



Original article

A late early to early middle Eocene mammal assemblage from Bayan Ulan (Inner Mongolia, China): Implication for the reassessment of the Arshantan Asian Land Mammal Age [☆]



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ABSTRACT

Paleogene mammal localities of North China are particularly well represented in the Erlian Basin, Inner Mongolia. Among them, the locality of Bayan Ulan is most famous for its late Paleocene Gashatan fauna. However, the younger Arshantan fauna of the same site is not well known, since no extensive study has been done so far. Here, we present a small mammal assemblage based on dental and tarsal material from a new Arshantan collection retrieved from the red beds of the late early to early middle Eocene Arshanto Formation at Bayan Ulan. It consists of at least six different taxa: the basal lagomorph *Dawsonolagus antiquus*, the large pantodont *Pantolambdodon* sp., the tapiroid *Schlosseria magister*, and the rhinocerotoids *Hyrachyus crista* and *Rhodopagus guoi* nov. sp. The assemblage is dominated by perissodactyls, especially Lophialetidae and Hyracodontidae. For the first time, p4-m1 of *Dawsonolagus antiquus*, tarsal material from *Pantolambdodon* sp., and lower dentition and tarsals of *Hyrachyus crista* are described and illustrated. Unlike other described Arshantan faunas, the Bayan Ulan Arshantan mammal assemblage has been collected exclusively from a single locality, which contributes to the reassessment of the misunderstood Arshantan Asian Land Mammal Age.

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1. Introduction

During the Eocene, faunas on the Mongolian Plateau (China and Mongolia) were dominated by perissodactyls and the overall faunal compositions reflect warm and humid conditions (Meng and McKenna, 1998). The taxonomical composition of the Arshantan Asian Land Mammal Age (ALMA) is quite different from that of the older early Eocene Bumbanian ALMA and more similar to the younger middle Eocene Irдинmanhan ALMA (Meng and McKenna, 1998). The Arshantan has been previously correlated to the entire Bridgerian North American Land Mammal Age (NALMA) (Luterbacher et al., 2004), combined with the Irдинmanhan as being equivalent to the Bridgerian (Lucas and Emry, 2001), or interpreted to mainly overlap with the Wasatchian and Bridgerian NALMA (Wang et al., 2010). While waiting for a redefinition of the Arshantan, we follow the last stratigraphic interpretation, in which

the Arshantan is correlated to the upper part of the Ypresian and the lower part of the Lutetian (Wang et al., 2019).

The first appearance of several placental mammal orders was recorded in the Bumbanian, among them the Perissodactyla which contained at that time only a few taxa on the Mongolian Plateau (Wang et al., 2011; Meng and Wang, 2014). Perissodactyla later dominated mammal assemblages during the Arshantan and the following Irдинmanhan and Sharamurunian ALMAs (Russell and Zhai, 1987; Tsubamoto et al., 2004; Wang et al., 2007).

The locality of Bayan Ulan (Fig. 1) – “Bayan”: rich, “Ulan”: red in Mongolian – is mostly known for its late Paleocene Gashatan “Bayan Ulan fauna” from the Nomogen Fm. (Russell and Zhai, 1987; Meng et al., 1998; Meng and Wyss, 2001). At the locality, a succession of around 110 m thick sediments is exposed, in which the following units are present according to Qi (1987): the Nomogen, Irдин Manha (containing Irдин Manha and Arshanto beds), Shara Murun, and Ulan Gochu formations. The age of the top deposits at Bayan Ulan should however be younger than the Ulan Gochu Fm. (Wang, 2003). The entire succession is exposed over several kilometers from the North of Bayan Ulan to the Holy Mesa area in the South (Fig. 2). The reddish clays of the Arshanto and

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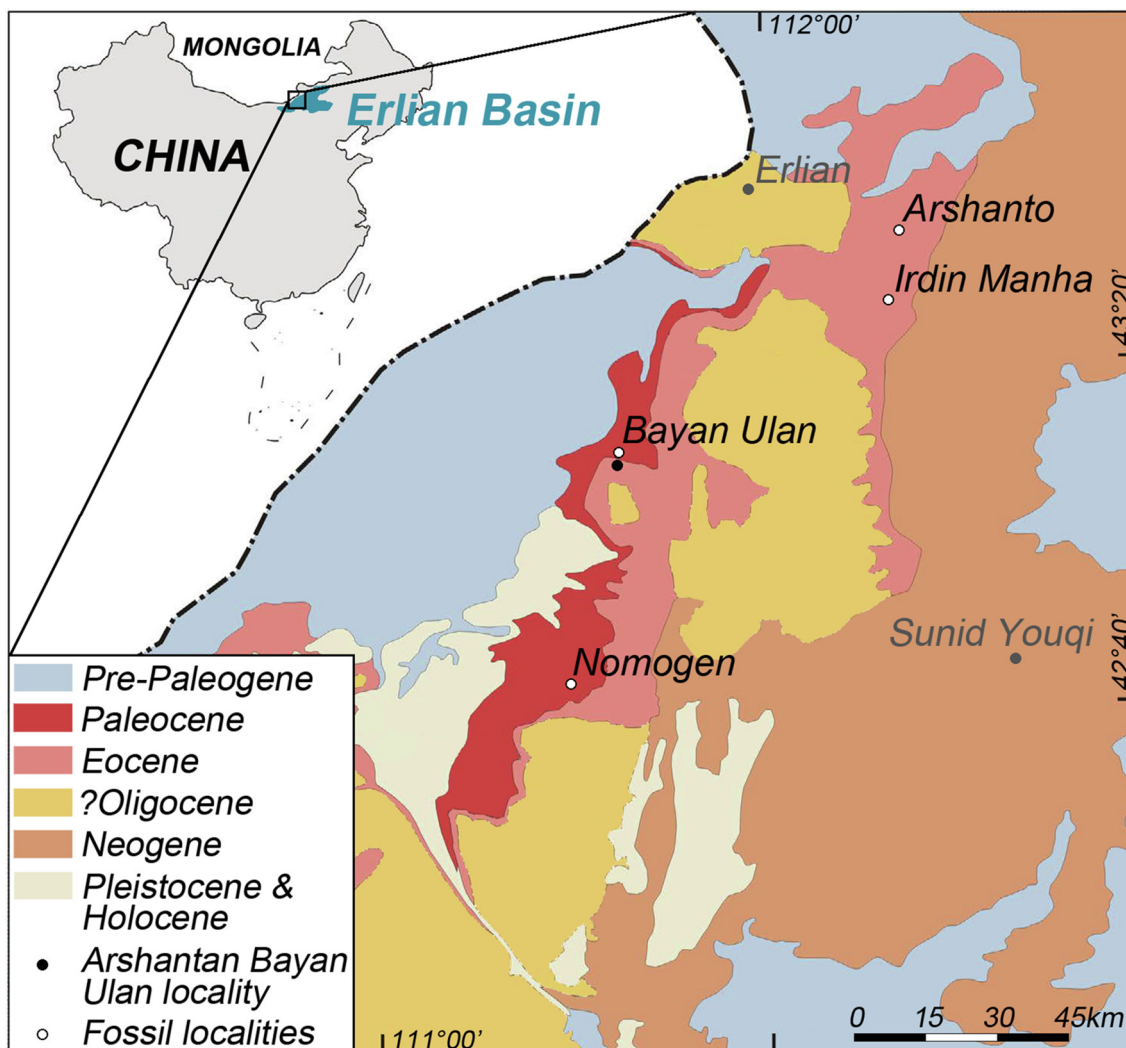


Fig. 1. Location of the Erlian Basin and geological map of the area with the Arshantan Bayan Ulan locality (N 43°07.870', E 111°35.299'). The cities of Erlian and Sunid Youqi, the type localities of the Irdin Manha, Nomogen, and Arshanto formations, and the Gashatan Bayan Ulan locality are shown. Modified from Wang et al. (2016a).

yellow sandstones of the Irdin Manha beds are equivalent to the Arshanto and Irdin Manha formations according to Meng et al. (1998, 1999); a disconformity is visible between both levels.

The Arshantan from Bayan Ulan is not described in detail in the overview of Asian Paleogene mammal sites by Russell and Zhai (1987), where only an abundant collection made from the Arshanto Fm. at Bayan Ulan is mentioned (p. 110) without a faunal listing. Also, Bowen et al. (2005) discovered tapiroid fossils just below the disconformity between the Arshanto and Irdin Manha formations at the locality, but no details are given. Mao and Wang (2012) mentioned that a single incisor of *Eudinoceras mongoliensis* was found at Bayan Ulan. So far, only Qi (1987) published a short list of mammals from the Arshanto beds (Arshanto Fm.; Meng et al., 1998) at Bayan Ulan, with *Rhodopagus* sp., *Lophialetes* sp., *?Mongolonyx prominentis*, *Hyrachyus crista*, *Breviodon minutus*, *Pantolambdodon* sp., and *Gobiatherium monolobatum*. This Arshantan fauna from Bayan Ulan was never described as a whole; the article by Qi (1987) only containing illustrations and descriptions of specimens from other Arshantan localities – apart from the upper dentition of *Hyrachyus crista*. Today, the Arshantan composite faunal assemblage, such as described by Lucas (2001) on material from mixed layers, needs revision (Meng et al., 2007).

The present paper contributes to a more detailed description of the Arshantan fauna from Bayan Ulan based on a new small collec-

tion. We describe the first Arshantan mammal assemblage collected exclusively at Bayan Ulan during the Sino-Belgian expeditions in Inner Mongolia. The material presented here, even though not extensive, was only recovered from the red beds of the Arshanto Fm. and therefore modestly contributes to the reassessment of the misinterpreted Arshantan ALMA.

2. Material and methods

The fossils described and illustrated in this paper were collected by handpicking at the Bayan Ulan locality (Inner Mongolia, China) on a surface of approximately a few hundred meters in diameter (coordinates N 43°07.870', E 111°35.299'). The material was collected by one of us (T.S.), with Dian-Yong Guo (Inner Mongolian Museum, Hohhot), Pei Jie Ning (Dinosaur Museum, Erlianhot), and Georges Lenglet and Eric Dermience (Royal Belgian Institute of Natural Sciences, Brussels) on September 20th and 28th 1995 in the red beds of the Arshanto Fm. The sampled horizons probably correspond to layers 4–6 of Qi's stratigraphy (1987: pp. 8–10), which has a maximum thickness of 25 m in Bayan Ulan.

Photographs of illustrated specimens have been done with a Canon 600D camera after coating most of the specimens with ammonium chloride, by using an electric version of the Teichert

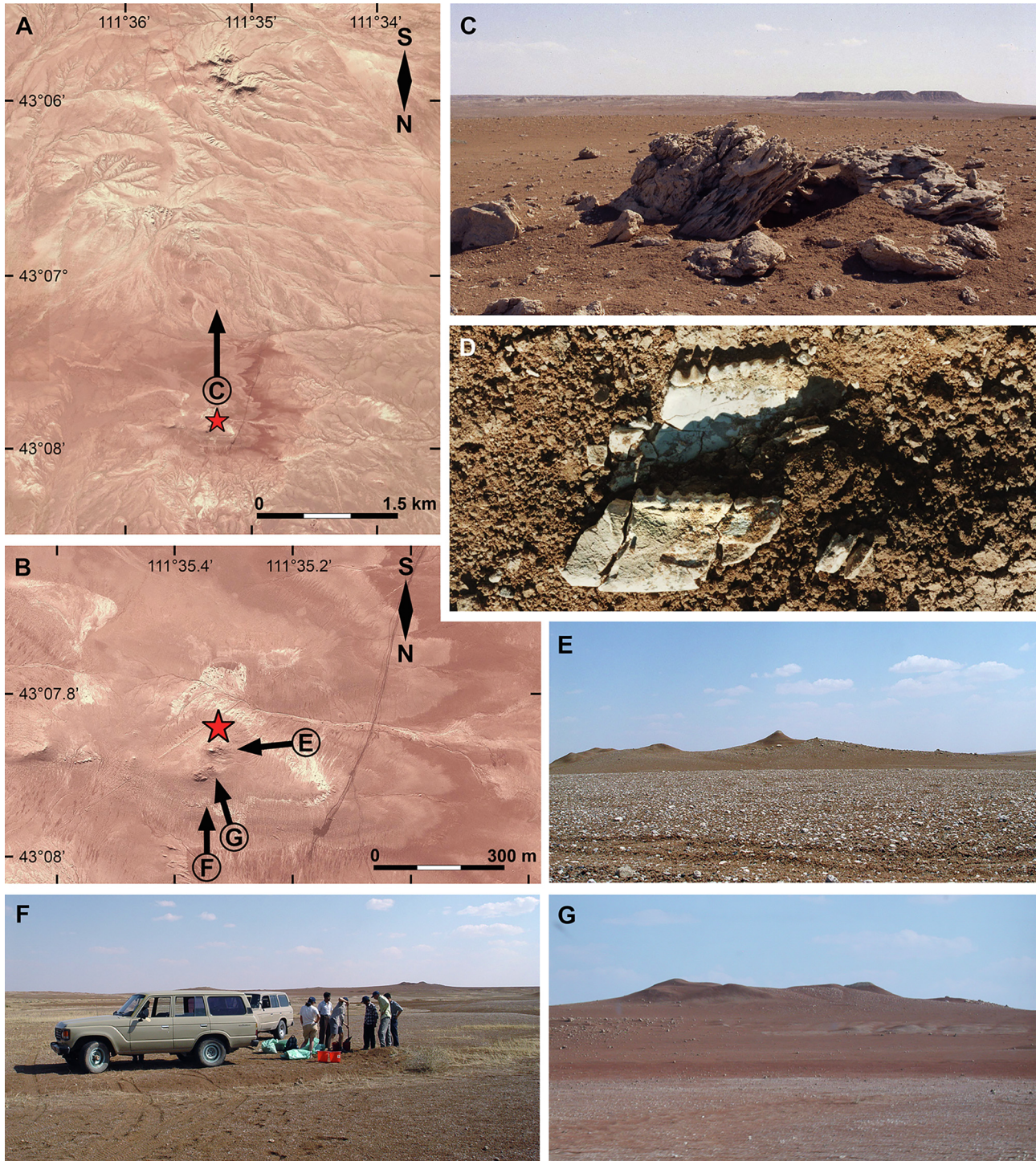


Fig. 2. Location of the Arshantan locality at Bayan Ulan. **A.** Bayan Ulan area in a South-North orientation (arrow C indicates the place and direction where picture C was taken). **B.** Close-up on the Arshantan locality indicated by a star near the Bayan Ulan hills (arrows E, F, and G indicate the places and directions where pictures E, F, and G were taken, respectively). **C.** Field surface at the Arshantan locality with main hills at the back (also visible on picture A), ca. 3.5 km to the South in the direction of Holy Mesa. **D.** Left and right dentary fragments of *Hyrachyus crista* (IMM-1995-BAYU-041) partially prepared in situ (the left fragment has been lost during the 1995 expedition). **E.** West side of the Bayan Ulan hills. **F.** Gashatan locality about 800 m North from the Bayan Ulan hills that are visible at the back. **G.** North side of the Bayan Ulan hills. Photographs A and B are adapted from satellite imagery (from Google Earth, Maxar technologies); C and D were taken in September 2000 and 1995, respectively (T. Smith); E and F in June 2004 (Z.-M. Zhang) and G (T. Smith).

set-up (1948). The specimen of the small lagomorph *Dawsonolagus antiquus* and p1 of *Schlosseria magister* have been photographed with a low environmental scanning electron microscope (ESEM) Fei Quanta 200 FEG. Some specimens were scanned with a RX Solutions EasyTom micro-CT scanner. All pictures are enhanced with Adobe Photoshop CS5.

To validate the correlation between dental and tarsal material, linear regression models (Figs. S1, S2; Appendix A) have been constructed for this work according to the method of Coillot et al. (2013). The models are based on the relationship between the length of the astragalus and calcaneum and the m1 surface area (maximal length multiplied with maximal width). The linear

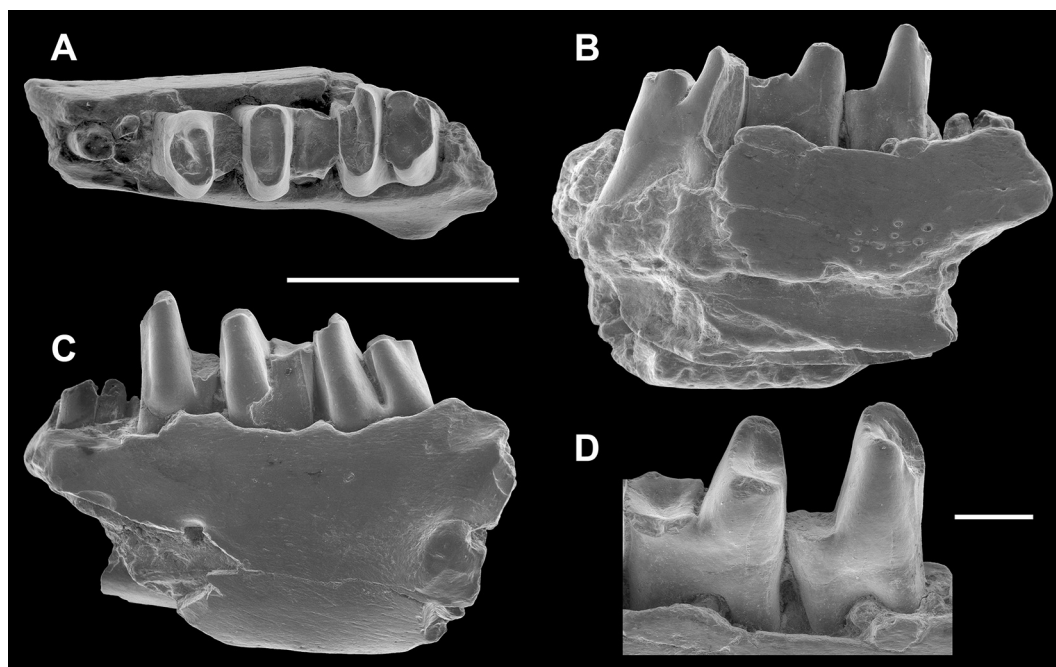


Fig. 3. *Dawsonolagus antiquus*. SEM microphotographs of specimen IMM-1995-BAYU-042, left jaw fragment with left p4-m2 and alveoli of p3 in occlusal (A), lingual (B) and labial (C) views, and enlarged view showing the morphology of p4 and m1 (D). Scale bars: 5 mm (A-C), 1 mm (D).

regression models are specifically applicable for Perissodactyla, since they are based on data from 26 different perissodactyl species, which represent all perissodactyl groups (Isectolophidae, Rhinoceroidea, Tapiroidea, Equoidea, Chalicotheriidae, and Bronthotheriidae). The following systematic classification is modified from Rose (2006).

Abbreviations: AMNH: American Museum of Natural History, New York, USA; IMM: Inner Mongolian Museum, Hohhot, China; BAYU: Bayan Ulan, Inner Mongolia, China.

3. Systematic palaeontology

Class Mammalia Linnaeus, 1758
 Infraclass Eutheria Gill, 1872
 Superorder Anagalida Szalay and McKenna, 1971
 Grandorder Glires Linnaeus, 1758
 Mirorder Duplicidentata Illiger, 1811
 Order Lagomorpha Brandt, 1855
 Genus *Dawsonolagus* Li, Meng and Wang, 2007
Dawsonolagus antiquus (Li, Meng and Wang, 2007)
 Fig. 3

Referred specimens: IMM-1995-BAYU-042, left dentary fragment with p4-m2, and roots of i1 and p3.

Description: The dentary is broken ventro-lingually exposing a horizontal root of a continuously growing incisor, which is clearly visible in lingual view. This root extends posteriorly at least to the level of the mid-length of m2. The crown of the double-rooted p3 is missing and the talonid surface of p4 is broken. The labial side of the p4 trigonid is slightly shorter compared to its lingual side, giving it an asymmetrical aspect in occlusal view by comparison with the m1-2 trigonids. The p4 has a distinct metaconid and the trigonid is higher than the trigonids of m1-2. Further, the trigonids and talonids become progressively wider labiolingually and shorter anteroposteriorly from p4 to m2. There is a progressive increase in tooth size and a widening of the grinding surfaces. The trigonids of m1-2 are oval in outline, and anteroposteriorly compressed,

while the talonids are slightly longer. The occlusal surfaces are concave. The lingual cusps are slightly higher compared to the labial ones and the dentary is twice as high as the tooth crowns.

Remarks: There is no alveolus trace for m3 posterior to m2, which means that one would expect the most posterior tooth to be m3. But the hypoconulid on m2 is not as distinct as one would expect on the most posterior tooth, the tooth has more the appearance of an m2 and, also, the relatively large size difference between the two most anterior teeth suggests that they are p4 and m1 (Li et al., 2007), which means that m3 was probably not yet erupted in this specimen. The molars have a lower degree in hypsodonty compared to most early to middle Eocene lagomorph taxa such as *Gobiolagus* and *Shamolagus* (Meng and Hu, 2004; Meng et al., 2005; Li et al., 2016). Also, the p4 trigonid is much higher relative to the m1-2 trigonids compared to *Strenulagus* from the middle Eocene Irudin Manha Fm. in the Erlian Basin, Inner Mongolia, China (Fostowicz-Freluk et al., 2015a), and its shape is different from *Lushilagus danjiangensis* from the middle Eocene of Henan (Tong and Lei, 1987). But some lagomorphs cannot be compared, as for instance *Arnebolagus leporinus* from the early Eocene of Tsagan Kushu in Mongolia, since it is only represented by an isolated P3 (Lopatin and Averianov, 2008) and an indeterminate lagomorph represented by tarsal bones from the early Eocene of Vastan, India (Rose et al., 2008).

Only the late early Eocene *Dawsonolagus antiquus*, found in the Arshanto Fm. at the Nuhetingboerhe locality, also in the Erlian Basin, Inner Mongolia (Li et al., 2007), has similar crown height, size, and its m2 is comparable in morphology and length ($L = 2.05$ mm) to the most posterior tooth on specimen IMM-1995-BAYU-042 ($L \sim 2.0$ mm). p4 and m1 of *D. antiquus* are here illustrated for the first time and show that p4 and the molars have a strong difference in height between trigonid and talonid, which is here interpreted as a primitive character.

Superorder “Ferae” Linnaeus, 1758
 Mirorder Cimolesta McKenna, 1975
 Order Pantodonta Cope, 1873

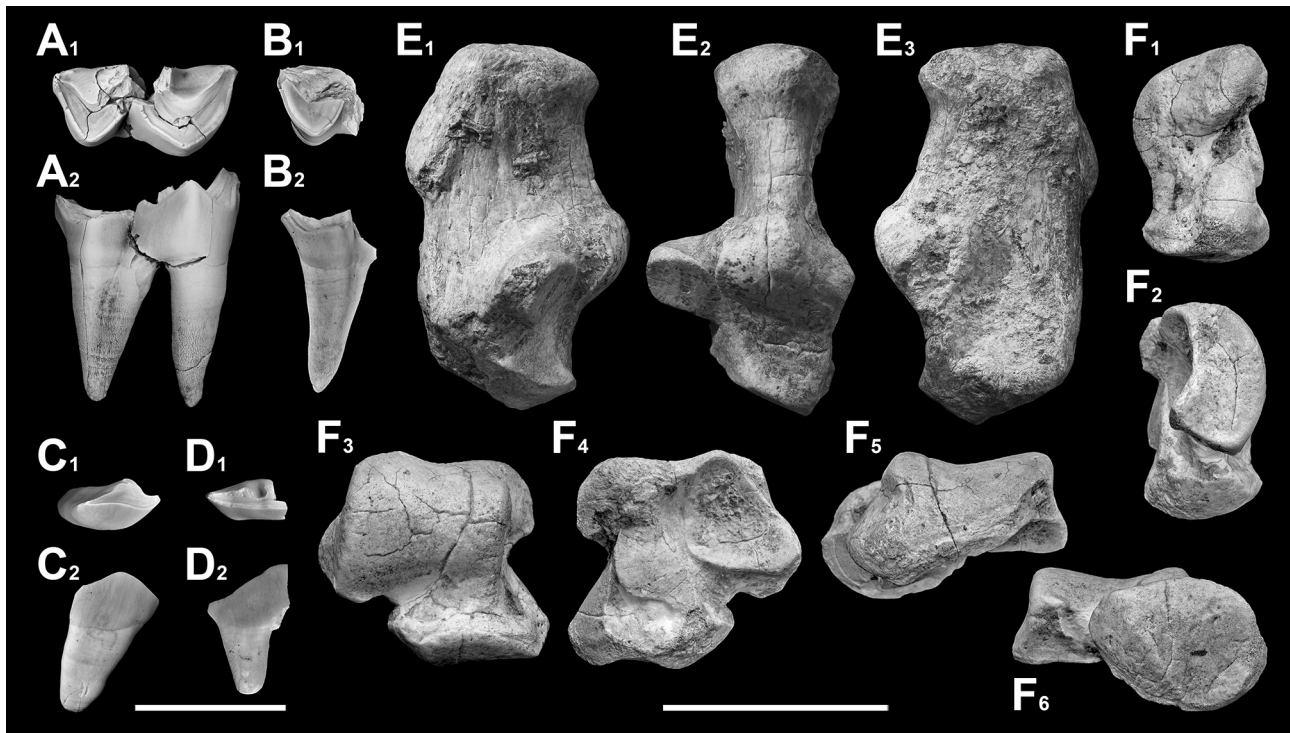


Fig. 4. *Pantolambdodon* sp. **A.** IMM-1995-BAYU-064, right lower molar in occlusal (A₁) and labial (A₂) views. **B.** IMM-1995-BAYU-066, talonid of right m1 in occlusal (B₁) and labial (B₂) views. **C.** IMM-1995-BAYU-065, right incisor in occlusal (C₁) and labial (C₂) views. **D.** IMM-1995-BAYU-067, posterior fragment of right p2? in occlusal (D₁) and labial (D₂) views. **E.** IMM-1995-BAYU-071, left calcaneum in medial (E₁), dorsal (E₂) and lateral (E₃) views. **F.** IMM-1995-BAYU-070, right astragalus in medial (F₁), lateral (F₂), dorsal (F₃), ventral (F₄), proximal (F₅) and distal (F₆) views. Scale bars: 2 cm (A–D) and 5 cm (E–F).

Family *Pantolambdodontidae* Granger and Gregory, 1934

Genus *Pantolambdodon* Granger and Gregory, 1934

Pantolambdodon sp.

Fig. 4

Referred specimens: IMM-1995-BAYU-064, right m2; IMM-1995-BAYU-065, right incisor; IMM-1995-BAYU-066, talonid of a right m1; IMM-1995-BAYU-067, posterior fragment of right p2?; IMM-1995-BAYU-075, lower molar? root; IMM-1995-BAYU-076, lower premolar? root; IMM-1995-BAYU-070, right astragalus; IMM-1995-BAYU-071, left calcaneum; IMM-1995-BAYU-077, right calcaneum; IMM-1995-BAYU-078, left calcaneum.

Description:

Lower dentition: The anterior ridge of the incisor is steeper than the posterior one due to the important wear of the tooth. The alleged p2 is labio-lingually compressed and shows a small fossa which is formed between an incipient “V”-shaped crest, a wide posterior ridge which is connected to a high conid and a short transverse ridge. The only complete lower molar is an m2, since it contains wear facets in the front and back. Specimen IMM-1995-BAYU-066, the talonid of an m1, has a rear wear facet which fits with the front wear of the m2 trigonid. The talonid of m1 is smaller compared to m2, it is slightly longer than wide. The double

Table 1

Comparison of the lower dentition of *Pantolambdodon* sp., *P. inermis*, *P. fortis*, and *P. bogdensis* (in mm).

		m1			m2			m3		
		total	trigonid	talonid	total	trigonid	talonid	total	trigonid	talonid
<i>P. inermis</i> AMNH 21558; type ¹	L	20	11.5	8.5	21.5	11.5	10			
	W	9.5	9	9	11	9.5	9			
<i>P. inermis</i> AMNH 22100; paratype ¹	L	20	11	9	22.7	13	9.5	26	15	11
	W	11	10	10	11.5	10.5	9.5	11.5	11	8
<i>P. inermis</i> AMNH 21748; paratype ¹	L							23	12.5	11
	W							9	9.5	7
<i>P. fortis</i> AMNH 26127; type ¹	L	29	16	13.5						
	W	13	12.5	13						
<i>P. fortis</i> V5687 ²	L	27.8	14.0	14.0						
	W	14.5	14.0	12.5						
<i>P. bogdensis</i> ³	L	11.5			13			14.0		
	W	7.5			7.0			8.5		
<i>Pantolambdodon</i> sp. IMM-1995-BAYU-064	L				24.2	~13.6	~10.6			
	W				12.4	~12.2	~10.5			
<i>Pantolambdodon</i> sp. IMM-1995-BAYU-066	L			9.8*						
	W			9.2*						

*estimated size; ~ approximate size; L, length; W, width.

¹ Granger and Gregory (1934).

² Qi (1987).

³ Dashzeveg (1980).

rooted second lower molar bears lophids which form double “V”-shaped crests, since the cristid obliqua extends extremely lingual towards the metaconid. The trigonid is much larger and higher compared to the talonid. Four cusps are present (the metaconid is broken). The paraconid is – after considerable wear – the highest cusp and both the metaconid and entoconid lie well behind the protoconid and hypoconid, respectively. The two posterior cusps are connected by the hypolophid. There is no trace of a hypoconulid on m1-2 and the lower molars lack basal cingulids.

Astragalus: The wide astragalus trochlea is not deeply grooved nor tilted. The astragalus neck is relatively short and broad. The head bears a navicular facet which is flat mediolaterally and slightly convex dorsoventrally with a concavity on the dorsal side. Lateral to this facet, a convex and elongated cuboid facet is present. The sustentacular facet is relatively wide mediolaterally and extends distally towards the narrow distal calcaneal facet. The ectal facet is large and concave and also relatively wide mediolaterally. It is separated from the sustentacular facet by an astragalus sulcus.

Calcaneum: The robust calcaneum has a tuber which is high dorsoventrally and narrow mediolaterally with a wider proximal end. A large swelling is seen on the ventral side of the tuber. The sustentacular facet is rounded and slightly concave, it is separated from the ectal facet by a narrow sulcus calcanei. The ectal facet is large and convex, with proximally a narrower, convex fibular facet. The lateral side of the calcaneum is concave, especially towards the distal end, and a distinct cavity is visible lateral to the ectal facet. The dorsal part of the cuboid facet is convex, while its ventral portion is concave. A narrow, triangular distal astragalus facet is visible between the cuboid facet and the sustentacular facet.

Remarks: The large lower molar trigonids compared to talonids, with high paraconids, is a characteristic of the pantodont family Pantolambdodontidae (Huang, 1995). The family contains the following genera: *Archaeolambda*, *Pantolambdodon*, *Guichilambda*, and *Nanlingilambda* (Huang and Chen, 1997; McKenna and Bell, 1997; Huang and Zheng, 2003). The angle of the lower molar “V”-shaped crests is most similar to *Pantolambdodon* (Granger and Gregory, 1934). Qi (1987: p. 10) already mentioned the presence of *Pantolambdodon* in the Arshantan of Bayan Ulan, but did not describe the material. Nevertheless, comparison with *P. inermis* and *P. fortis* (Granger and Gregory, 1934), *P. zhui* (Ding et al., 1987), and *P. bogdensis* (Dashzeveg, 1980) is difficult, since the dental material from Bayan Ulan is rather limited. The size of the material is most similar to *P. inermis* (Table 1), but the m1 talo-

nid is longer than wide, while it is the opposite for *P. inermis*. Also, m2 of *Pantolambdodon* sp. is larger in size.

The only known skeleton of the family Pantolambdodontidae is referred to *Archaeolambda tabiensis* (Wang et al., 2016a, 2016b). It was described by Huang (1977), its astragalus showing some similarities with the one here described: the astragalus trochlea is shallowly grooved and not tilted, the neck is very short, and no astragalus foramen seems to be present. The head and neck of the astragalus of *A. tabiensis* which is illustrated by Huang (1977: pl. III 6a-b) seem to be broken, which is why the astragalus appears to be narrower compared to that of *Pantolambdodon* sp. The tarsal bones described here are tentatively referred to *Pantolambdodon* sp., based on the large size, morphology, and occurrence at the same locality as the above described dentition.

Superorder Ungulatomorpha Archibald, 1996

Grandorder Ungulata Linnaeus, 1766

Order Perissodactyla Owen, 1848

Suborder Tapiromorpha Haeckel, 1866

Infraorder Ceratomorpha Wood, 1937

Superfamily Tapiroidea Gray, 1825

Family Lophialetidae Matthew and Granger, 1925

Genus *Schlosseria* Matthew and Granger, 1926

Schlosseria magister (Matthew and Granger, 1926)

Fig. 5

Referred specimens: IMM-1995-BAYU-009, right p1; IMM-1995-BAYU-011, anterior fragment of left m3; IMM-1995-BAYU-012, left and right dentary fragment with molar? roots; IMM-1995-BAYU-013, right dentary fragment with roots of p2-4?; IMM-1995-BAYU-022, left maxilla fragment with erupting M3 and roots of M1-2; IMM-1995-BAYU-025, right jaw fragment with m3 and posterior root of m2?; IMM-1995-BAYU-026, right fragment with anterior part of an erupting m3 and alveoli of m1-2; IMM-1995-BAYU-027, front part of the mandible, with roots of two incisors; IMM-1995-BAYU-030, right mandible fragment with alveoli of p1-3; IMM-1995-BAYU-031, left jaw fragment with roots of m?; IMM-1995-BAYU-040, right jaw fragment with roots of m?; IMM-1995-BAYU-047, right fragment with roots of m1, damaged m2, and anterior part of erupting m3; IMM-1995-BAYU-049, left mandible fragment with roots of premolars?; IMM-1995-BAYU-050, right jaw dentary with dp4? and erupting m1?; IMM-1995-BAYU-051, right dentary fragment with m2, anterior part of erupting m3, and posterior root of m1; IMM-1995-BAYU-058, right

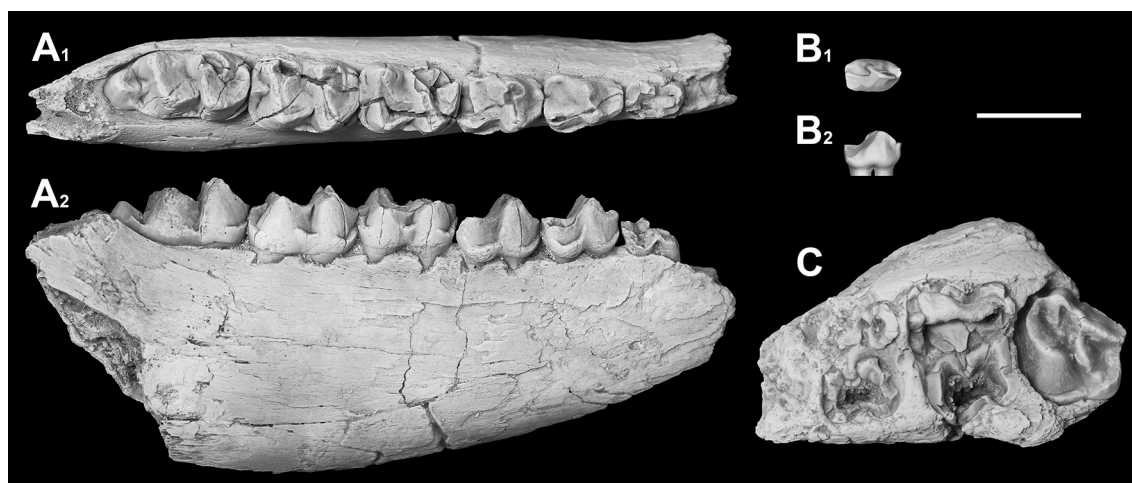


Fig. 5. *Schlosseria magister*. A. IMM-1995-BAYU-058, right jaw with p2-m3 and alveoli of p1 in occlusal (A₁) and labial (A₂) views. B. IMM-1995-BAYU-009, isolated right p1 in occlusal (B₁) and labial (B₂) views. C. IMM-1995-BAYU-022, fragment left maxilla with M3 and alveoli of M1-M2 in occlusal view. Scale bar: 1 cm.

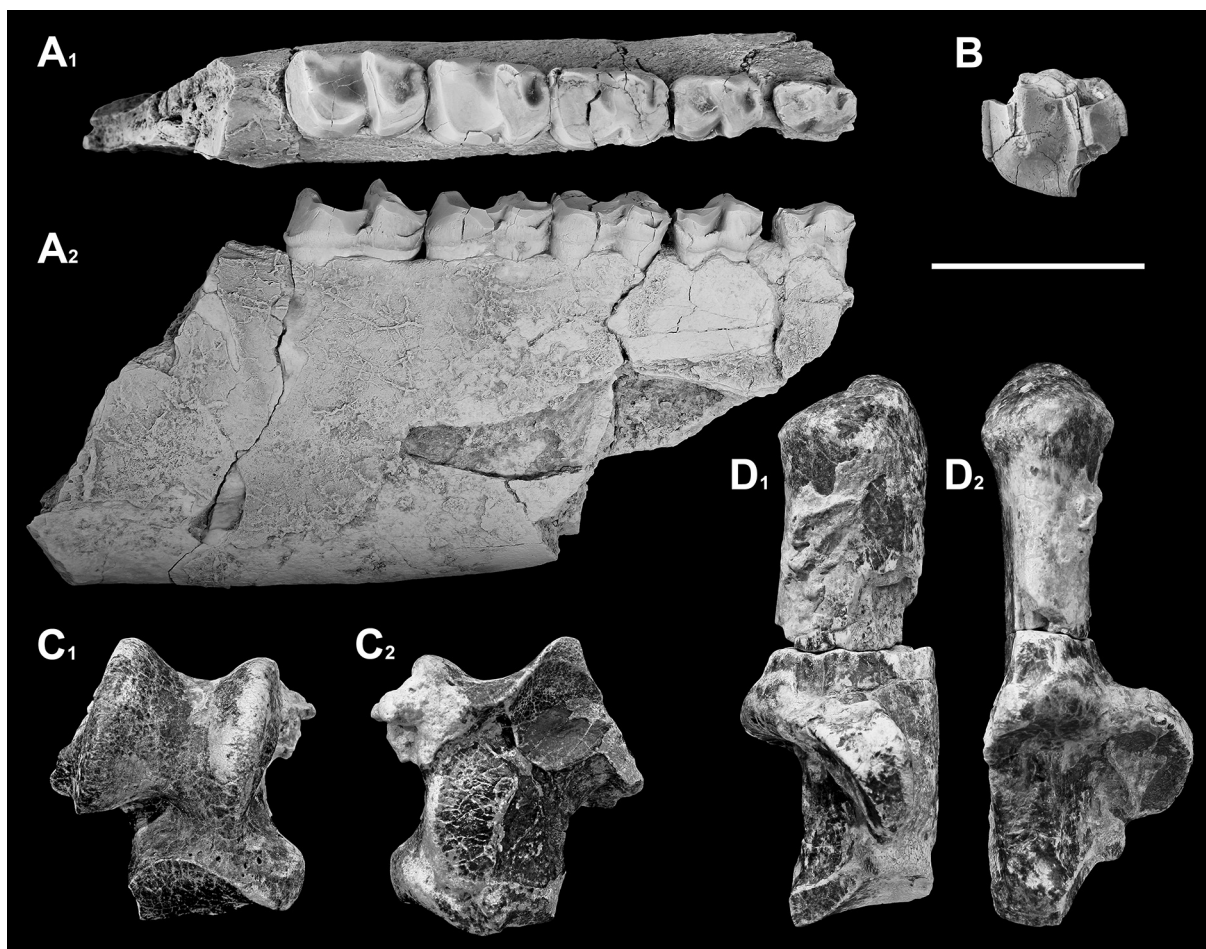


Fig. 6. *Hyrachyus crista*. **A.** IMM-1995-BAYU-041, partial right jaw with p3-m3 in occlusal (A₁) and labial (A₂) views. **B.** IMM-1995-BAYU-068, M3 in occlusal view. **C.** IMM-1995-BAYU-004, right astragalus in dorsal (C₁) and ventral (C₂) views. **D.** IMM-1995-BAYU-044, right calcaneum in dorsal (D₁) and medial (D₂) views. Scale bar: 3 cm.

mandible with p2-m3 and alveoli of p1; IMM-1995-BAYU-072, left jaw fragment with roots of m1-2 and anterior part of erupting m3.

Remarks: A well-developed hypoconulid on m3, distinct paracristids and cristid obliqua on lower molars, and flat metacones on upper molars are typical features of the Asian endemic family Lophialetidae (Radinsky, 1965, 1969; Missiaen and Gingerich, 2012). The dentition is similar to that of the well-described Irindmanhan lophialetid *Lophialetes expeditus*, but smaller in size (Matthew and Granger, 1925; Radinsky, 1965). Because the trend in hypsodonty is less comparable to *L. expeditus*, the present material is referred to the closely related *Schlosseria magister*. Only specimen IMM-1995-BAYU-022 is slightly different morphologically from *S. magister*, showing a small bulge on M3 which is positioned on the anterior side of the metaloph. Its presence can possibly be explained by morphological variability, since this is also visible on specimen AMNH 20245 (*S. magister*), even though Radinsky (1965) did not mention this feature.

Superfamily Rhinoceroidea Gray, 1825

Family Hyracodontidae Cope, 1879

Genus *Hyrachyus* Leidy, 1871

Hyrachyus crista (Qi, 1987)

Fig. 6

Referred specimens: IMM-1995-BAYU-019, right maxilla fragment with damaged P3-4?; IMM-1995-BAYU-020, left maxilla fragment with damaged P3-4?; IMM-1995-BAYU-021, right maxilla fragment with roots of M2 and M3; IMM-1995-BAYU-041, right

dentary fragment with p3-m3; IMM-1995-BAYU-068, damaged M3?; IMM-1995-BAYU-004, right astragalus; IMM-1995-BAYU-043, right astragalus fragment; IMM-1995-BAYU-024, left astragalus; IMM-1995-BAYU-032, right astragalus; IMM-1995-BAYU-044, right calcaneum.

Description:

Lower dentition: The lower premolar and molar trigonids of IMM-1995-BAYU-041 are narrower than the talonids. The lingual basal cingulids are absent and the labial ones are interrupted at the protoconid and hypoconid levels. The premolars are submolariform – they lack the entoconid – and their talonids bear a small ridge running from the hypoconid extending lingually halfway the talonid width. On the molars, the hypolophid is slightly more oblique, relative to the long axis of the tooth, compared to the protolophid, with the metaconid and entoconid positioned more posteriorly relative to the protoconid and hypoconid. The paralophid and cristid obliqua are prominent, the latter touches the protolophid slightly lingual to the protoconid at approximately half the metaconid height. The m3 hypoconulid is absent, only a small posterior cingulid is present. Transverse Hunter-Schreger bands (HSBs) are seen on the base of the teeth, while vertical HSBs are seen towards the top, and cross-ridges can be observed on the occlusal surfaces of the lower molars, which is best visible on m3.

Upper dentition: The upper premolars (P2-4) are triangular in outline, but the crowns are badly preserved in this collection. Specimen IMM-1995-BAYU-021 shows a broader lingual root on M3,

Table 2Comparison of the lower dentition of *Hyrachyus crista* and *H. modestus* (in mm).

	p3		p4		m1		m2		m3	
	L	W	L	W	L	W	L	W	L	W
<i>H. modestus</i> A.M. No. 11651 ¹					15.5	10.4	18.6	12.1	20.4	11.0
<i>H. modestus</i> A.M. No. 12667 ¹			14.4	8.4	17.7	11.9				
<i>H. crista</i> IMM-1995-BAYU-041	11.8	7.6	13.4	9.4	17.6	12.1	18	12.6	20.5	12.3

L, length; W, width.

¹ Wood (1934).**Table 3**Measurements of the upper dentition of *Hyrachyus crista*, *H. modestus*, and *H. tongi* (in mm).

	P4		M1		M2		M3	
	L	W	L	W	L	W	L	W
<i>H. modestus</i> A.M. No. 11651; right ¹	12.6	17.2	15.3	18.5	21.4	18.6	18.0	21.1
<i>H. modestus</i> A.M. No. 11651; left ¹	12.3	17.1	15.2	18.9	17.8	20.9	18.2	20.9
<i>H. tongi</i> V13100 ²	13.0	17.4	16.5	17.2	20.0	19.6	17.1	19.4
<i>H. crista</i> V5722 ³	13.5	17.5	17.5	19.0	21.4	21.4	18.4	19.0
<i>H. crista</i> V5723 ³	14.5	18.3	19.2	20.0	23.5	22.6		

L, length; W, width.

¹ Wood (1934).² Huang and Wang (2002).³ Qi (1987).

compared to M2, which allows to identify specimen IMM-1995-BAYU-068 as M3. The lingual part of this tooth bears an incomplete protoloph and metaloph. Both are curved posteriorly. Also, a section of the anterior basal cingulum is visible. The tooth exhibits transverse HSB and the occlusal surfaces bear cross-ridges. The protoloph and metaloph are worn from the front.

Astragalus: The trochlea is longer (higher) than wide and deeply grooved. A relatively deep fossa is present on the lateral side of the trochlea to receive the fibula. The lateral process is partially broken on IMM-1995-BAYU-004 but well preserved on the three other astragali. The medial process is broken on IMM-1995-BAYU-004 and replaced by a calcareous concretion. It is also not well-preserved on the other astragali. The lateral trochlear crest is slightly more tilted, relative to the long axis of the foot bone, in comparison to the medial crest. The distal end of the latter almost touches the navicular facet. The astragalar neck is relatively long. The ectal facet is deeply concave, practically as wide as long, and it extends laterodistally in a narrow, convex strip (or lappet; Bai et al., 2017). The slightly convex, proximodistally elongated sustentacular facet is separated from the ectal facet by a narrow astragalar sulcus. The former extends distally towards the narrow distal calcaneal facet, but it is unclear whether they connect. The medial part of the narrow cuboid facet is concave, while the lateral portion is convex. The quadrilateral navicular facet is saddle shaped with a small convexity on the ventral end. A prominent tubercle is visible proximomedial to the navicular facet, with a cavity between the tubercle and the astragalar trochlea.

Calcaneum: The tuber calcanei is long, relatively slender medio-laterally, and not very high dorsoventrally. The ectal facet consists of a small, convex, proximomedially facing part and a concave, distally facing portion, which extends distally where it also articulates with the astragalus. A pit for the fibula can be clearly observed proximal to the ectal facet. Also, a shallow depression is visible on the lateral side next to the ectal facet. The concave sustentacular facet is “bean”-shaped, it faces ventrodistally and is tilted slightly medial. The sustentaculum is, in medial view, proximally thicker than on the distal end. The cuboid facet on the distal end of the calcaneum is concave dorsoventrally, more convex lateromedially, and it bears a concavity on the dorsomedial side. A relatively long and narrow distal astragalar facet is positioned medial

to the cuboid facet, it has a flat portion that is facing medioventrally and a convex, short, more ventrally facing part.

Remarks: A combination of the loss of m3 hypoconulid, a relatively long paralophid and cristid obliqua, and the presence of transverse HSB, vertical HSB, and cross-ridges is characteristic for the genus *Hyrachyus* (Radinsky, 1966, 1967; Koenigswald et al., 2011). Even though *Hyrachyus* species are often distinguished based on size and characteristics of the upper dentition (Wood, 1934; Huang and Wang, 2002), we assign this material to *Hyrachyus crista* based on its size and the locality where it was found – since the holotype of *H. crista* comes from the same horizon at Bayan Ulan (Qi, 1987). It is the first time that lower teeth and tarsal material from *H. crista* are described. The lower dentition of *H. crista* is wider compared to *H. modestus* (Table 2). The upper dentition of *H. crista* has however a similar size compared to the late early to early middle Eocene *H. modestus* from North America and the middle Eocene *H. tongi* from Shanxi, China (Table 3). Huang and Wang (2002) proposed that *H. crista* may be a junior synonym to *H. modestus* based on size and the fact that the main characteristic of *H. crista* (a distinct crochet on M3) is seen on other *Hyrachyus* species.

The lower dentition of *H. crista* can be correlated with the above described tarsal bones (which all have a brownish colour, different from all other tarsal material in this collection) based on abundance and size (Figs. S1, S2; Appendix A). Obviously, several bones belong to the same individual. The calcaneum and astragali articulate well and their overall shape is similar to that of the North American *H. modestus* (Bai et al., 2017). The calcaneum of *H. crista* does differ in bearing a more distinct pit for the fibula, the tuber calcanei is dorsoventrally somewhat lower, and the astragalar ectal facet is longer proximodistal (Bai et al., 2017). *H. crista* was a fairly good runner based on the relatively long and slender tuber calcanei.

Genus **Rhodopagus** Radinsky, 1965*Rhodopagus guoi* nov. sp.

Figs. 7–9

Derivation of the name: Named in memory of Dian-Yong Guo (Inner Mongolian Museum), who was part of the expedition team and discovered several specimens in Bayan Ulan.

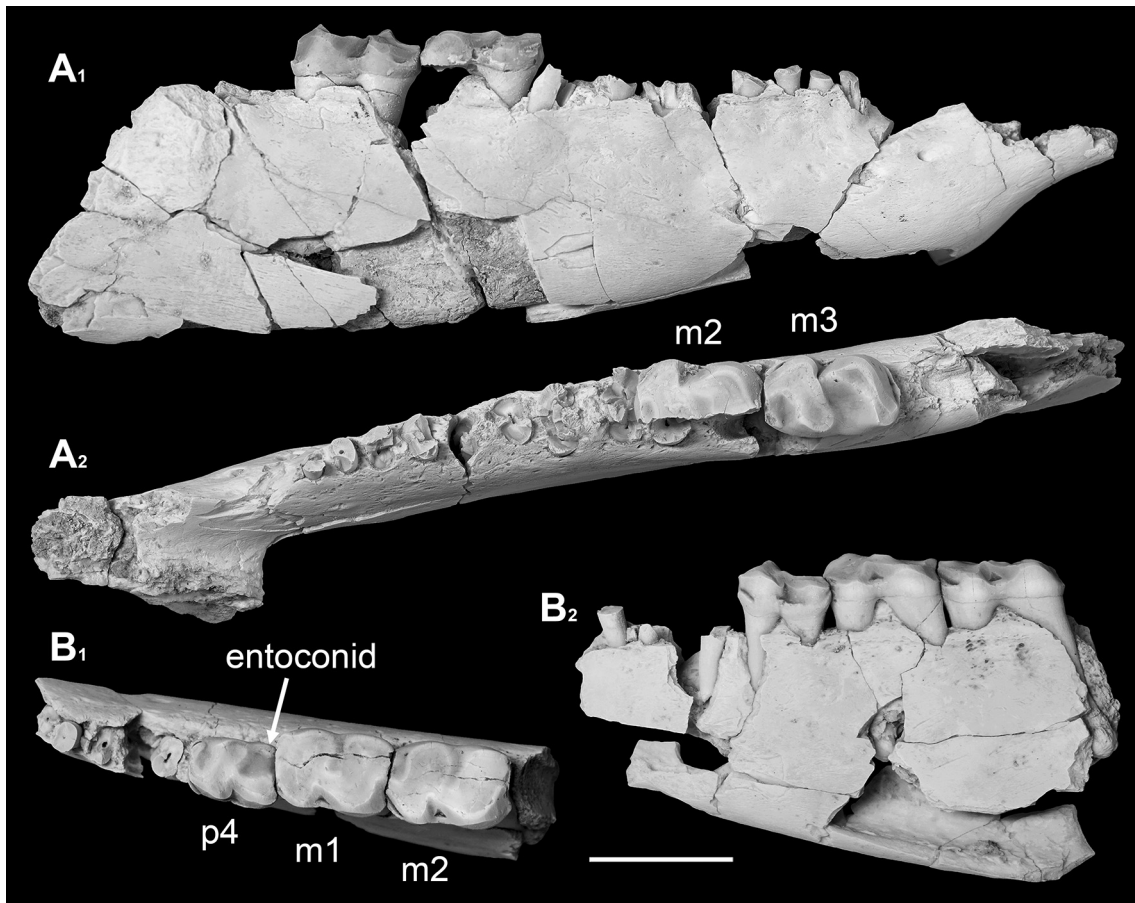


Fig. 7. *Rhodopagus guoi* nov. sp., holotype IMM-1995-BAYU-016. **A.** Right jaw fragment bearing m2-3 and the alveoli of p2-m1, in labial (A₁) and occlusal (A₂) views. **B.** Left mandible fragment with p4-m2 and alveoli of p2-3, in occlusal (B₁) and labial (B₂) views. Scale bar: 1 cm.

Holotype: IMM-1995-BAYU-016, right dentary with m2-m3, roots of p2-m1 and symphysis, and left dentary fragment with p4-m2 and roots of p2-3.

Referred specimens: IMM-1995-BAYU-006, right maxilla fragment with DP4-M1, alveoli of DP3, and roots of M2; IMM-1995-BAYU-007, left dentary fragment with dp3-4 and m1 and right jaw fragment with dp4-m1 and roots of dp3; IMM-1995-BAYU-010, right dentary fragment with alveoli of dp2-3?; IMM-1995-BAYU-014, mandible fragment with two mental foramen; IMM-1995-BAYU-015, left maxilla fragment with M2 and cavity for the M3; IMM-1995-BAYU-016, right dentary with m2-m3 and roots of p2-m1, and left dentary fragment with p4-m2 and roots of p2-3; IMM-1995-BAYU-017, left unerupted p2, p3-4, and a separate fragment with the roots of dp3-4; IMM-1995-BAYU-018, left m3; IMM-1995-BAYU-023, right fragment of M1?; IMM-1995-BAYU-028, left mandible fragment with alveoli of p2 and two mental foramen; IMM-1995-BAYU-029, left jaw fragment with roots of p3-4?; IMM-1995-BAYU-033, right M3; IMM-1995-BAYU-034, left M2; IMM-1995-BAYU-035, left anterior side of M3; IMM-1995-BAYU-036, left dentary fragment with p2-4; IMM-1995-BAYU-037, left posterior and labial sides of M1?; IMM-1995-BAYU-038, right dentary fragment with p3-m2; IMM-1995-BAYU-039, left P4 and M1 (crown lost), roots of DP4; IMM-1995-BAYU-048, left dp3 and broken dp4; IMM-1995-BAYU-059, right maxilla fragment with lingual part of M2? and lingual root of M1?; IMM-1995-BAYU-060, right maxilla fragment with P2 (broken crown) and alveoli of P1.

Type locality and Horizon: Bayan Ulan, Erlian Basin, Nei Mongol, China; red beds of Arshanto Formation, Arshantan ALMA, early Eocene to earliest middle Eocene.

Measurements: See Tables 4 and 5.

Diagnosis: Species of *Rhodopagus* which is larger in size compared to *Rhodopagus minimus*, *Rhodopagus radinskyi*, and *Yimengia zdanskyi*; differs from *Yimengia* by the presence of p3-4 entoconids and a non-molariform P4 which bears a continuous, “V”-shaped protoloph-metaloph loop; p2-3 protolophids are shorter compared to *Yimengia yani*; differs from *Y. zdanskyi* by the near equal height of the m2-3 protolophids and hypolophids; unlike *R. minimus* and *R. radinskyi*, the distinct cristid obliqua of lower premolars and molars contact the protolophid lingual to the protoconid; the lower molars do not exhibit swollen root tips as *R. minimus*.

Description:

Lower dentition: The first lower premolar is absent. A diastema is present in front of the double rooted p2. This tooth bears two posterior cusps, the protoconid and metaconid, connected by an extremely short protolophid. A distinct paracristid and cristid obliqua are present. The latter connects the protoconid to the relatively low hypoconid. The trigonid is wider and longer than the talonid. A short posterolingual cingulid is visible on the latter and there is a short labial cingulid. The p3 is similar to p2, but the spacing between the protoconid and metaconid is larger. Both cusps are connected by a high and posterolingually trending protolophid. The lower hypoconid is positioned posterolabial to the protoconid and a prominent cristid obliqua connects the two cusps. The talonid is not as long as the trigonid and bordered by a weak posterolingual cingulid. The latter is raised at the posterior end as an incipient entoconid. The second lower molar erupts prior to p3, visible on specimen IMM-1995-BAYU-038. This specimen contains the roots of dp3 and dp2 (Fig. 9). The p4 is comparable to p3, though the talonid and trigonid are approximately equal in length

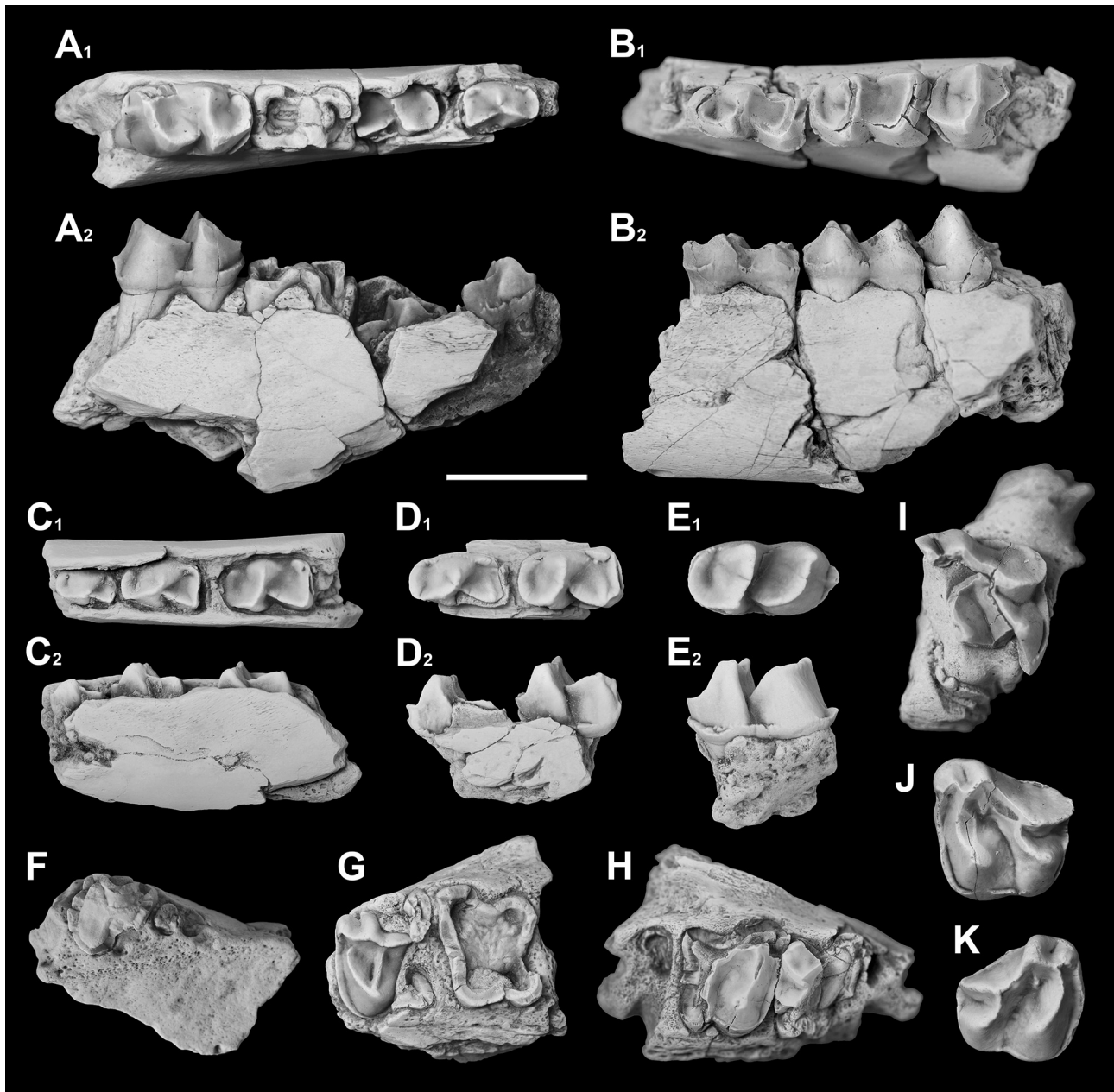


Fig. 8. *Rhodopagus guoi* nov. sp., lower and upper dentition. **A.** IMM-1995-BAYU-038, right jaw fragment with p3-4 (erupting) and m1-2 in occlusal (A₁) and labial (A₂) views. **B.** IMM-1995-BAYU-007, left dp3-4 and m1 in occlusal (B₁) and labial (B₂) views. **C.** IMM-1995-BAYU-036, left p2-p4 in occlusal (C₁) and labial (C₂) views. **D.** IMM-1995-BAYU-017, left p3-4 in occlusal (D₁) and labial (D₂) views. **E.** IMM-1995-BAYU-018, left m3 in occlusal (E₁) and labial (E₂) views. **F.** IMM-1995-BAYU-060, right maxilla fragment with P1-2 in occlusal view. **G.** IMM-1995-BAYU-039, left P4 and M1 (lost crown), roots DP4 in occlusal view. **H.** IMM-1995-BAYU-006, right maxilla fragment with damaged DP4-M1 and alveoli of DP3 and M2 in occlusal view. **I.** IMM-1995-BAYU-015, left maxilla fragment with M2 in occlusal view. **J.** IMM-1995-BAYU-034, left M2 in occlusal view. **K.** IMM-1995-BAYU-033, right M3 in occlusal view. Scale bar: 1 cm.

and an entoconid is present. The latter is positioned posterior to the metaconid and lingual to the hypoconid, which is lower than the protoconid and metaconid. The protoconid is positioned more labially compared to p3, while the metaconid is shifted lingually. The protolophid is, therefore, longer and oriented more labiolingual. The cristid obliqua (metalophid) connects the hypoconid to the middle base of the protolophid and the hypolophid is absent. The p4 bears posterior, anterior, and labial cingulids. The latter is interrupted at the level of the hypoconid and protoconid.

The lower molars are much wider anteroposteriorly compared to p4. The root tips of m1-2 are not swollen (Fig. 9). They bear prominent cristid obliqua (metalophids) and paralophids. The trigonids and talonids are practically equal in width and the poste-

rior cusps are slightly lower compared to the anterior ones. The protolophid is V-shaped (in posterior and anterior view) with the metaconid and protoconid being the highest points; it is slightly higher compared to the cristid obliqua (metalophid). The metaconid and ectoconid are positioned more posteriorly relative to the protoconid and hypoconid, respectively. The cristid obliqua (metalophid) reaches the protolophid lingual to the protoconid. The hypolophid is progressively more oblique, relative to the long axis of the tooth, from m1 to m3. The lower molars bear small posterior, anterior, and labial cingulids. The latter is interrupted at the level of the protoconid and hypoconid. Specimen IMM-1995-BAYU-016 seems to have a small void behind the most posterior tooth, but no roots are seen on the X-ray scan, this is probably

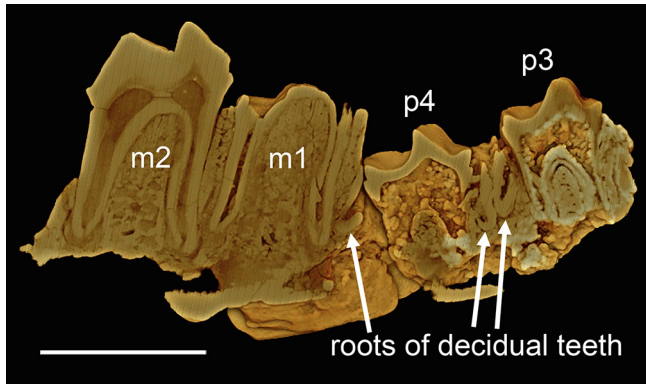


Fig. 9. *Rhodopagus guoi* nov. sp., micro-CT scan of specimen IMM-1995-BAYU-038, left p3–m2, showing roots of dp3–4. Scale bar: 1 cm.

the beginning of the coronoid process. Unlike the m3 on this lower jaw fragment, specimen IMM-1995-BAYU-018 bears a more distinct posterior cingulid, which is elevated into a small prominence and connected to the base of the hypolophid by a small ridge, possibly caused by the degree of wear or variability within the taxon.

The third and fourth deciduous lower premolars are molariform, with weak labial cingulids which are interrupted at the basis of the protoconid and hypoconid. The trigonids are narrower labi-

olingly relative to the talonids. The dp3 trigonid is narrower and more elongated compared to dp4. The former bears a relatively low and long paralophid. On dp3–4, the posterior transverse lophid is more oblique, relative to the long axis of the tooth, compared to the protolophid. There seems to be a “ridge” on dp4, anterior to the entoconid, which is oriented towards the metaconid.

Upper dentition: P1 was present as it can be inferred from specimen IMM-1995-BAYU-060, a right maxilla fragment that preserves the two roots of P1 and a broken double rooted P2. Based on the disposition of the roots, P1 was longer than wide whereas P2 is wider than long. Unfortunately, the crown of P2 is missing, preventing any description of its cusp morphology. A micro-CT scan of specimen IMM-1995-BAYU-039 gives no indication of a new tooth beneath the most posterior tooth, therefore, the specimen contains P4 (which is unerupted), the roots of DP4, and a broken M1. There is a continuous “V”-shaped protoloph-metaloph loop on P4. The two lophids have about the same height with the metaloph being a little shorter and less developed than the protoloph. The loop bears a single lingual cusp, the protocone, since the hypocone is lacking. The metaloph-ectoloph junction is higher compared to the intersection of the protoloph and ectoloph. The former is positioned anterior to the metacone, while the latter is located at the level of the preparacrista. The prominent, convex paracone has approximately the same height as the protocone. The slightly lower metacone is flattened and the antero-

Table 4
Measurements of the lower dentition of *Rhodopagus guoi* nov. sp. (in mm).

		p2	p3	dp3	p4	dp4	m1	m2	m3
IMM-1995-BAYU-007 ^{left}	L			8.8		~8.8	–		
	W			4.7*		5.5	5.9 ^(tr)		
IMM-1995-BAYU-007 ^{right}	L					~8.9	–		
	W					5.6	5.9 ^(tr)		
IMM-1995-BAYU-016 ^{left}	L	–	–		6.5		~8.0	~8.9	
	W	–	–		4.7		6.0	6.0	
IMM-1995-BAYU-016 ^{right}	L	–	–		–		–	9.3*	9.6
	W	–	–		–		–	–	5.8
IMM-1995-BAYU-017	L	5.2*	~6.5		~7.4				
	W	~2.8	~4.0		4.4				
IMM-1995-BAYU-018	L								10.8
	W								5.7
IMM-1995-BAYU-036	L	~4.2	~5.8		~6.5				
	W	~2.8	~3.6		~4.0				
IMM-1995-BAYU-038	L		5.7		6.4*		–	9.4	
	W		3.5		4.3*		–	5.6	
IMM-1995-BAYU-048	L			8.6		–			
	W			~4.9		–			

*estimated size; ~ approximate size; (tr) trigonid; L, length; W, width.

Table 5
Measurements of the upper dentition of *Rhodopagus guoi* nov. sp. (in mm).

		P1	P2	P3	P4	M1	M2	M3
IMM-1995-BAYU-006	L					9.0*		
	W					9.2*		
IMM-1995-BAYU-015	L						9.9*	
	W						10.6*	
IMM-1995-BAYU-033	L							9.2
	W							9.3
IMM-1995-BAYU-034	L						10.2	
	W						10.4	
IMM-1995-BAYU-037	L					9.2*		
	W					9.6*		
IMM-1995-BAYU-039	L				6.2*	–		
	W				~7.6	–		
IMM-1995-BAYU-059	L						9.8*	
	W						–	
IMM-1995-BAYU-060	L	–	5.7*					
	W	–	6.3*					

*estimated size; ~ approximate size; L, length; W, width.

posteriorly oriented metastyle is relatively long. The distinct parastyle is rounded and lower compared to the main cusps. Basal cingula run from the parastyle, around the anterior, lingual, and posterior side, towards the metastyle. The labial cingulum is broken on specimen IMM-1995-BAYU-039, but its presence is indicated at the base of the paracone. Maxilla fragment IMM-1995-BAYU-006 possibly contains DP4, which is molariform. The metaloph runs posterolingually.

The upper molars bear a distinct, rounded parastyle, separated from the larger paracone. The M2 paracone is the highest cusp, while the others cusps and the parastyle have more or less the same height. The teeth bear neither metaconules nor paraconules. The protoloph is curved less posteriorly compared to the metaloph. The labio-lingually flattened metacone is positioned posterior to the ectoloph-metaloph junction. There is a non-continuous basal cingulum, which is interrupted at the parastyle, paracone, protocone, and hypocone. M2 is slightly larger in size than M1 and M3. The posterior side of M3 is labio-lingually narrower compared to that of M1-2, giving the last molar a more triangular shape. The parastyle is smaller on M3, compared to M2. M3, also, bears a protoloph which is longer compared to the metaloph and the junction of the former and the ectoloph is much lower relative to the metaloph-ectoloph junction. M3 has small bulge on the lingual side of the ectoloph, between the protocone and metacone.

Remarks: The lower and upper dentitions can be associated based on the distribution of the material in the field, abundance, similar size, and morphological compatibility. However, we are cautious with the more fragmentary upper dentition and focus on the lower teeth for the identification of this material. The lophodont lower molars bear anteriorly extending cristid obliqua and no twinned metaconids, while the upper molar paraconules are absent, this is exclusive to Ceratomorpha (comprising Tapiroidea and Rhinoceroidea; Radinsky, 1964; Hooker, 1989). The upper molars have a typical wear pattern – protoloph worn down from the top and metaloph from in front – which is seen in Lophialetidae and primitive Rhinoceroidea (Radinsky, 1965). The continuous protoloph-metaloph loop on P4 is seen in the rhinocerotoid genus *Triplopus* and most members of the early to middle Eocene Asian endemic family Lophialetidae (Radinsky, 1965; Wang et al., 2011). The retention of the ancestral transverse HSB configuration seen in the material is similar to Lophialetidae and other taxa – such as *Rhodopagus* and *Pataecops* –, but different from what is generally known for Rhinoceroidea (Koenigswald et al., 2011). However, the absence of an m3 hypoconulid, clearly distinguishes this taxon from lophialetids (Radinsky, 1965). All previously mentioned characteristics apply for *Rhodopagus* (Radinsky, 1965; Koenigswald et al., 2011), a genus with a controversial phylogenetic position. *Rhodopagus* was provisionally assigned to the family Lophialetidae (Radinsky, 1965), but Lucas and Schoch (1981) transferred it to the Hyracodontidae, whereas Hooker (1989) considered it as closely related to the Deperetellidae. McKenna and Bell (1997) classified the genus into the Hyracodontidae. *Yimengia* which could be ancestral to *Rhodopagus* is similar in morphology (Wang, 1988).

Rhodopagus minimus (Matthew and Granger, 1925), *Rhodopagus radinskyi* (Gabunia and Kukhaleishvili, 1991), *Rhodopagus laiwuensis* (Qi and Meng, 1983), and *Rhodopagus zdanskyi* (Lucas and Schoch, 1981) were previously recognized. But the two latter were transferred to *Yimengia* by Wang (1988) when he described *Yimengia yani*.

According to Wang (1988), *Yimengia* differs from *Rhodopagus* in having: no entoconid on the lower premolars, more triangular lower molar trigonids, cristid obliqua (metalophid) that contact the protolophid lingual to the protoconid, no protoloph-metaloph loop on the upper premolars, less prominent parastyles and paracones, and an older age. But several of these arguments are not

valid. First, since, P4 of the type species *Y. yani* does bear an (almost) complete protoloph-metaloph loop, Wang (1988) states: “the base of the lingual side of the metaloph reaches the protocone”. But P4 of *Y. yani* is somewhat worn, making it unclear if there would be a complete loop on a fresh P4. If the loop is not continuous, then the difference could be due to variability or development of the loop within a single genus, as is for instance the case in *Schlosseria* (Wang et al., 2011). Second, the m3 trigonid of *R. minimus* is also relatively triangular in cross-section (Radinsky, 1965) and in a slightly different position the trigonids of m1-2 also look more similar in shape to *Yimengia* (Lucas and Schoch, 1981). This means that such an interpretation is strongly dependent of the orientation of the specimen, but also of the wear of the teeth that is different from the holotype of *Y. yani* (Wang, 1988). Third, the m1-3 cristid obliqua of *R. minimus* do seem to connect slightly lingual to the protocone, but less than in *Yimengia* (Radinsky, 1965). It is possible that *Rhodopagus* and *Yimengia* are not distinct genera. We therefore refer this material to *Rhodopagus* (Radinsky, 1965) because this name would have the priority in case of synonymy.

Rhodopagus guoi nov. sp. from Bayan Ulan differs from *R. minimus* by its larger size, the lack of swollen root tips, the molar proto- and hypolophids are more tilted relative to the antero-posterior axis of the tooth, the stronger cristid obliqua reaches the protolophid more lingual to the protocone, and the M2-3 metalophs bend stronger towards the posterior side (Radinsky, 1965). *R. radinskyi* is smaller in size compared to *R. guoi* nov. sp., its cristid obliqua touches the protolophid more labially, the P4 protoloph-metaloph loop seems to be less V-shaped, the M3 postmetacrista is shorter and oriented more labially, while the posterior end of the tooth is longer and less rounded (Gabunia and Kukhaleishvili, 1991).

R. guoi nov. sp. presents several characteristics that are absent in *Yimengia*, such as a p3-4 entoconid and a continuous protoloph-metaloph loop on the upper premolars (Wang, 1988). Also, the p2-3 protolophids of *Y. yani* are longer and the lower molars are wider (Wang, 1988). The lower dentition of *Y. laiwuensis* has different proportions: p3-4 are similar in size, but m1 is narrower, while m2-3 are wider (Qi and Meng, 1983). *Yimengia zdanskyi* is also smaller in size and its m2-3 protolophids are distinctly taller than the hypolophids (Lucas and Schoch, 1981).

4. Discussion

The new collection from Bayan Ulan has very few small-sized species, possibly due to a collecting bias, since all fossils were collected by handpicking at the surface and within a very short time frame (Table 6). Consequently, the collection does not represent the complete Arshantan fauna from Bayan Ulan. However, it brings new information regarding: (i) the morphology and taxonomical validity of some specific taxa, and (ii) the Arshantan faunal composition and its biostratigraphic correlations.

4.1. New data on the Arshantan Bayan Ulan fauna

Our results provide additional morphological information for the species *Dawsonolagus antiquus*, *Pantolambdodon* sp. and *Hyrachyus crista*. The lower jaw fragment of the basal lagomorph *D. antiquus*, found at Bayan Ulan, contains the first illustrated p4 of this species that is regarded as the earliest true lagomorph (Fostowicz-Frelik et al., 2015b).

Dental material of *Pantolambdodon* is very limited, making it difficult to compare the different species of *Pantolambdodon*. Therefore, the material from Bayan Ulan is tentatively named *Pantolambdodon* sp. Interestingly, the astragalus and calcaneum of *Pantolambdodon* were previously not known. This new collection

Table 6
Arshantan faunal assemblage from Bayan Ulan.

Class Mammalia Linnaeus, 1758
Infraclass Eutheria Gill, 1872
Superorder Anagalida Szalay and McKenna, 1971
Grandorder Glires Linnaeus, 1758
Mirorder Duplicidentata Illiger, 1811
Order Lagomorpha Brandt, 1855
<i>Dawsonolagus antiquus</i> Li, Meng, and Wang, 2007
Superorder “Ferea” Linnaeus, 1758
Mirorder Cimolesta McKenna, 1975
Order Pantodonta Cope, 1873
Family Pantolambdodontidae Granger and Gregory, 1934
<i>Pantolambdodon</i> sp.
Superorder Ungulatomorpha Archibald, 1996
Grandorder Ungulata Linnaeus, 1766
Order Perissodactyla Owen, 1848
Suborder Tapiromorpha Haeckel, 1866
Infraorder Ceratomorpha Wood, 1937
Superfamily Tapiroidea Gray, 1825
Family Lophialetidae Matthew and Granger, 1925
<i>Schlosseria magister</i> Matthew and Granger, 1926
Superfamily Rhinoceroidea Gray, 1825
Family Hyracodontidae Cope, 1879
<i>Hyrachyus crista</i> Qi, 1987
<i>Rhodopagus guoi</i> nov. sp.

contains more postcranial material than the above illustrated astragali and calcanea. At least the patella, metacarpals, and navicular of *Pantolambdodon* sp. are also present. These can be used in future studies on the locomotion of *Pantolambdodon*.

Qi (1987) already recognized the occurrence of *Hyrachyus crista* at Bayan Ulan. This species is similar in size to the here described dental and tarsal material of *Hyrachyus*. The new specimens are therefore assigned to the same species. It is, however, the first time that the lower dentition and tarsal bones of *Hyrachyus crista* are described and illustrated. Other postcranial bones of *H. crista* are present in the collection including several tibia and a cuboid.

The material is largely dominated by small perissodactyl remains, which is typical for the Arshantan. One new species can be recognized, *Rhodopagus guoi* nov. sp. The dental material is dominated by *R. guoi* nov. sp. (36.5%) that differs from *Rhodopagus minimus*, *R. radinskyi*, *Yimengia yani*, *Y. laiwuensis*, and *Y. zdanskyi*. Our review of the literature raises the question whether *Yimengia* and *Rhodopagus* are separate genera, because many differences highlighted by Wang (1988) are not valid such as, for example, the upper premolar continuous protoloph-metaloph loop that is (almost) complete on *Y. yani* and *Rhodopagus*. Moreover, this loop can be variable within a species, this is for instance the case for the Lophialetidae *Schlosseria magister*, *Minchenoletes erlianensis*, and *Lophialetes expeditus* (Radinsky, 1965; Wang et al., 2011).

The dentition of the well-known lophialetid *Schlosseria magister* is also well represented (30.8%). The high abundance of *R. guoi* nov. sp. and *S. magister* assumes that their tarsal material is present in the collection. Based on the linear regression models, a large portion (75%) of the tarsal bones can be associated with *R. guoi* nov. sp. and/or *S. magister* (Figs. S1, S2; Appendix A). These astragali and calcanea display a range of moderate sizes, but morphological differences are difficult to observe. At the moment it doesn't seem possible to separate the material in two groups, therefore the material was not included in this study. The astragali and calcanea of *R. guoi* nov. sp. are probably very similar to those of *S. magister*, which were illustrated by Matthew and Granger (1926).

4.2. Arshantan faunal composition

The Arshantan ALMA is one of the most difficult land mammal ages to characterize. In the past, the difficult stratigraphic correla-

tion between mammal localities, mixing of material from different horizons, and the use of multiple names for the same beds have confused literature. For example, the well-known genus *Schlosseria* has been erroneously reported from the Irдин Manha Fm. by Radinsky (1965), Qi (1987), and Lucas (2001). This was due to incorrect stratigraphic subdivision, notably of the Camp Margetts area (Meng et al., 2007), confusion due to unclear terminology between the Arshanto, Irдин Manha, and Houldjin formations (Wang et al., 2010), the possibility of admixture from older layers (Wang et al., 2012), or presence of Arshantan relics in younger horizons (Li et al., 2016).

Russell and Zhai (1987: pp. 110–111) list, in their extensive overview of the Paleogene of Asia, the “Fauna of the Arshanto Formation”, which is a mixed assemblage from different Arshantan localities and possibly even different formations (e.g., the Irдинmanhan *Lophialetes expeditus* is reported from the Arshanto Fm.). Qi (1987) provides an overview of the Arshantan fauna in which he describes and illustrates material from multiple localities, but some fossils come from the younger Irдин Manha Fm. (Meng et al., 2007). Therefore, the Arshantan composite fauna of Lucas (2001), based on Russell and Zhai (1987) and Qi (1987), is in need of revision.

New materials of fossil mammals have been reported from the Arshanto Fm. in recent years, such as mesonychids (Jin, 2012), pantodonts (Mao and Wang, 2012), rodents (Li and Meng, 2015), and perissodactyls (Bai et al., 2018). Furthermore, these new materials, much better stratigraphically located, were discovered from the six different mammal-bearing layers reported from the Arshanto Fm. (Wang et al., 2010). Wang et al. (2019) updated a faunal list of 31 species and also briefly discussed the Arshantan ALMA.

It is difficult to make an assessment using previously published material that potentially has an erroneous stratigraphic origin. Therefore, the new collection from Bayan Ulan is useful in such a revision, since all material comes from the Arshanto Fm. at one single locality. The basal lagomorph *Dawsonolagus antiquus* was previously only recorded from the Arshantan of Nuhetingboerhe, a locality ca. 30 km North-East from Bayan Ulan and is here confirmed as belonging to the Arshantan assemblage. *Schlosseria magister* has been shown as restricted to the Arshantan (Li et al., 2007; Meng et al., 2007; Bai et al., 2011). *Pantolambdodon* and *Hyrachyus* are also found in the Irдинmanhan (Huang and Wang, 2002; Li et al., 2016) and should be included in both the Arshantan and Irдинmanhan composite faunas. However, *Hyrachyus crista* as well as *Rhodopagus guoi* nov. sp. seems until now restricted to the Arshantan.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary information

Supplementary information (including Figs. S1, S2 and Table S1) associated with this article can be found online, at: <https://doi.org/10.1016/j.geobios.2020.11.001>.

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