those two genera (Ziegler et al. 2007). The main reason why “*Mioechinus*” *gobiensis* was originally classified as *Mioechinus* was the prominent metaconule on M1 and M2 (Qiu 1996), a feature that was later observed in *Palaeoscaptor* or *Amphechinus*. Considering the determination of *Mioechinus* species (Mein and Ginsburg, 2002; Ziegler 2005), this species is unlikely to be classified as *Mioechinus*. *Amphechinus bohlini* Bi, 2000 and *Parvericius buk* Ziegler et al., 2007 are very likely recent junior synonyms of “*M.*” *gobiensis*. The former is similar in size and morphology to “*M.*” *gobiensis*, but the naming thesis do not compare them, and many type specimens do not have any upper jaw or scattered upper tooth, which is confusing (Bi 2000); the latter is named and assigned to *Parvericius* on the basis of the anteroposteriorly compressed trigonid of the m1 and m2 (Ziegler et al. 2007), but this feature was also found in *Untermannerix copiosus* from Middle to Late Miocene, *A. minimus* (Bohlin, 1942; Rich 1981) and “*M.*” *gobiensis*. The morphology of the metaconule is also very variable (Qiu 1996). The tooth morphology of *Oligoechinus lanzhouensis* is not fundamentally different from *Palaeoscaptor* nor *Amphechinus*, and since most Oligocene to Miocene Erinaceinae material do not preserve C-P3, this taxon may just be a new species belonging to *Palaeoscaptor* or *Amphechinus*, not a new genus.

### Conclusion

*Sonidoletes wendusui* is a new erinaceine taxon from the Early Miocene of Inner Mongolia in China showing special dental features whose dietary signal suggests it may feed on snails or coleopteran insects. The Asian Erinaceinae displayed a high diversity from the Late Oligocene to the Early Miocene, striving to occupy different ecological niches and compete with other subfamilies of the Erinaceidae.

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