



The late Eocene hyracodontid perissodactyl *Ardynia* from Saint Jacques, Inner Mongolia, China and its implications for the potential Eocene–Oligocene boundary

Bin Bai^{a,b,*}, Yuan-Qing Wang^{a,c}, Zhao-Qun Zhang^{a,c}

^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, 100044, China

^b State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, 210008, China

^c College of Earth Science, University of Chinese Academy of Sciences, Beijing, 100049, China

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Abstract

Saint Jacques is a classic Oligocene fossil locality in China, which was first investigated by P. Teilhard de Chardin and E. Licent in 1923. All the fossil mammals previously reported from the area are Oligocene in age. Here we report some new material of the hyracodontid *Ardynia* from two lower horizons in the Saint Jacques area. These new specimens represent two species: *Ardynia praecox* Matthew and Granger, 1923 and *A. ordosensis* n. sp. A right lower jaw of *Ardynia praecox* with complete i1–c shows that i2 is the largest. The new species, *Ardynia ordosensis*, is characterized by a moderately hypsodont M1 with a pillar-like “crista” and the metaloph connecting the ectoloph distal to the metacone, characters that are more similar to those of *A. altidentata* than to any other species in *Ardynia*. The stratum bearing Ergilian *Ardynia* extends the deposits at Saint Jacques down to the upper Eocene. In combination with early Oligocene microfossils from the strata overlying the upper Eocene *Ardynia*-bearing layers, it is reasonable to conclude that the Saint Jacques section may bracket, or likely document, the Eocene–Oligocene transition.

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Keywords: Saint Jacques; Inner Mongolia; Hyracodontid; *Ardynia*; Ergilian; Eocene–Oligocene boundary

1. Introduction

The classic Oligocene Saint Jacques locality (San-tao-ho) is located on the right bank of the Yellow River, near Dengkou County (Li and Ting, 1983; Russell and Zhai, 1987), and about 2 km east of Balagong of Hangjin Banner, Ordos, Inner Mongolia (Fig. 1). It was first investigated by Teilhard de Chardin and Licent in 1923 during their survey in Ordos (Teilhard de Chardin and Licent, 1924a, 1924b, 1924c). The deposits at Saint Jacques were preliminarily regarded as Pliocene at the beginning (Teilhard de Chardin and Licent,

1924b, 1924c), and were revised to the Oligocene based on the occurrence of *Paraceratherium* (= *Baluchitherium*) soon afterward (Teilhard de Chardin and Licent, 1924a; Qiu and Wang, 2007). Later, Teilhard de Chardin (1926) reported mammalian fossils from Saint Jacques, found in two layers of the section that were clearly shown in a sketch. However, he considered the mammalian fauna from the different beds at Saint Jacques to be homogeneous (Russell and Zhai, 1987). After the exploration by Teilhard de Chardin and Licent, this area was rarely investigated except for a short visit by the Sino-Soviet Paleontological Expedition in 1959 (Chow and Rozhdestvensky, 1960) and IVPP crews in 1977 and 1978 (Wang, 1987). The mammalian fossils from Saint Jacques were commonly considered to be of early Oligocene age, and the lithology was roughly equivalent to the lower member of the Wulanbulage Formation in Qianlishan district (Wang, 1987, 1997).

* Corresponding author at: Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, 100044, China.

E-mail address: baibin@ivpp.ac.cn (B. Bai).

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Fig. 1. Distribution of *Ardynia* and *Prohyracodon* in Eurasia. 1, Saint Jacques, Inner Mongolia; 2, Erden Obo, Inner Mongolia; 3, Nom Khong, Inner Mongolia; 4, Linxia Basin, Gansu Province; 5, Lunan Basin, Yunnan Province; 6, Ergilin Dzo, Mongolia; 7, Khoer Dzan, Mongolia; 8, Dzamynd Ude, Mongolia; 9, Chelkar Teniz, Kazakhstan; 10, Benara, Georgia; 11, Transylvania, Romania.

In the past several years, IVPP crews have organized extensive, continuous explorations in Saint Jacques, and collected a large number of fossil mammals from different levels and sites. Unlike the previous interpretation of an early Oligocene age for the strata in the Saint Jacques section, preliminary analyses now suggest that the lithological sequence of Saint Jacques contains deposits of late Eocene through late Oligocene age. Some new specimens of the carnivore *Palaeogale sectoria* have been reported recently (Wang and Zhang, 2015), and studies on other groups are still underway.

Here we report new material of the hyracodontid *Ardynia* from two lower horizons in the Saint Jacques area, which confirms the presence of upper Eocene deposits there. The hyracodontid *Ardynia*, characterized by high crowned teeth and cursorial adaptation of the postcrania, was usually restricted to late Eocene Ergilian. Together with the unequivocal early Oligocene mammals from the higher stratigraphic levels, it can be hypothesized that the Saint Jacques section may bracket, or likely document, the Eocene–Oligocene transition.

2. Materials and methods

The new material includes a left M1 associated with a juvenile left mandible with dp3–dp4, m1 (IVPP V 23860), a nearly complete right mandible with left i1–2, right i1–3, c, and p2–m3

(IVPP V 23858), and a fragmentary right mandible with p4–m1 (IVPP V 23859).

During the recent fieldwork, relatively numerous faults have been recognized in the Saint Jacques area, which cut the Paleogene sediments into a number of blocks of various sizes. To avoid mixture of fossils collected from different horizons due to miscorrelation between different blocks, and for the sake of convenience, we labeled these blocks from A-block to W-block, and subdivided the strata of each block in its own sequence. IVPP V 23858 and V 23859 were collected from the layer L2 of L-block, and V 23860 was from the middle part of the layer D1 of D-block. The L-block and D-block consist of four layers (L1–L4) and eight layers (D1–D8), respectively, in ascending order. The strata of L-block are predominately brownish red beds of silty mudstone and gray/yellow siltstone. The strata of D-block are predominately brownish red beds of silty mudstone. The topmost horizon of L-block is considered to be correlated with or slightly lower than the basal part of D-block based on our field observation and correlation.

Micro-CT was utilized in order to acquire horizontal sections of the tooth crown in different levels. Scanning was carried out using 225 kV micro-computerized tomography (developed by the Institute of High Energy Physics, Chinese Academy of Sciences (CAS)) at the Key Laboratory of Vertebrate Evolution and Human Origins, CAS. IVPP V 23860 with M1 and dp3–m1

(parameters of dp3-m1 in parentheses) was scanned with beam energy of 120 kV (130 kV) and a flux of 120 μ A at a resolution of 13.33 μ m (36.07 μ m) per pixel using a 360° rotation with a step size of 0.5° and an unfiltered aluminium reflection target. A total of 720 transmission images were reconstructed in a 2048 \times 2048 matrix of 1536 slices using a two-dimensional reconstruction software developed by the Institute of High Energy Physics and Institute of Automation, CAS. The three-dimensional reconstructions were performed using software VG Studio 2.1. It is necessary to mention that the real worn surfaces of the teeth in *Ardynia* are uneven, irregular, and not in the same plane as showed by the horizontal sections of CT images.

Institutional abbreviations: AMNH FM, American Museum of Natural History, Fossil Mammal, New York; IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing; PIN: Paleontological Institute, Russian Academy of Sciences, Moscow; PSS: Paleontologo-stratigraphic Section of the Geological Institute, Mongolian Academy of Sciences, Ulaanbaatar.

3. Systematic paleontology

Order Perissodactyla Owen, 1848

Family Hyracodontidae Cope, 1879

Ardynia Matthew and Granger, 1923

Type species: *Ardynia praecox* Matthew and Granger, 1923.

Included species: *A. kazachstanensis* (Beliajeva, 1952), *A. altidentata* Qiu et al., 2004, *A. ordosensis* n. sp.

Emended diagnosis (modified from Radinsky, 1967): Medium-sized hyracodontid. Length of M1-3 about 60 mm or much longer in *A. altidentata*. Cheek teeth relatively high crowned: crown height index higher than 1.1. Incisors spatulate, increasing in size from I3 to I1, and i2 larger than i1 and i3. Canine incisiform and smaller than I3/i3. Relatively long postcanine diastema. P1/p1 lost; p2 reduced or completely lost. P3-4 non-molariform, with protoloph-metaloph loop; p3-4 molariform. M1-2 relatively long and narrow with oblique protoloph and variably developed “cristae”. M3 metacone extremely reduced or lost. Trigonids of lower molars triangular. Boundary between the crown and the root undulating. Horizontal ramus of the mandible procumbent anteriorly. Manus tridactyl.

Relationships: *Ardynia* is an endemic Asian hyracodontid, and ranges from late Eocene to late Oligocene. Radinsky (1967) proposed its close affinity with *Triplopus*, which may be derived from a more basal group than *Hyrachyus* (Bai et al., 2017), whereas Qiu and Wang (2007) suggested that early–middle Eocene *Pataecops* and *Rhodopagus* (Radinsky, 1965; Wang et al., 2011) may represent the “ancestor-form” of *Ardynia*. Both Prothero et al. (1986) and Wang et al. (2016) proposed a sister-group relationship between *Ardynia* and North American *Triplopidus* in the phylogenetic analysis of Rhinoceroidea. *Ardynia* is characterized by relatively high-crowned

teeth, which are more hypsodont than those of other hyracodontids (Radinsky, 1967).

Ardynia praecox Matthew and Granger, 1923

1923 *Ardynia praecox* – Matthew and Granger, p. 2, fig. 1.

1925 *Ardynia praecox* – Matthew and Granger, p. 6, figs. 6-8.

1952 *Ardynia praecox* – Beliajeva, p. 129, figs. 3-7; pl. 3, figs. 1, 2; pl. 4, figs. 1-3, 5.

1952 *Ergilia pachypterna* – Gromova, p. 99, figs. 1-3.

1952 *Parahyracodon mongoliensis* – Beliajeva, p. 122, fig. 1; pl. 1, figs. 1, 2; pl. 2, fig. 2.

1965 *Ardynia praecox* – Radinsky, p. 33, figs. 19, 20.

1991 *Ardynia mongoliensis* – Dashzeveg, p. 40, figs. 18:1a-1c, 19 (in part).

1991 *Ardynia praecox* – Dashzeveg, p. 39, fig. 17.

Holotype: AMNH FM 19156, a left maxilla with P2-M1, an isolated M3.

Referred specimens: AMNH FM 20358: right mandible with p3-m3; AMNH FM 26039: associated skull, lower jaw, and manus; PIN 473-366 etc.: right calcaneum and other postcrania; PIN 473-255: lower jaw with right i3, left and right p3-m3; PSS 27-99: right lower jaw with p3-m3; PSS 21-19: left lower jaw with p3-m3.

New material: IVPP V 23858: a lower jaw with left i1-2, right i1-3, c, and p2-m3; V 23859: a fragmentary right mandible with p4-m1. Both specimens are from the layer L2 of L-block, Saint Jacques, Ordos, Inner Mongolia. Late Eocene. Field number of IVPP V 23858: 110921WYQ01 (N 40° 15.885', E 107° 06.735'); field number of IVPP V 23859: 110921LSJ01 (N 40° 15.891', E 107° 06.810').

Diagnosis: Medium-sized hyracodontids. Lower incisors with i2 prominently larger than i1 and i3. p2 highly reduced or absent. Premolar series shortened. M1-2 metalophs connecting to the midpoint of the ectoloph mesial to the metacone.

Differential diagnosis: Differs from *A. kazachstanensis* in having i2 prominently larger than i1 and i3, p3-4 relatively smaller, and in lacking the buccal cingula of the lower cheek teeth. Differs from *A. altidentata* and *A. ordosensis* in having M1-2 with a much smaller crista, the metaloph of M1-2 connecting the midpoint of the ectoloph and distally extended. Further differs from *A. altidentata* in having less hypsodont teeth, and a smaller size.

Description:

The mandible is relatively slender (Fig. 2A, B). The horizontal ramus is procumbent anteriorly with the posterior border of the symphysis situated anterior to p2. In dorsal view (Fig. 2C), the symphyseal region is expanded anteriorly in the incisive part and slightly constricted posteriorly. The ventral border of the horizontal ramus is convex, and the height of the horizontal ramus gradually increases from p2 (19.6 mm) to m2/3 (31.1 mm). Eight mental foramina or foramina are present on the right mandible with the largest one below the canine, five below the diastema, and two below the premolars (Fig. 2A). The angular process is broken off, and the vessel notch is nearly indiscernible. On the medial side of the preserved vertical ramus there is a relatively large, low mandibular foramen situated at the level below the alveolar border (Fig. 2B).

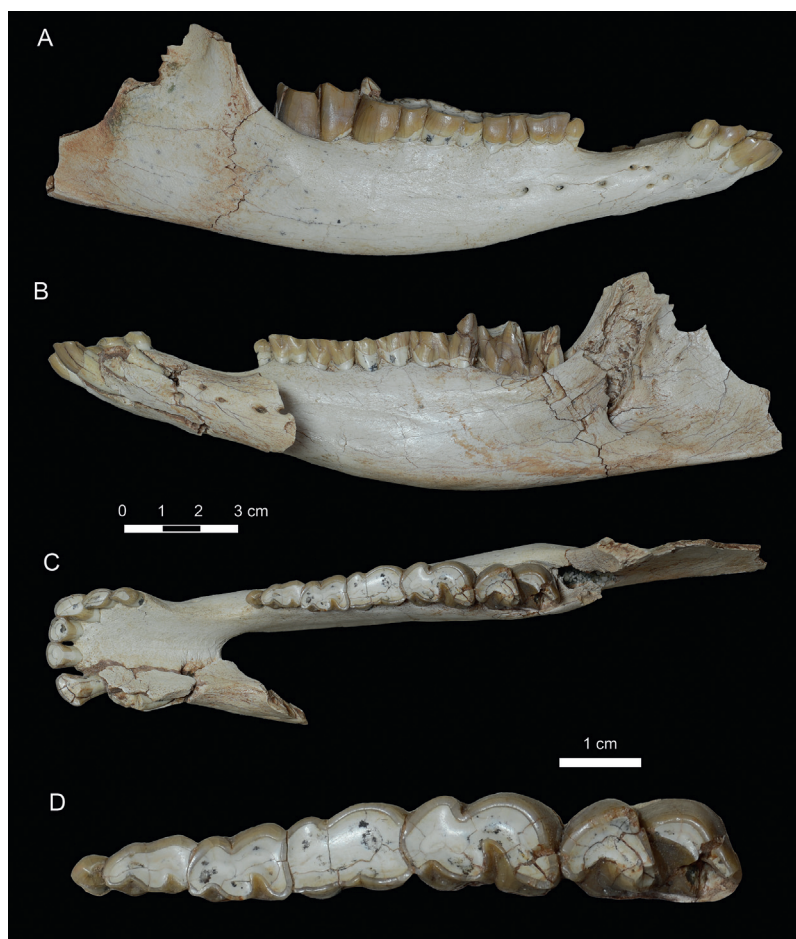


Fig. 2. The lower jaw and teeth of *Ardynia praecox* (IVPP V 23858). The lower jaw of *A. praecox* in (A) lateral, (B) medial, and (C) dorsal views. The right p2-m3 of *A. praecox* in (D) occlusal view.

The three incisors and the canine are closely appressed, with i2 the largest and the canine smallest (Fig. 2C). The incisors are moderately worn. The i1 is roughly rounded on the crown with the mesiodistal length slightly greater than the buccolingual width. The buccal surface is convex laterally and longitudinally. The buccal enamel is thicker, more distally extended, and considerably higher than the lingual enamel. The cingulum is lacking. The i2 is roughly oval in outline with the length considerably greater than the width. Other features of i2 are same as those of i1. The i3 is similar to i2 and overlapped by the latter on the mesial end, but is slightly smaller than i1. The canine is incisiform, laterally compressed as in i2-3, overlapped by i3 on the mesial end, and bears a small worn facet on the lingual side. However, the buccal and lingual enamels of the canine are equally distally extended. The incisor and canine measurements of IVPP V 23858 from the right mandible are as follows (length/width in mm): i1 (7.3/6.3), i2 (9.7/7.2), i3 (7.0/6.2), and c (7.1/4.7). The postcanine diastema is long (29.2 mm) and forms a blunt ridge, which is widely bowed lingually. Slightly anterior to the p2 is the narrowest part of the horizontal ramus with the height of 17.4 mm (Fig. 2A).

The p1 is absent. The single-rooted p2 is rather small, nodule-like, and bears an indistinct basin distally (Fig. 2D; Table 1). The p3 and p4 are moderately worn. The trigonid of p3 is triangular

in outline with a high paraconid. The metaconid is distolingual to the protoconid and the protolophid is relatively oblique. The talonid is slightly wider than the trigonid and the hypoconid is prominent, extending a hypolophid lingually with a pointed end. The inconspicuous ectoflexid is a very shallow groove. The cingulum is absent. The buccal enamel is thicker than the lingual one, as in the anterior teeth. The p4 is molariform with a well-developed hypolophid and relatively large entoconid. The trigonid is similar to that of p3, whereas the talonid is pronouncedly wider and slightly longer than the trigonid. The ectoflexid is distinct and forms a narrow groove (Fig. 2A). The boundary between the crown and the root undulates on the lingual side (Fig. 2B).

The m1 is heavily worn (Fig. 2D). The talonid is slightly wider and considerably longer than the trigonid. The ectoflexid is distinct and relatively deep. The mesial and distal borders of m1 lack the enamels at heavily worn stage. The m2 is moderately worn and generally similar to p4. The trigonid is triangular with an angled junction between the protolophid and the paralophid. The talonid is wider and longer than the trigonid. The hypolophid is oblique and the cristid obliqua connects to the protolophid lingual to the protoconid. The joint between the cristid obliqua and the hypolophid is smoothly curved. The m3 is partially broken at the metaconid and entoconid, and not completely erupted.

Table 1

The comparative measurements of *Ardynia praecox* and *A. kazachstanensis*. The data of PSS 21-19 and PIN 1463-169 are from Dashzeveg (1991, table 10).

	<i>Ardynia praecox</i>			<i>A. kazachstanensis</i>
	IVPP V 23858	AMNH FM 21764 (cast of PIN 473-255)	PSS 21-19	PIN 1463-169
p2 L	4.8		6.0	7.5
p2 W	4.3		3.8	5.0
p3 L	12.1	13.3	10.0	15.0
p3 TrdW	6.2	7.4	5.0	9.0
p3 TadW	7.2	9.2	8.5	10.0
p4 L	12.8	14.2	13.5	16.0
p4 TrdW	8.1	9.2	9.8	10.0
p4 TadW	9.5	10.4	11.0	12.0
m1 L	15.2	17.6	15.5	17.0
m1 TrdW	9.9	11.2	9.8	12.0
m1 TadW	10.9	11.7	11.0	13.0
m2 L	18.8 ^a	22.0	19.0	21.0
m2 TrdW	11.3	13.3	12.0	12.0
m2 TadW	12.9	12.5	13.0	13.0
m3 L	21.9 ^a	22.9	22.0	21.0
m3 TrdW	11.6	10.5	12.6	12.0
m3 TadW	12.6 ^a	12.4	13.0	12.0
p3-m3 L	79.2	90.0	81.0	90.0
p3-p4 L	23.9	27.6	23.5 ^a	31.0
m1-m3 L	55.3	62.4	55.0	59.0
Ratio (%)				
p3-4/m1-3	43.2	44.2	42.7	52.5
p3-4/p3-m3	30.2	30.6	29.0	34.0

Abbreviations: L: length; W: width; TrdW: Trigonid width; TadW: Talonid width (all measurements are in mm).

^a Approximate values.

The tooth is less worn than m2 but generally similar to the latter in morphology. However, the trigonid is about as long as the talonid, and the cristid obliqua extends from the hypoconid to the protoconid, separated from the latter by a shallow notch. The joint between the hypolophid and the cristid obliqua is slightly more angled. A weak cingulum is present at the lingual opening of the trigonid. The crown-root boundary is undulated.

Comparisons and discussion:

Matthew and Granger (1923) first erected *Ardynia praecox* from the Ardyn Obo of Mongolia on the basis of a heavily worn maxilla with P2-M1 and an isolated M3 (Fig. 1). Later, Matthew and Granger (1925) described a right mandible with heavily worn p2-m3 from the same locality. Gromova (1952) erected a new genus and species *Ergilia pachypterna* from Ardyn Obo of Mongolia on the basis of some postcranial skeletons; later, Gromova (1960) assigned some postcranial skeletons to another species *Ergilia kazachstanica* from central Kazakhstan. Simultaneously, Beliajeva (1952) created a new genus and species *Parahyracodon mongoliensis* mainly on the basis of a lower jaw from Ardyn Obo of Mongolia, and named *P. kazachstanensis* for a mandible from the late early Oligocene of Chelkar Teniz, Kazakhstan (Russell and Zhai, 1987; Qiu et al., 2004) (Fig. 1). In his revision of hyracodontids, Radinsky (1967) considered both *Ergilia* and *Parahyracodon* to be junior synonyms of *Ardynia*, *Ergilia pachypterna* and *Parahyracodon mongoliensis* are synonymous with *Ardynia praecox*, and *Ergilia kazachstanica* is synonymous with *Ardynia* (= *Parahyracodon*) *kazachstanensis*. Thus, Radinsky (1967) considered only *Ardynia praecox* and *A.*

kazachstanensis to be valid species, and distinguished them by a relatively larger p3-4 in the latter. Radinsky (1967) also briefly mentioned and illustrated some additional material of *Ardynia* collected by the Central Asiatic Expedition (CAE) of the American Museum of Natural History from the Erlian Basin (Radinsky, 1967, figs. 19, 20). This material includes an associated skull, mandible, and manus of *Ardynia praecox* (AMNH FM 26039) from “Middle Gray” at the Erden Obo (=Urtyu Obo) (field number: 747), and a lower jaw of *A. kazachstanensis* (AMNH FM 26183) from “Baron Sog” beds at Nom Khong Obo (Wang et al., 2012).

Dashzeveg (1991), however, considered *Ardynia mongoliensis* to be a valid species and synonymized *A. kazachstanensis* with *A. mongoliensis*, although he agreed with Radinsky (1967) in regarding *Ergilia* and *Parahyracodon* as junior synonyms of *Ardynia*. Dashzeveg (1991) assigned a right mandible with p3-m3 and an alveolus of p2 (PSS 27-99) to *A. praecox*, and further distinguished *A. praecox* from *A. mongoliensis* by having: p2 with two roots, the length ratio of p3-4 to m1-3 = 53%, and the lack of the cingulum. He further reassigned several specimens (AMNH FM 20358 and 26039), identified as *A. praecox* by Matthew and Granger (1925) and Radinsky (1967), to *A. mongoliensis* mainly on the basis of their single rooted p2. However, the diagnosis of *A. mongoliensis* proposed by Dashzeveg (1991) is based mainly on AMNH FM 26183, a mandible with complete anterior teeth, that was discovered from the Erlian Basin by CAE and referred to *A. kazachstanensis* by Radinsky (1967).

Dashzeveg (1991) doubted the referral of AMNH FM 20358 to *Ardynia praecox*, because the holotype of *A. praecox* was

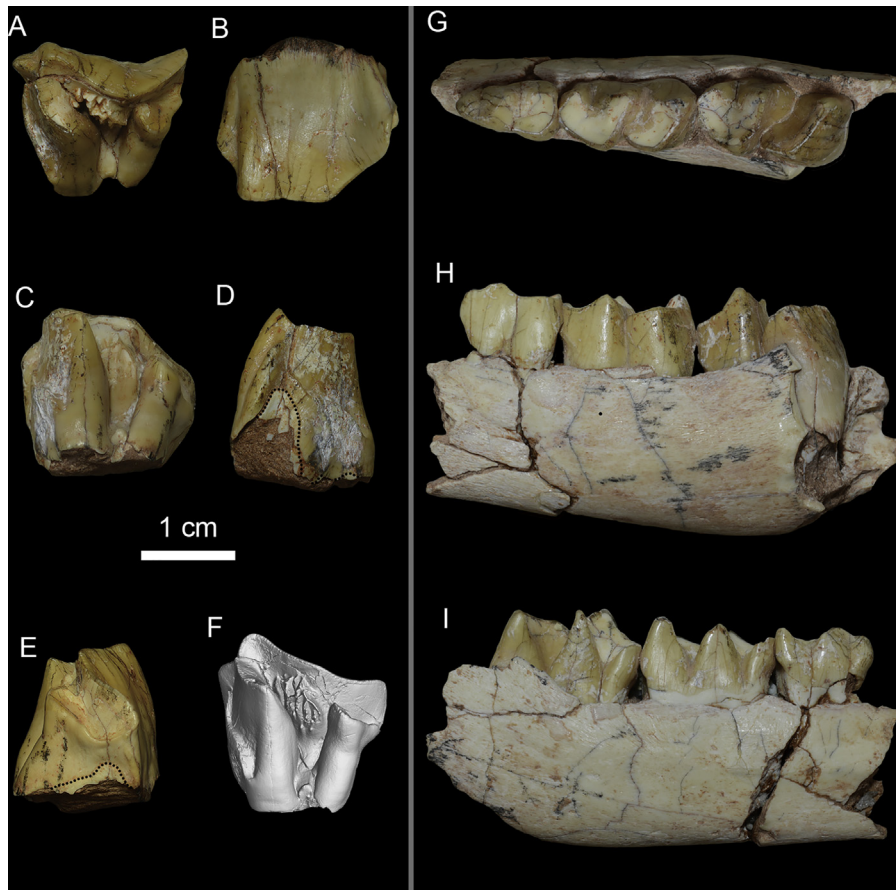


Fig. 3. *Ardynia ordosensis* n. sp., left M1 (IVPP V 23860-1) in (A) occlusal, (B) buccal, (C) lingual, (D) mesial, (E) distal, and (F) occlusolingual views; the dotted lines in (D) and (E) show the undulation of the crown/root boundaries; left juvenile mandible with dp3-dp4 and m1 (IVPP V 23860-2) in (G) occlusal, (H) buccal, and (I) lingual views.

then only known from a heavily worn P2-M1 and an isolated M3 (Matthew and Granger, 1923, 1925). However, the associated skull and mandible of *Ardynia praecox* (AMNH FM 26039) from Erden Obo of the Erlian Basin justifies the inclusion of AMNH FM 20358 in *A. praecox*. Further, the holotype of “*Parahyracodon mongoliensis*” is nearly identical to the mandible of AMNH FM 20358 as suggested by Radinsky (1967), except that the latter has a shorter dentition due to interstitial wear and a curved rather than a straight ventral border of the horizontal ramus. Thus, we agree with Radinsky (1967) in regarding “*Parahyracodon mongoliensis*” as a junior synonymy of *A. praecox*. As a result, some specimens described by Dashzeveg (1991) as *A. “mongoliensis”* (e.g., PSS 21-19, Dashzeveg, 1991, fig. 19) should be included in *A. praecox* (Table 1). Radinsky (1967) considered the holotype of “*Parahyracodon mongoliensis*” (PIN 473-255) to be larger than *A. praecox* on the basis of the measurements provided by Beliajeva (1952, table 1; see also Dashzeveg, 1991) (Table 1). However, the ratio of p3-4 length to m1-3 length in “*P. mongoliensis*” is similar to the ratio in *A. praecox* (Table 1), and the difference in size between “*P. mongoliensis*” and *A. praecox* may be attributed to the intraspecific variation. Further, the new mandible of *A. praecox* with complete anterior teeth (IVPP V 23858, described above) from Saint Jacques shows charac-

ters that are distinguishable from those of *A. kazachstanensis*, supporting the validity of *A. kazachstanensis*.

The morphology of the new mandible from Saint Jacques is nearly identical to that of previously described material of *A. praecox* (= *A. mongoliensis*) (Matthew and Granger, 1925; Beliajeva, 1952; Dashzeveg, 1991). Both have a relatively wide symphyseal region with a posterior border situated anterior to p2, a single-rooted p2, molariform p3-4, relatively reduced premolars, and a triangular trigonid. Based on the new material with complete anterior teeth, *A. praecox* is clearly different from *A. kazachstanensis* in having i2 prominently larger than i1 and i3, and the posterior border of the symphyseal region situated anterior to p2 (Beliajeva, 1952; Radinsky, 1967). Radinsky (1967) also noted that *A. kazachstanensis* has a relatively larger p3-4 than in *P. praecox*. The ratio of p3-4 length to m1-3 length in *A. praecox* ranges from 41.2% to 46.4%, whereas that of *A. kazachstanensis* is around 52% based on PIN 1463-169 and AMNH FM 26183 (Dashzeveg, 1991, table 10) (Table 1). Thus, we agree with Radinsky (1967) that *A. kazachstanensis* is a valid species.

Ardynia ordosensis n. sp.

(Fig. 3)

Etymology: The specific name refers to the Ordos Basin, where

Table 2

Measurements of *Ardynia ordosensis* (IVPP V 23860) and *A. ordosensis?* (PSS 27-26). The data of PSS 27-26 are from Dashzeveg (1991, table 11).

	M1			dp3			dp4			m1		
	L	W	H	L	TrdW	TadW	L	TrdW	TadW	L	TrdW	TadW
<i>A. ordosensis</i> IVPP V 23860	20.0	16.5	18.3 ^a	11	4.5	6.7	13.8	7.1	7.6	15.3	8.5 ^a	9 ^a
<i>A. ordosensis?</i> PSS 27-26				10		7	12		8	14.8		8.8

Abbreviations: L: length; W: width; H: height at the paracone; TrdW: Trigonid width; TadW: Talonid width (all measurements are in mm).

^a Approximate values.

the holotype was discovered.

Holotype: IVPP V 23860-1, a left M1.

Paratype: IVPP V 23860-2, a juvenile left mandible with dp3-dp4 and m1.

Horizon and locality: The upper part of the middle layer of “D1” at “D-block”, Saint Jacques, Ordos, Inner Mongolia. Late Eocene? Field number: 150918MHD01 (N 40° 15.928', E 107° 07.381').

Diagnosis: *Ardynia* with the crista of M1 enlarged and pillar-like with several small, longitudinal crests and/or tubercles on the apical part; metaloph of M1 reduced, connecting the ectoloph distal to the metacone.

Differential diagnosis: The new species differs from *A. praecox* in having a stronger crista, a metaloph relatively shorter and connecting to the ectoloph distal to the metacone on the pre-ultimate upper molars; it differs from *A. altidentata* in being smaller and relatively less hypsodont; it differs from *A. kazakhstanensis* in lacking the buccal cingula of the lower cheek teeth.

Description:

M1: The tooth crown is complete and unworn, whereas the roots are lost. The crown is relatively high, and the hypsodonty index is about 1.11, which is calculated from the height of the paracone divided by the width of the crown (Table 2). The tooth is considerably longer than wide, and the length of the buccal side is greater than that of the lingual side. The paracone is the highest cusp, and a distinct paracone rib is gradually diminishing towards the base of the crown. The parastyle is reduced, rib-like, lower than the paracone, and mesially placed to the latter. The groove between the parastyle and the paracone rib is distinct. The protoloph and the ectoloph form sharp, continuous ridges. The metacone is slightly lower than the paracone, strongly lingually depressed, and slightly buccal to the level of the protocone on the unworn tooth (Fig. 3A, B). The postmetacrista is even longer than the centrocrista, strongly deflected buccally, and descends to a prominent metastyle. The protocone is nearly as high as the paracone, with its lingual side slanted buccally at an angle of about 75° relative to horizontal plane (Fig. 3D). Mesial to the protocone there is a shallow constriction at the base of the protoloph. The protoloph is slightly bowed mesially, connecting the protocone and the paracone. The hypocone is much lower than the protocone, and distally slanted in lingual view (Fig. 3C). In distal view, the lingual wall of the hypocone is buccally slanted at the base and nearly vertical at the top (Fig. 3E). The metaloph is rather short and weak, extending from the hypocone to the

ectoloph at a point distal to the metacone, but separated from the ectoloph by a shallow notch (Fig. 3A, E, F). A weak ridge descends distobuccally from the hypocone to the distal border. The postfossette is relatively long, narrow, and shallow. The most conspicuous feature of M1 lies in that the “crista” is well-developed and enlarged into a pillar extending to the base of the crown on the lingual side of the centrocrista (Fig. 3A, C, F). The apical part of the “crista” is furrowed by several small, longitudinal crests and/or tubercles, whereas the basal part is smooth (Fig. 3F). There is a small cusp at the lingual base of the median valley. The cingulum is only present on the mesial side, unevenly ascending from the mesial base of the protocone to the parastyle (Fig. 3A, D). The boundary between the crown and the root is distinctly undulated, which is more prominent on the mesial side. In mesial view, the crown height of the buccal side (7.4 mm) is less than half the height of the crown on the lingual side (about 16.8 mm) (Fig. 3D). Although the boundaries between the crown and the root are partially broken off on other sides, the undulation is less prominent than on the mesial side.

In a slightly worn condition, as inferred from the horizontal section of the crown by CT scanning (Fig. 4A, B), the lingual enamel of the protocone is much thicker than the buccal enamel of the ectoloph, and there is a strong protoloph, a well-developed “crista” with tubercles, and a weak metaloph not in contact with the ectoloph. In a relatively heavier worn condition (Fig. 4A, C), the metaloph connects to the ectoloph in a relatively distal position, and is separated from the “crista” by a deep notch. At the level of the middle height of the crown (Fig. 4A, D), the metaloph becomes wider and is separated from the “crista”, which nearly lacks tubercles, by a pointed notch. Further, the parastyle is less projected mesially, and the mesial part of the protocone shows a shallow notch due to the constriction at the base of the protoloph. In a heavier worn condition (Fig. 4A, E), the posthypocrista extends buccodistally, and the notch mesial to the protocone becomes much deeper. The parastyle is nearly confluent with the paracone. Near the root, the crown is relatively short and wide (Fig. 4A, F).

A juvenile left mandible, IVPP V 23860-2, preserves dp3-m1 with m1 partially erupted (Fig. 3G–I; Table 2). A short diastema is preserved anterior to dp2. We interpreted the dentition as dp3-dp4 and m1 rather than dp2-dp4 for the following reasons: the p2 of *Ardynia* is usually highly reduced or absent; although a double-rooted p2 was occasionally present (Dashzeveg, 1991, fig. 17), its size (6 × 4 mm) is much smaller than the first deciduous tooth of V 23860-2. Further, the third tooth of V 23860-2 has a relatively high crown, visible in the damaged mandible on the buccal side (Fig. 3H), whereas the deciduous teeth have a

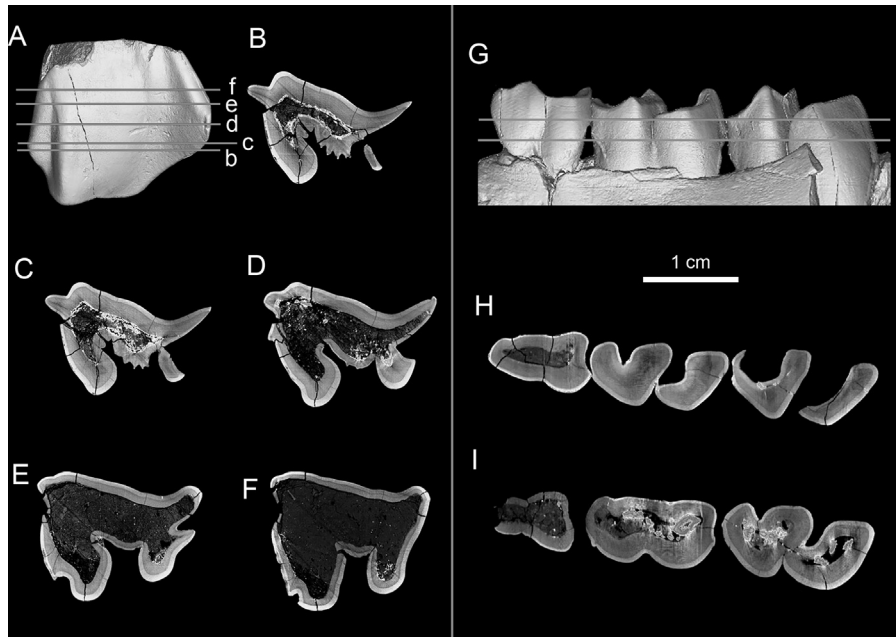


Fig. 4. Horizontal section of M1 (IVPP V 23860-1) and dp3-m1 (IVPP V 23860-2) of *Ardynia ordosensis* n. sp. (A) buccal view of left M1 with the lines showing the position of horizontal section in (B–F) from the apical to the basal parts of the crown; (G) buccal view of left dp3-m1 with the lines showing the position of horizontal section in (H, I) from apical to the basal parts of the crown. In horizontal section, the external light-colored, narrow rim is enamel, and the internal, gray, relatively wide ring is dentine. The dark areas filled with the matrix are pulp cavities.

relatively low crown. Finally, the enamel of the third tooth in V 23860-2 is thicker than those of the preceding teeth as showed in the horizontal sections (Fig. 4H, I), and has a relatively darker coloured enamel (Fig. 3G–I). These differences can be attributed to the permanent versus the deciduous teeth.

dp3: The crown is triangular in outline with a mesially pointed apex. The trigonid is nearly unworn with a high, conical paraconid mesially placed. The metaconid is close to the protoconid but more distally situated. The talonid is shallow, moderately worn, and considerably wider than the trigonid. The entoconid is higher and more distally placed than the hypoconid; thus the hypolophid is oblique. The ectoflexid is indistinct and represented by a shallow, indistinct groove. The cingulum is absent. The boundary between the crown and the root undulates on the lingual side.

dp4: The tooth is subrectangular in outline, relatively long and narrow. The trigonid is triangular in outline with a high, mesiolingually placed paraconid. The metaconid is as large as the protoconid, and more distally situated than the latter. The protolophid is oblique and straight, whereas the paralophid is smoothly curved. The trigonid is deep and extends to the base of the crown in lingual view (Fig. 3I). The talonid is slightly wider and shallower than the trigonid, but as long as the trigonid. The hypolophid is nearly parallel to (or slightly more oblique than) the protolophid, and the cristid obliqua connects the protolophid in a relatively high position lingual to the protoconid. The ectoflexid is distinct and forms a deep groove. The cingulum is absent. The boundary between the crown and the root undulates on the lingual side as in dp3, and rises considerably towards the mesial side.

m1: The tooth is similar to dp4 in morphology except relatively wider. The trigonid is moderately worn, whereas the talonid is unworn. The unworn talonid of m1 is consistent with the unworn M1, and occludes perfectly with the basin formed by the protoloph and the “crista”. As a result, we concluded that the two specimens may represent the same individual, an interpretation further supported by the fact that they were discovered from the same spot. A short cristid obliqua extends mesially from the hypoconid, and then descends slightly lingually to the distal wall of the protolophid (Fig. 3G, H). The hypolophid is more oblique than the protolophid, and gradually inclines mesially from the entoconid to the hypoconid.

At the slightly worn stage of m1 (Fig. 4G, H), the buccal enamel is thicker than the lingual, and the talonids of dp3–4 are slightly longer than the corresponding trigonids. At the moderately worn stage of m1 (Fig. 4G, I), the hypolophid of m1 is less oblique than in less worn condition, and the buccal sides of the hypoconid are more rounded. Further, the heavily worn dp4 lacks the mesial enamel and has thin distal enamel for the adaptation of interstitial wear.

Comparisons and discussion:

Qiu et al. (2004) named *Ardynia altidentata* from the late Oligocene of the Jiaozigou Formation, Linxia Basin, Gansu Province, China. Although the known material of *Ardynia altidentata* was composed of isolated teeth, the species clearly differs from other species of *Ardynia* by a larger size, more hypsodont molars, M2 with well-developed “crista”, the metaloph connecting the ectoloph in a position distal to the metacone, and lower molars with ectoflexid shifted mesially. The M1 of *A. ordosensis* is very similar to M2 of *A. altidentata* in having a well-developed, pillar-like “crista” extending to the base of

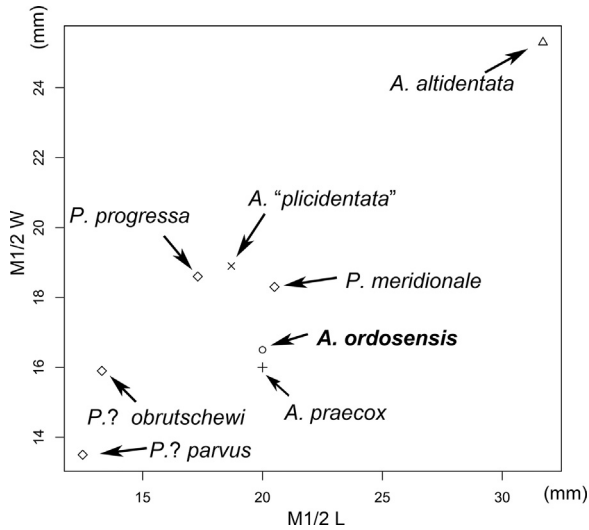


Fig. 5. Scatter plot for M1/2 size of *Ardynia* and *Prohyracodon* (in mm). The data for *A. altidentata* and *A. "plicidentata"* are from M2, whereas others are from M1. Measurements of *Ardynia* species are from Qiu et al. (2004), Beliajeva (1952), and Gabunia (1964). Measurements of *Prohyracodon* species are from Dashzeveg (1991, 1996) and Chow and Xu (1961).

the crown, the metaloph connecting to the ectoloph distal to the metacone, and a constriction situated mesial to the protocone. In contrast, the unworn M2 of *A. praecox* has a small crista and crochet, and a long metaloph connecting to the midpoint of the ectoloph mesial to the metacone (Beliajeva, 1952; Qiu et al., 2004). The moderately worn M2 of *A. praecox* further differs from the moderately worn M1 of *A. ordosensis* (Fig. 4D) in having a relatively longer metaloph distally extended, and a much smaller crista (Beliajeva, 1952; Qiu et al., 2004). The similarities between *A. ordosensis* and *A. altidentata* suggest a close phylogenetic relationship. However, *A. ordosensis* is different from *A. altidentata* in being less hypsodont and much smaller in size (Fig. 5). Further, it has upper molars with a pillar-like “crista” in a rudimentary condition and furrowed by several small, longitudinal crests and/or tubercles, lower molars with metaconids relatively narrow and not lingually grooved, and ectoflexids situated in the middle of the buccal side. *Ardynia kazachstanensis* is only known from lower dentitions, which hampers the comparison with *A. ordosensis*. But the buccal cingula of the lower cheek teeth in *A. kazachstanensis* are relatively distinct, whereas those of *A. ordosensis* lack the cingula.

Dashzeveg (1991) assigned to *Ardynia* sp. two mandibles with p3-m1 (PSS 27-26, 21-23) collected from the Sevkul and Ergilin Members of the Ergilin Dzo Formation, Khoer Dzan (Fig. 1). He noticed the peculiar characters of these specimens in having the p2 totally lost, cingulum absent, and a short diastema between the canine and the premolars. However, we have interpreted the short diastema and shallow horizontal ramus as juvenile features. The “p3-m1” of PSS 27-26 is more likely dp3-m1, which are very similar to the corresponding teeth of IVPP V 23860 in the morphology and size (Table 2). Both of them have a triangular dp3, relatively long and narrow dp4, and the talonid longer than the trigonid in m1. The shallower horizontal ramus in IVPP V 23860 is attributed to a slightly younger individual with m1 only partially erupted in the jaw. As

a result, we tentatively assigned the mandible (PSS 27-26) to *A. ordosensis*? Whether or not the other mandible (PSS 21-23) should be assigned to *A. ordosensis* is uncertain, due to the lack of first-hand observation and a figure.

4. Comments on other miscellaneous material of *Ardynia*

Gabunia (1964) erected a new species, *Ardynia plicidentata*, from the early late Oligocene Benara fauna of Georgia on the basis of a DP3 or DP4 and an M1 or M2 (Russell and Zhai, 1987; Lucas and Emry, 1999; Métais et al., 2016) (Fig. 1). *Ardynia plicidentata* was diagnosed by the wrinkled enamel in the area of the crochet, but Radinsky (1967) regarded wrinkled enamel as a variable character and referred these specimens to *Ardynia* sp. We agree with Radinsky (1967) in assigning this material to *Ardynia* sp., pending the discovery of more complete material. However, *Ardynia "plicidentata"* is different from other species of *Ardynia* in having a less oblique protoloph and a length roughly equal to the width on M1/2 (Fig. 5).

Qiu et al. (2004) described a right m3 of *Ardynia* sp. (IVPP V 13851) from Jiaozigou Formation, Linxia Basin, Gansu Province, China. Its small size and morphology is more similar to *A. praecox* and *A. kazachstanensis* than to *A. altidentata*, as pointed out by Qiu et al. (2004). Furthermore, the identification of the specimen as m3 was further supported by the trigonid being as long as the talonid, and the cristid obliqua extending mesially to the protoconid as in m3 of *A. praecox*. However, without more material, we agree to assign the specimen to *Ardynia* sp.

Dashzeveg and Hooker (1997) reported a left m1/2 of *Ardynia* sp. from the Mergen Formation of Mergen, Mongolia. The tooth is very similar to that of *P. praecox*, but is about 30% smaller than the m1 of the latter, more brachyodont (Dashzeveg and Hooker, 1997), and has a prominent cingulum at the base of the ectoflexid. The Mergen fauna has been considered typical of the Irindmanhan, but Dashzeveg and Hooker (1997) proposed that the fauna might be slightly older than typical Irindmanhan. Thus, the earliest record of *Ardynia* is likely extended to the early middle Eocene based on its appearance in the Mergen fauna.

Qiu and Wang (2007) suggested that *Prohyracodon? parvus* and *P. obrutschewi*, named by Dashzeveg (1991, 1996) from the Sevkul and Ergilin Members of the Eriglin Dzo Formation in Khoer Dzan and Dзамын Ude are more similar to *Ardynia* than to *Prohyracodon* from Transylvania, Romania and Lunan Basin, Yunnan Province (Wood, 1929; Chow and Xu, 1961) (Fig. 1). However, both of them are similar to *Prohyracodon* in having M1-2 nearly as long as wide or wider than long (Fig. 5), upper molars with more prominent paracone ribs mesially curved, and relatively larger, more separated parastyles. In contrast, *Ardynia* has M1-2 considerably longer than wide, upper molars with reduced, nearly straight paracone ribs, and relatively small parastyles less separated from the paracones. However, a relatively short protoloph and a strongly lingually depressed metacone in *Prohyracodon? parvus* and *P. obrutschewi* are very similar to those of *Ardynia*. Thus, we ten-

tatively consider species *P. parvus* and *P. obrutschewi* to be valid species of *Prohyracodon* in query based on the known materials.

5. Biostratigraphy

The holotype of *A. praecox* was collected from the Ardyn Obo Formation at Ardyn Obo by CAE in 1922, when the Ardyn Obo fauna was considered to be Oligocene in age. However, the term “Ergilin Dzo Suite = (formation),” equivalent to the Ardyn Obo Formation, was more frequently used by many researchers (Russell and Zhai, 1987; Dashzeveg, 1991; Tsubamoto et al., 2008, 2011). Dashzeveg (1991) recognized six members of the Ergilin Dzo Formation in the Eastern Gobi Desert of Mongolia, ranging from upper Eocene to lower Oligocene. The Sevkhul and Ergilin Members of the Ergilin Dzo Formation are the main horizons on which the Ardyn Obo fauna was based. Dashzeveg (1991) further proposed that the Eocene–Oligocene boundary in the Eastern Gobi Desert is at the base of the Ergilin Member. However, because the Chadronian of North American Land Mammal Age has been transferred from the early Oligocene to the late Eocene (Swisher and Prothero, 1990), the initially early Oligocene deposits in Asia have been consequently transferred to the latest Eocene (Berggren and Prothero, 1992; Ducrocq, 1993; Wang, 1997). The Ergilian was regarded as the latest Eocene Asian Land Mammal Age (Meng and McKenna, 1998; Vandenbergh et al., 2012).

A. praecox was reported from both the Ergilin Member and the underlying Sevkhul Member of the Ergilin Dzo Suite. Whether the Sevkhul Member is middle Eocene or upper Eocene is uncertain, although some authors considered the whole Ergilin Dzo Formation as upper Eocene (Emry et al., 1998; Tsubamoto et al., 2008). Considering the gradual change of the mammalian fauna between the Ergilin and Sevkhul Members with many shared taxa (Russell and Zhai, 1987; Dashzeveg, 1993), we regard both the Sevkhul Member and the Ergilin Member as upper Eocene. Thus, the distribution of *Ardynia praecox* was confined to the late Eocene, most probably the latest Eocene Ergilian. As a result, the horizon bearing the mandible of *P. praecox* from L-block in Saint Jacques is correlated to the latest Eocene Ergilian, in contrast with the previous notion that the deposits in Saint Jacques are exclusively Oligocene.

The basal layer of D-block is correlated with or slightly higher than the topmost strata of L-block based on our field observation. The layer D3, which is higher than D1, is most likely early Oligocene in age based on the presence of *Desmatolagus gobiensis*, *Karakoromys decessus*, *Selenomys mimicus*, and others. Hence the underlying D1 and D2 should range from the latest Eocene to the earliest Oligocene, and the fieldwork suggests that the deposits are continuous without prominent hiatus in D1–2. *Ardynia ordosensis* from the middle part of the layer D1 has a closer similarity to late Oligocene *A. altidentata* than to late Eocene *A. praecox*, but the precise age of the layer bearing *A. ordosensis* is hard to determine based on present evidence, waiting for the results of paleomagnetic study. Thus, it is reasonable to suggest that the Eocene–Oligocene boundary is likely present within D1–2 of D-block in Saint Jacques.

6. Conclusions

New material of *Ardynia* from Saint Jacques of Inner Mongolia was attributed to *A. praecox* and *A. ordosensis* n. sp. A right lower jaw of *Ardynia praecox* with complete anterior teeth shows that i2 is the largest among the incisors and the canine, the horizontal ramus is procumbent anteriorly, and the mandibular foramen is located below the level of the alveolar border. *Ardynia ordosensis*, represented by a left M1 associated with a juvenile mandible with dp3-m1, is characterized by the well-developed “crista” on M1, the metaloph connecting the ectoloph distal to the metacone, and the undulated boundary between the crown and the root. Ergilian *Ardynia* from Saint Jacques first indicates the existence of late Eocene deposits in the area, and further implies that the Eocene–Oligocene boundary is likely present near the strata bearing *Ardynia ordosensis*. The determination of the Eocene–Oligocene boundary at Saint Jacques awaits further analyses of the microfossils and paleomagnetic results from L-block and D-block.

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