A new fossil Erinaceidae from the Shajingyi area in the Lanzhou Basin, China

Zhichao LI^{1,2}, Yongxiang LI², Xiangxu XUE², Wenhou LI², Yunxiang ZHANG² and Fu Yang³

- 1 Earth Science and Resources College, Chang'an University, Xi'an 710064, China
- 2 State Key laboratory of Continental Dynamics, Department of Geology, Northwest University, Xi'an 710069, China
- 3 key laboratory of coal resources exploration and comprehensive utilization, ministry of land and resources, Xi'an 710021, China

Abstract.---Here, we describe a new primitive Erinaceidae species, *Oligoechinus lanzhouensis* n. gen. n. sp., based on a specimen from late Oligocene strata of the Lanzhou Basin, Gansu Province. Its characteristics are as follows: the M1 width is longer than the length, the metastyle extends far disto-labially, the posterior margin has strong curve and a distinct metaconule that is connected to the protocone by a postprotocrista is located in the centre of the tooth. The posterior arm of the metaconule is poorly developed. In the P4, the pterion of the metastyle is less developed and the metacone is carinate. In addition, *O. lanzhouensis* has a premolar larger than the canine tooth (P2 > C) and P3 had no molarisation, characters also possessed by *Erinaceus*. Overall, *O. lanzhouensis* was similar to *Mioechinus* based on architectural tooth features, demonstrating a closed genetic relationship. Fossil Erinaceidae are relatively rare before the Miocene. The discovery of *O. lanzhouensis* provides an important insight into the origin of *Mioechinus* in China and the early evolution of the Erinaceidae. Our analysis shows that a relatively recent ancestor of *Mioechinus* had probably existed in the early Oligocene and that *O. Lanzhouensis* was likely an ancestral type of *Mioechinus gobiensis*, and its systematic position should be located at a transitional position between *Amphechinus* and *Mioechinus*.

Key words: Erinaceidae, Oligoechinus, Lanzhou basin, Oligocene

E-mail: lzc 369@126.com

1 Introduction

Members of the Erinaceidae are insectivores that have survived from the Palaeocene to the present, and are widely distributed and well adapted in tropical rain forests, semi-desert and desert areas. In general, the Erinaceidae includes three subfamilies, the Hylomyinae, Erinaceinae and Brachyericinae. The Erinaceidae lived from the Palaeocene to the Eocene and were frequently singled out from the three subfamilies mentioned above and classified into the Galericinae or Echinosoricinae because of their ambiguous relationship with modern hedgehogs (Li and Qiu, 2015). Fossil Erinaceinae are rarely found in China. So far, a total of 11 genera have been found and most belong to a single genus. Early fossil materials are limited; taxa discovered from the Palaeogene include Luchenus and Eochenus from the Eocene and Metexallerix and Palaeoscaptor and Amphechinus from the Oligocene (Tong and Wang, 2006; Wang and Li, 1990; Qiu and Gu, 1988; Huang, 1984; Wang et al., 1981, Daxner-Höck et al., 2017). Furthermore, because complete fossils are rarely discovered, we cannot conduct detailed comparisons and our understanding on early Erinaceidae animals is limited (Li and Qiu, 2015). In recent years, field trips to the Lanzhou basin have led to the discovery of some animal fossils, of which an Erinaceidae fossil from the Oligocene had distinct early Erinaceidae characteristics and should be considered a new genus. This discovery provides important materials for research on the composition of early mammals in the Lanzhou basin and the origin and evolution of the Erinaceidae.

2 Geologic setting

The Lanzhou basin is located in the conjunction of the Tibet Plateau cold region, the Eastern monsoon region and the arid region of northwest China (Dmitrienko et al., 2018). It is a special geographic area that has yielded a large number of animal fossils from Cenozoic strata, including faunal series such as the Nanpoping fauna, Xiagou fauna, Lanzhou fauna, Miaozuizi fauna, Zhangjiaping fauna, Duitinggou fauna, Quantougou fauna and Xingjiawan fauna (Xie, 1991; Qiu and Gu, 1988; Flynn et al., 1999; Qiu et al., 2000; Qiu et al., 2001; Wang and Qiu, 2000; Wang et al., 2001;

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Xie, 2004; Xie and Zhao, 2011; Zhang et al., 2012, 2014; Wang et al., 2017, Han et al., 2018). The Oligocene in the Lanzhou basin contained the upper Yehucheng and lower Xianshuihe formations (equivalent to the Hanjiajing and Ganjiatan formations). A study of the Lanzhou basin sedimentary faces showed that the Oligocene developed from lacustrine and deltaic deposits (Yue et al., 2001). The upper member of the Yehucheng Formation consists of brownish-red mudstone, sandstone and laminated green mudstone that yield abundant fossils including gastropods, ostracods and small fish. In contrast, the Hanjiajing Formation consists mainly of greyish-white to greyish-yellow sandstone that contains Steneofiber sp., Paraentelodon sp., Schizotherium ordosium, Aprotodon lanzhouensis and massive remains of rodents known as the Nanpoping fauna (Qiu et al., 1997; Xie, 2004). The new fossils described here were found in the laminated green mudstone of the lower member of the Ganjiatan Formation, which is above the greyish-white to greyish-yellow sandstone of the lower Nanpoping fauna and below the brownish-red mudstone of the upper Ganjiatan (Fig. 1). According to paleomagnetic data, the age range of Nanpoping fauna is from 29.5 to 31.5 Ma and the age of Xiagou fauna is about 26 Ma (Yue et al., 2003; Zhang, 2015). Thus, we speculated that the age range of the new Erinaceidae fossils found in the Lanzhou basin was between 26 and 29.5 Ma and belong to the early-late Oligocene.

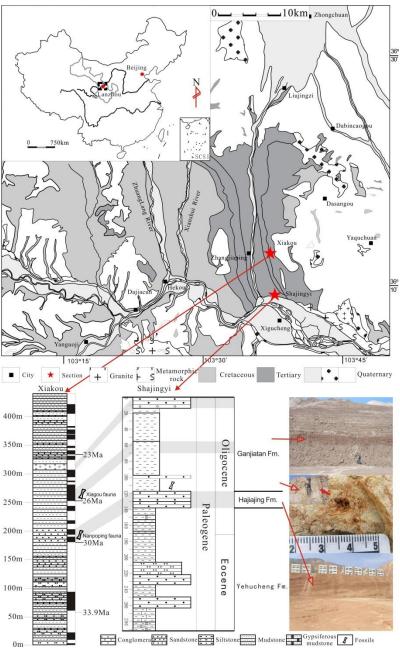


Fig. 1. Maps showing the fossil location and stratigraphic column (modified from Zhang, 2015; China basemap after China National Bureau of Surveying and Mapping Geographical Information).

3 Systematic paleontology

Class MAMMALIA Linnaeus, 1758

Order EULIPOTYPHLA Waddell, Okada and Hasegawa, 1999

Suborder Erinaceomorpha Gregory, 1910

Family Erinaceidae Von Waldheim, 1817

Subfamily Erinaceinae Von Waldheim, 1817

Genus Oligoechinus new genus

Type species.--- Oligoechinus lanzhouensis n. gen. n. sp.

Diagnosis.---Same as for species.

Etymology.--- Genus name after the Oligocene, where the specimen was found.

Occurrence.---Lanzhou Basin, Gansu Province, China; late Oligocene.

Oligoechinus lanzhouensis n. gen. n. sp. (Figs. 2.27-2.31)

Holotype.—The specimen is preserved at Northwest University in Xi'an, China and specimen number NWUV1404. The material contained a fragment of the right upper jaw with one canine tooth, three premolar teeth and one molar tooth.

Diagnosis.—Compared with other genera of the Erinaceidae and Oligoechinus, the M1 has a distinct metaconule that has no postbrachium or antebrachium. The P3 has a triangular crown with no molarisation, and P2 is evidently larger than C.

Etymology.---The species name is derived from 'Lanzhou'.

Description.---The specimen only includes a part of the right upper jaw as the jaw bone was too thin to be repaired and only the C-M1 teeth were repaired. The tip of C was destroyed during repair. P2 has a clear outward tilt, which probably suffered from the pressure of the diagenetic process. The trailing end of the P3 implant under the bottom of P4 and the tip of P3 were slightly damaged as revealed by scanning electron microscopy. The anterior cingulum was slightly damaged. The M1 is relatively complete.

C is small and short with a low crown that is elliptically cylindrical. The tip of C is rather blunt. The cingulum of the lateral tongue is well developed.

P2 is larger than C, has a triangular crown and is unicuspid. The cingulum developed in the anterior, posterior and lingual lateral portions and becomes wide at the back tooth. The protocone is low and is an intumescent cingulum on the back of lingual side.

P3 is similar to P2 and is slightly bigger than P2 and has a triangular crown. P3 is unmolarised, and the main apical development is in the outside middle of the tooth. It is tall with a wide base and possesses a strip of edge on the front and back edges. The back edge extends to the bottom of P4 and is covered. The front edge extends to the anterior cingulum. The inner side of the tooth is shrunken, becoming narrow and small with a low and small protocone. The girdle is developed in the front, back and lingual sides and is expanded on the back of the lingual side.

P4 is larger and more stout than P3 and has molarisation. Its crown is an oblique rectangle with a clear trailing-edged curve leading to a gently concave edge. The parastyle is weak and can only be an inflated former cingulum. The sturdy paracone is the tallest of all the tooth tips. It is stout and strong and has a dental ridge that stretches out of the paracone. The back edge of the paracone connects with the front edge of the metacone. The metacone presents a ridge that intensely projects a straight, posterior-lateral stretch to the metastyle, becoming lower in height and making the outside and back side of the crown wider. The pterion of the metastyle is not developed. The protocone is half the height of the paracone. The preparacrista is well preserved. The hypocone is weak and low and located behind the protocone near the lateral tongue, which is relatively independent of the protocone. The hypoconal flange is wide and large. Cingulum is well developed in the front side, back side, outside, whereas that in the lingual side is weak but inflated in the back.

The M1 is nearly square in shape, is bigger than P4 and is longer than it is broad. The trailing edge curve is prominent, and the maximum bending department is located in the middle of trailing edge; the outer edge does not bend. The crown has four bunodont cusps. The protocone is the most robust cusp, and the prong bends slightly to the side of the cheek. The hypocone is as big as the paracone, and both are smaller than the protocone and metacone. The parastyle is weak and is likely an inflated fore-tooth cingulum. There is no mesostyle, ridged metastyle connection with the postmetacrista, which projects backwards. The preprotocrista connects the protocone with the protoconule and extends to the front of the paracone, where there is an inconspicuous protoconule that shrinks into the ridge. The postprotocrista extends to the middle of the crown and connects with the metaconule. The metaconule is small but relatively independent and outstanding and is located in the middle of crown. It is short, cylindrical and disconnected from the paracone, metacone and hypocone. The front and back arms are not developed. The front and back of the hypocone are shrunken, resulting in a wide distance between the trailing edge and the post-cingulum. Its forearm connects with the postprotocrista, and the lingual side is inflated. The trigon basin is broad and deep, and the protocone extends to the valley between the

paracone and metacone. The hypoconal flange is located in the valley between the metaconule and hypocone, due to the shrinkage of buccal side of the hypocone. The hypoconal flange is medially developed. The cingulum is developed in the front, back and cheek side, and it is weak in the lingual side

4 Comparison and discussion

The P4 of the new species is molarised, and its crown has four cusps. The paracone is the tallest of the cusps, the metacone is weak and the hypocone is developed. The M1 is square in shape with no mesostyle. All these features confirm that the specimen belongs to the Erinaceidae. Only two genera are known from the Eocene in China, Eochenus and Luchenus (Wang and Li, 1990; Tong and Wang, 2006). Eochenus sinensis is the only species found in China from the late to middle Eocene, which has the existing characters of a P1: C is clearly bigger than P1, P4 is not molarised, the metaconule of M2 clearly developed and the leading and trailing edges differ from Oligoechinus. Species belonging to the Luchenus from the early Eocene are from the Chaling Formation. They differ from Oligoechinus in the P1, have a small P2, the P3 crown is triangular, the metastyle edge of the P4 is prominent, the hypocone is evidently molarised and is the biggest upper cheek tooth. The hypocone of the M1 behind the protocone has a weak edge projecting to the protocone, and the metaconule post-edge extends to the metastyle. The evidence shows that E. sinensis and species belonging to the Luchenus have a P1 that is not degraded and that the metaconule in the cheek teeth have a clear front and back edge, which shows a more original character. The new species has no P1, the metaconule in the M1 connects with the post-edge of the protocone and the metaconule is relatively independent with no front-back edge. These results imply a relatively advanced character.

The known species from the Oligocene include *Palaeoscaptor*, *Metexallerix* and *Amphechinus* (Huang, 1984; Qiu and Gu, 1988; Wang et al., 1981; Daxner-Höck et al., 2017), whereas species from European and American areas that have similar characters include those belonging to the *Galericinea*, *Apulogalerix*, *Galerix* and *Parasorex* (Fig. 2) (Mein and Suarez, 1993; Ziegler, 2005; Furio etal., 2010; Federico and Flaviano, 2013; Klietmann et al., 2014; Jerome et al., 2015).

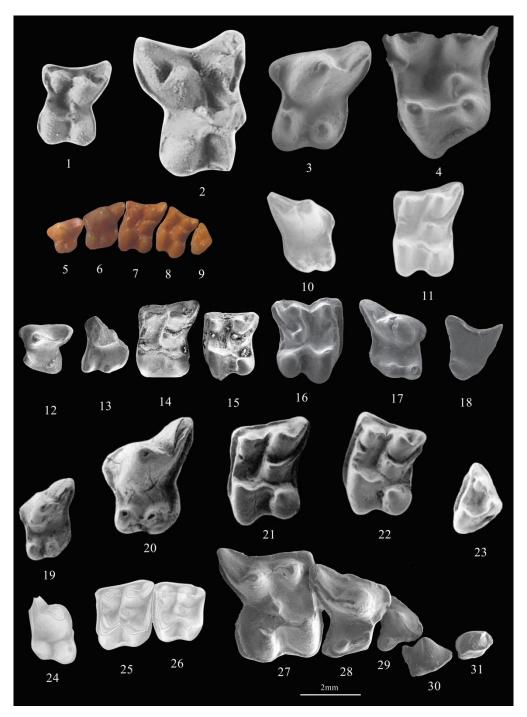


Fig. 2. Plate.

(1) 1, Amphechinus microdus, left M1, PIN 4516/467, from Kazakhstan; 2, Amphechinus akespensis, right M1, PIN 210/774, from Kazakhstan, Early Miocene; (2) 3–4, Galericinae gen. et sp., 3 P4, NMA 2012-16/2058, 4 M2, NMA 2012-15/2058, from Germany, Early Miocene; (3) 5–9, Apulogalerix pusillus, left P3–M3, from Gargano, late Miocene; (4) 10–11, Galerxi ibericus, right P4–M1, OTU-1.71 and OTU-1.69, from Iberian peninsula, late Miocene; (5) 12–15, Parasorex sp. 12, 13 left P3, MAFI 2015.30.1 and PM2014.1, 14-15 left M1–M2, MAFI 2015.41.1 and MAFI 25015.37.1, from Hungary, middle Miocene; (6) 16–18, Parasorex depereti, 16-17 right M1–P4, CPM53 and CPM48, 18 left D3, DSG/URT-053/40, from Sardinia, Pliocene; (7) 19–23, Parasorex socialis, left P3–M3, NHMA P10-400B1, NHMA P10-401A1, NHMA P10-402A4, NHMA P10-403D1 and NHMA(P10-404B5), from Germany, middle Miocene; (8) 24–26, Lantanotherium sannigueli, 24 right P4, IVPP V 9731.10, 25-26 left M1–M2, IVPP V 9731.11 and IVPP V 9731.11, from China, late Miocene; (9) 27–31, Oligoechinus sp. right C, P2–M1, NWUV1404, from China, late Oligoecne. Scale bar represents 2 mm.

The palaeoscaptor are distributed in Inner Mongolia, Xinjiang and Gansu Provinces in China, but most of them preserved the lower jaw. A *Palaeoscaptor rectus* found in the Xiagou section of the Lanzhou Basin was a juvenile, and only the lower jaw was preserved so it cannot be directly compared with *Oligoechinus* (Wang and Qiu, 2000). However, it is easy to distinguish the differences between the two species: the M1 in adult individuals of *Palaeoscaptor rectus* is larger at 5.9 mm length and 3.3 mm

width, and the M1 and M2 have no metaconule. The M1 in O. lanzhouensis is smaller at 3.3 mm length and 3.8-mm width, with a clear metaconule.

Metexallerix spp. have been found in Xinjiang, in the Gansu Province of China. Metexallerix gaolanshanensis is the representative Metexallerix species found in the Gaolan Mountain region, located in the southeast corner of the Lanzhou Area (Qiu and Gu, 1988). When compared with Oligoechinus, we found that M. gaolanshanensis is a unique insectivore within this genus. It is large in size, the P4 is larger than the M1 at 6.2 mm long and 4.4 mm wide, the upper dental formula is 3*1*2*2 and there are two premolars, which are distinct from the others. The latter is small and has three premolars which is distinct from former.

Amphechinus was widely distributed throughout Asia, Europe, Africa and America until the Miocene. Many Amphechinus fossils have been found in the Gansu area of China, including Amphechinus cf. A. minimus (Table 1) and an undefined species (preserved fossil teeth were damaged and scattered) (Wang and Qiu, 2000). A new survey shows that the genotype species of Amphechinus is Palaerinaceus arvernensis Aymard that was first described by Viret in 1938. Its M1 and M2 have no metaconules, which was long considered a distinct character of Mioechinus and Amphechinus. For example Rich (1973) and Engesser (1980) used this standard to describe a Late Neogene hedgehog species in Turkey. Some researchers took the view that the I1 was not amplified as a distinct character in Mioechinus and Amphechinus, which led to some species being classified based on their M1 and M2 metaconule as Amphechinus, and even some hedgehog species were classified based on the metaconule as Amphechinus in late period (Butler, 1956). Therefore, some species of Amphechinus are ambiguous (Ziegler, 2005, 2007). Meanwhile, the previously described Amphechinus specimen was based on a preserved underjaw, few maxilla are saved and most of them only have a text description without relevant plates. Hence, it's difficult to conduct detailed species-specific comparisons (Lopatai, 2004). After collecting masses of materials, we found some scattered premolars, defined as M1s of Amphechinus as they had distinct metaconules. A comparative analysis follows.

Table 1. Measurements of Oligoechinus and comparison with other species.

Type	Oligoechinus Lanzhouensis L*W	Mioechinus oeningensis Lydekker,1886 L*W	M. sansaniensis Lartet,1851 L*W	M. tobieni Engesser,1980 L*W	M. gobiensis Qiu, 1996 L*W	Amphechinus cf. A. minimus Bohlin, 1942 L*W
P2	1.5*1.1	2.4*2.2	2.0*1.5	1.9*1.3	0.6*0.65	
Р3	1.8*1.6	2.9*2.4	2.0*2.1	2.0*2.2	1.19*1.21	0.98*0.82
P4	2.8*2.9	5.5*4.6	3.3*4.7	3.3*3.9	1.83*2.28	
M1	3.3*3.8	4.9*6.0	4.3*4.7	4.2*4.4	2.21*2.58	

Note: L=length, W=width. units=mm.

The M1 of *Oligoechinus* compared with that of *A. microdus* (Fig. 2.1) shows that *Oligoechinus* has no parastyle, the metacone is almost as big as the paracone, the metacone is located right behind the paracone and has no tongue side bias, the metaconule is predominant and connects with the protocone at the back crista and the hypocone front crista connects with the protocone back crista. The latter metacone is taller and stronger than the paracone and has a tongue side bias, the parastyle is small and the protoconule is carinate. A well-developed protoconule back crista projects to the base of the metacone, there is a small swelling akin to a metaconule in the middle of crown and the protoconule and metaconule have disappeared because of crown abrasion.

The comparison between M1 of *Oligoechinus* and that of *A. akespensis* (Fig. 2.2) show that *Oligoechinus* has an equal altitude paracone and metacone, the metacone is stouter than the paracone and there is no tongue side bias. The parastyle is undeveloped, the cingulum in the front side is closed to buccal side and expanded, the protoconule is present as a ridge and connects with the protocone front crista and the metaconule is distinct and connects with the protoconule back crista. The latter has a taller and stouter metacone than the paracone, the metacone is closed to the tongue side and the metastyle is small and connects with the paracone by a low ridge paracone front crista. The middle part of the paracone projects to the back of the tongue, the centrocrista front arm pterion is well developed and the metaconule is teardrop shaped and angled slightly towards the paracone. The front ridge of the paracone extends to the protoconule but does not connect with it. There is an isolated metaconule bias to the tongue side in the binding site between the hypocone and protocone.

It is obvious that *Oligoechinus* is distinct from some species of *Amphechinus* that had a metaconule. To avoid any classification confusion, we agree with the opinions of Qiu (1996) and Ziegler (2005, 2007), who used the earliest defined characters of M1–M2 with no metaconules to identify the two species *Amphechinus* and *Mioechinus*. That is to say, the M1 and M2 of *Mioechinus* have distinct metaconules while in *Amphechinus* they are missing.

In this way, *Oligoechinus* is different from *Amphechinus* cf. A. minimus as follows: the former canine tooth is columnar, low and short with a blunt prong. The P3 is bigger than C and its paracone

has obvious front and back crista. The M1 has a clear metaconule, its hypocone is not isolated and the hypocone front crista connects with the protocone back crista. The latter is a small individual, but C tapers obliquely, its major point is towards the front side and the cusp is slightly recurving. The P3 has a crown similar in size to the large C, the chewing surfaces of the trigon exist on the paracone, protocone and embryonic hypocone.

Data are limited on the *Galericinea*. The latest research reported on only one piece of P4 and an M1 with a broken outer edge (Figs. 2.3-2.4) (Klietmann, 2014). After our comparison, we discovered that the hypocone in P4 of *Oligoechinus* was located behind the protocone and was close to the tongue side and that a weak crista connected the protocone and hypocone. In M1, the metaconule connects with the protocone back crista and is divided from the metacone by a trench.

Apulogalerix, Galerix and Parasorex (Figs. 2.5-2.23) are the special live branches from the Oligocene to the Pliocene (Bohlin, 1942; Tong and Wang, 2006; Federico et al., 2013; Zijlstra et al., 2015; Jerome et al., 2015). The differences between Oligoechinus and the upper three species are as follows: the metaconule of new species' M1 connects with the protocone, the hypocone connects with the protocone back crista and the mataconule's post-brachium is not developed. Although the metaconule of Apulogalerix, Galerix and Parasorex are well developed with a strong forearm and posterior arm, its posterior arm extends to the cingulum in the back side, and the protocone has few connections with the metaconule.

Oligoechinus has large differences when compared with the species already found from the Oligocene. As such, it is likely a new species found in the Lanzhou area from the Oligocene epoch. Miocene species that have similar structural features to Oligoechinus are the Lantanotherium and Mioechinus, except that these species existed from the Oligocene to Miocene.

Lantanotherium (Figs. 2.24-2.26) is widely distributed throughout China, including Yuannan and Jiangsu Provinces (Qiu and Li, 2015). It is different from *Oligoechinus* (Figs. 2.27-2.31), as the protocone of the P4 is relatively independent from the hypocone. Although its M1 and M2 have metaconules, they are relatively independent and not connected with any major points: the back crista of the hypocone does not project outside and the posterior edge is not curved.

The *Mioechinus* was classified as belonging to the Erinaceidae from the earliest finds in Miocene strata of Europe and Turkey. *Mioechinus* discovered from Europe and Middle-East include *M. oeningensis* (Lydekker, 1886), *M. sansaniensis* (Lartet, 1851) and *M. tobieni* (Engesser, 1980). Only one species has been found in China, *M. gobiensis* (Qiu, 1966), from Inner Mongolia and Gansu Province. Fortunately, one *M. gobiensis* was found in the Qauntougou section of the Xiajie area in the Lanzhou basin (Qiu, 2000)

A comparative study has shown that *Oligoechinus* is closely related to *M. gobiensis*. There are three teeth between the I3 and P4. The pterion of the P4 metastyle is undeveloped. The width of the M1 is greater than the length, and a remarkable feature is the metaconule connects with the protocone and is separated from the metacone by a deep valley. The hypocone fore-crista connects with the paracone post-crista and the hypocone has no post-arm. The cingulum is well-developed.

A previous report has shown that although there are a large number of *Mioechinus*, there are relatively few details. Except for some early reports, only Ziegler (2005) provided information on a large number of scattered Miocene fossil *Mioechinus* materials from Germany. Hence, after conducting a detailed comparison of previous materials (Table 1; Fig. 3), we found the following differences: European species are oversized as a whole, *M. oeningensis* is the biggest individual with an M1 width up to 6 mm, followed by *M. sansaniensis* and *M. tobieni* who have an M1 width over 4 mm. In addition, *M. gobiensis* from China are the smallest with a P2–P4 distance of less than 2 mm and an M1 width less than 3 mm. However, the *Oligoechinus* individual from the Lanzhou basin is in-between being smaller than the European Erinaceidae and larger than the *M. gobiensis* from China. At the same time, its teeth characters are also different from both of them.

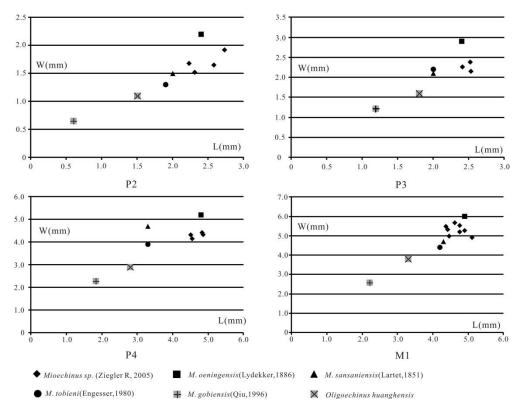


Fig. 3. Scatter diagrams showing length and width of P2-M1 of *Oligoechinus* and Mioechinus species.

L=length, W=Width. (1) Black diamond include relevant specimens of Mioechinus sp. (Ziegler R, 2005), NHMA P6, P18, P35, from Petersbuch, middle Miocene; (2) Black Square symbols represent *M. oeningensis* (Lydekker, 1886), from Öhningen, Miocene; (3) Black triangle symbols represent *M. sansaniensis* (Lartet, 1851), from Sansan, Miocene; (4) Black circle represent *M. tobieni* (Engesser, 1980), from Yeni-Eskihisar, Miocene; (5) Shaded cross symbols represent *M. gobiensis* (Qiu, 1996), V10332, from Inner Mongolia, middle Miocene; (6) Shaded Fork symbols represent *Oligoechinus*, NWUV1404, from Lanzhou, late Oligocene.

Compared with *M. oeningensis* (Fig. 4.1), *Oligoechinus* has the following characters. C is smaller than P2. P2 has one major point with an edge cusp and a well-developed cingulum. P3 has no molarisation, a triangular crown and the cups of the paracone are sharply pointed front and back with two crista. The back crista extends to the front cingulum. The protocone is weak. P4 has a well-developed postcingulum, the front crista of the protocone does not extend to the forepart of the paracone and the hypocone has a wide pterion. The metacone back crista of the M1 projects back outwards, the outer edge does not curve, its metaconule is coniform and the parastyle is undeveloped.

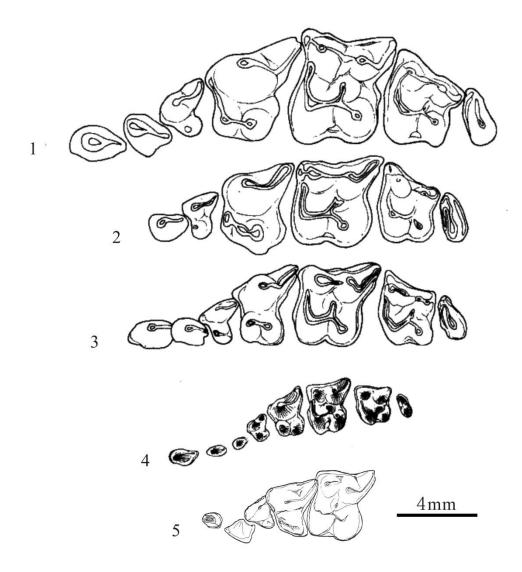


Fig. 4. Comparison between *Oligoechinus* and *Mioechinus* species.
(1) 1, *M. oeningensis* (Lydekker, 1886), from Öhningen, Miocene; (2) 2, *M. sansaniensis* (Lartet, 1851), from Sansan, Miocene; (3) 3, *M. tobieni* (Engesser, 1980), from Yeni-Eskihisar, Miocene; (4) 4, *M. gobiensis* (Qiu, 1996), V10332, from Inner Mongolia, middle Miocene; (5) 5, *O. huanghensis*, NWUV1404, from Lanzhou, late Oligocene.

Oligoechinus differs from M. sansaniensis (Fig. 4.2) as follows. In Oligoechinus, the P2 has a triangular crown with edge cusps. The P3 has no molarisation, its paracone has a fore-crista and post-crista, the protocone is weak and its fore-cingulum and lingular cingulum are developed. The P4 hypocone is distinctly smaller than the protocone, the hypoconal flange is wide and deep and the fore-crista of the protocone is developed. The M1 has a relatively large width:length ratio, its metaconule is coniform and there is no parastyle. The post-crista projects backwards and the maximum crook of post edge is located in the middle of the post-edge.

Oligoechinus differs from M. tobieni (Fig. 4.3) as follows: in Oligoechinus, C is larger than P2, P2 has a triangular crown, has edge cusps and the cingulum is developed. P3 has no molarisation with a triangular crown and a weak protocone. The cingulum in P4 developed in the front, back and outside, and expanded at back side close to the tongue side. The hypocone is smaller than the protocone and the back side of M1 is hardly curved.

Oligoechinus differs from M. gobiensis (Fig. 4.4) as follows: Oligoechinus is larger, C is smaller than P2 and P2 has a triangular crown. Its paracone is developed and the cingulum in the tongue side is expanded and close to the front side. The P3 also has a triangular crown, a sturdy paracone with front and back cristae. The back crista does not project outwards and the cingulum in the tongue side is developed. The protocone of the front crista is developed in P4, the hypocone is behind the protocone and is closer to the tongue side.

A comprehensive analysis shows that *Oligoechinus* (Fig. 4.5) is different from other Oligocene species. Although it is similar to *Mioechinus*, there still distinct differences between them and it should

be classified as a new genus.

5 Systematic position and environmental analysis

From the analysis described above, *Oligoechinus* is distinctly different from previously discovered species. Its teeth from C to M1 gradually increase and become wide and long. It also has special, perhaps original characteristics. The M1 has a metastyle that projects powerfully backwards and outwards. It has a remarkable metaconule, its protocone connects with the metaconule by the protocone back crista and the hypocone front crista connect with the protocone back crista. These characters are similar to *Mioechinus*. However, it has a special character: C is smaller than P2, showing that *Oligoechinus* has a character similar to *Erinaceus koloshanensis* and *E. olgae*. Considering its unique characters, some plesiomorphy and yield in the Oligocene, we named it *Oligoechinus*.

From the early systematic position raised by Butler (1948), *Mioechinus* in the Miocene is a branch that evolved from *Amphechinus* in the Oligocene (Fig. 5). This new *Oligoechinus* species discovered in this time has both similar and dissimilar characters with the early *Amphechinus* and late *Mioechinus* in terms of tooth structure, which matches with its early-late Oligocene yield. Therefore, *Oligoechinus* probably belongs to a transition style between *Amphechinus* and *Mioechinus*.

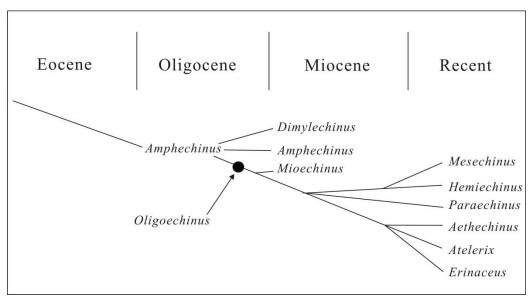


Fig. 5. Postulated phylogeny of Erinaceinae (after Butler 1948; He, 2012).

Amphechinus belongs to the family Erinaceidae, which lived in desert and arid environments and we can speculate that Oligoechinus would have also (Wang and Qiu, 2000; Qiu, 2000). According to previous analyses, including a plant coexistence analysis and sporopollen analysis (Sun et al., 2004; Yao et al., 2010), and research on phytoliths in strata from the same period that contained fossil Populus davidiana Dode cuticles, the climate in the Lanzhou basin at that time period was considered to be moist, warm and sub-humid with an abundant precipitation. Other researchers believe that this area was subtropical arid or a periodically drought stricken climate (Geng, 2001), or had a mild environment that was semi-arid and semi-warm-humid forest with some expansive prairie regions (Xie, 2011). Recent studies have shown that Lanzhou could be late-early Oligocene (Li et al., 2016), and given the background environment, we suggest that the new Oligoechinus existed in a semi-arid and semi-humid environment that was slightly dry.

6 Conclusions

- 1. The new fossil Erinaceidae, a yield from the bottom of the Ganjiatan Formation from the Oligocene in the Shajingyi area of Lanzhou Basin, is different from previously discovered members of the Erinaceinae. It should be a new genus for the Oligocene of China, named *O. lanzhouensis*.
- 2. O. lanzhouensis is both similar and dissimilar to early Amphechinus and late Mioechinus based on tooth structure, and it probably represents a transitional type that evolved from the early type of the Eocene to the advanced type of the Miocene.
- 3. The new species could be a representative animal living in a transition period from an early semi-arid to a semi-humid environment to a late partially dry environment in the early Oligocene.

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About the first author

LI Zhichao, male; born in 1988 in Xi'an City, Shaanxi Province; doctor; graduated from Northwest University; research assistant of Chang'an University. He is now interested in the study on Paleontology and environment in the Lanzhou and Weihe basin. Email: lzc_369@126.com; Phone: 15091150580.