A new species of the "condylarth" *Hyopsodus* from the middle Eocene of the Erlian Basin, Inner Mongolia, China, and its biostratigraphic implications

BIN BAI, YUAN-QING WANG, XIN-YUE ZHANG, and JIN MENG

The "condylarth" genus *Hyopsodus* is diverse and abundantly represented in Eocene mammalian faunas of North America. In contrast, fossil specimens of *Hyopsodus* are rather sparse in Eurasia. Only four species of *Hyopsodus* are known from Asia and two from Europe, as compared to the 18 species of *Hyopsodus* described from North America. Here, we report a new species of *Hyopsodus*, *Hyopsodus arshantensis* sp. nov., from the middle part of the Arshanto Formation in the Erlian Basin, Inner Mongolia, China. The holotype and only specimen of the new species, a right mandible with m1–m2, exhibits a unique combination of characters on m1–m2 not present in other species of *Hyopsodus*, including a moderately lophodont crown, a long trigonid without a paraconid, an obliquely aligned protolophid, an angle between the cristid obliqua and the posthypocristid slightly greater than 90°, a midline position of the hypoconulid, and a relatively large entoconid. The m1–m2 morphology of *H. arshantensis* is intermediate between specimens of *Hyopsodus* from the Wasatchian and Uintan North American Land Mammal Ages (NALMA), and is comparable to that of *Hyopsodus* from the Bridgerian NALMA. Moreover, its relatively large size is near the size range present among the late Bridgerian species of *Hyopsodus*. Based on those similarities, in combination with a few fossil mammals from overlying layers, the middle part of the Arshanto Formation could be correlated in part to the late Bridgerian, and the upper part of the Arshanto Formation may bracket the time interval equivalent to the Bridgerian/Uintan boundary. That proposed correlation and somewhat different faunas recognized within the Arshanto Formation suggest that it may be necessary to subdivide the Arshantan Asian Land Mammal Age (ALMA) and/or redefine the Arshantan/Irdinmanhan ALMA boundary in future comprehensive studies.

Key words: Mammalia, *Hyopsodus*, "condylarth", Eocene, Arshanto Formation, Erlian Basin, China.

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Introduction

The "condylarth" *Hyopsodus* is an archaic ungulate known from the early Eocene to the late Eocene (Archibald 1998).

Hyopsodus is included in Hyopsodontidae, a likely polyphyletic group comprising 20 small-sized Paleocene and Eocene genera (Zack et al. 2005b; Rose 2006; Halliday et al. 2017). Hyopsodontids were considered to be ancestral to artio-

dactyls (Simpson 1945), allied with afrotheres (Godinot et al. 1996; Zack et al. 2005a) or related to South American ungulates (Cifelli 1983; Muizon and Cifelli 2000). *Hyopsodus* is indeed abundant and diverse in early–middle Eocene North American faunas, and comprises up to 39% of the identified specimens from the Bridger Formation in the US National Museum of Natural History collection (Gazin 1976; West 1979). A brief revision of *Hyopsodus* recognizes 16 valid species from North America (Archibald 1998), but that work omitted *H. lovei* from the earliest Uintan North American Land Mammal Age (Flynn 1991). Taking advantage of the abundance and stratigraphic distribution of *Hyopsodus*, it has been used in evolutionary studies (Gingerich 1974, 1976; Redline 1997) and stable isotope analyses to reconstruct paleoenvironments in combination with other mammalian groups (Secord et al. 2008). More recently, the cranial endocast and inner ear morphology of *Hyopsodus* have been reconstructed through the use of X-ray computed microtomography (Orliac et al. 2012; Ravel and Orliac 2015). While it is well known from North American deposits, *Hyopsodus* is much rarer in the Eocene deposits of Asia and Europe. Six species of *Hyopsodus* and *Asiohyopsodus confuciusi* (represented by fragmentary maxillae and mandibles) have been reported from the early–middle Eocene of Eurasia (Hooker and Dashzeveg 2003; Tong and Wang 2006), and the validity of some of those Asian species assigned to *Hyopsodus* is controversial (Kondrashov and Lucas 2004).

Here we report a new species of *Hyopsodus* and an indeterminate species of *Hyopsodus* from the early middle Eocene Arshanto Formation in the Erlian Basin, Inner Mongolia, China. These two fragmentary mandibles represent the first record of *Hyopsodus* from the Arshanto Formation, which is the basis of the Arshanto fauna and the Arshantan Asian Land Mammal Age (Wang et al. 2019b; Speijer et al. 2020). Based on comparisons with other species of *Hyopsodus* from North America and Eurasia, we further investigate its biostratigraphic implications and propose a probable new correlation between Arshantan and Bridgerian/Uintan NALMA.

Institutional abbreviations.—ACM, Amherst College Museum (Pratt Museum), Amherst, USA; AMNH FM, American Museum of Natural History, Fossil Mammals, New York, USA; IVPP V, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China.

Other abbreviations.—NALMA, North American Land Mammal Ages; ALMA, Asian Land Mammal Age. We follow standard convention in abbreviating tooth families as I, C, P, and M, with upper and lower case letters referring to upper and lower teeth, respectively.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:F753C4DF-C373-41DB-BE98-B9B2B7AE3C36

Material and methods

The holotype specimen of the new species (IVPP V 28282) was unearthed from the middle part of the Arshanto Formation at Chaganboerhe in the Erlian Basin, Inner Mongolia, China. The holotype comes from a brownish-red silty mudstone with small calcareous nodules, which is equivalent to the mammalian horizon AS-4 of the Arshanto Formation (Wang et al. 2010). The second specimen identified as *Hyopsodus* sp. (IVPP V 28283) was collected from the upper level of the lower part of the Arshanto Formation at Nuhetingboerhe. The stratigraphic horizon that produced the second specimen is a brownish-red, muddy siltstone, and is equivalent to the mammalian horizon AS-2 of the Arshanto Formation (Wang et al. 2010). Three species of *Hyopsodus* previously reported from China are compared with the new material and figured, including *H. turpanensis*, *H. fangxianensis*, and *H. huashigouensis*.

X-ray micro-computerized tomography. The scanning was carried out using the 225 kV micro-CT scanner facility (developed by the Institute of High Energy Physics, Chinese Academy of Sciences) at the Key Laboratory of Vertebrate Evolution and Human Origins, Chinese Academy of Sciences (Wang et al. 2019a). The specimens were scanned with beam energy of 120 kV and a flux of 120 µA. The resolution per pixel for IVPP V 4355 (holotype of *H. turpanensis*) and IVPP V 12005 (holotype of *H. fangxianensis*) are 21.956 µm and 18.820 µm, respectively. A 360° rotation with a step size of 0.5° was used. A total of 720 projections were reconstructed in a 2048×2048 matrix of 1536 slices using a two-dimensional reconstruction software developed by the Institute of High Energy Physics, Chinese Academy of Sciences. The three-dimensional reconstructions were created using the software VG Studio 3.2.

Systematic palaeontology

Order "Condylarthra" Cope, 1881

Family Hyopsodontidae Trouessart, 1879

Genus *Hyopsodus* Leidy, 1870

Type species: *Hyopsodus paulus* Leidy, 1870, Bridger Basin, Wyoming, USA, early–middle Eocene.

Hyopsodus arshantensis sp. nov.

Fig. 1A.

ZooBank LSID: urn:lsid:zoobank.org:act:79A0AB22-A930-4159-8F B8-BBD321777F76

Etymology: In the reference to the Arshanto Formation, where the new species was found.

Holotype: IVPP V 28282, a right mandible with m1–m2.

Type locality: Chaganboerhe, Erlian Basin, Inner Mongolia, China.

Type horizon: Upper level of the middle part of the Arshanto Formation (AS-4), Arshantan ALMA, middle Eocene.
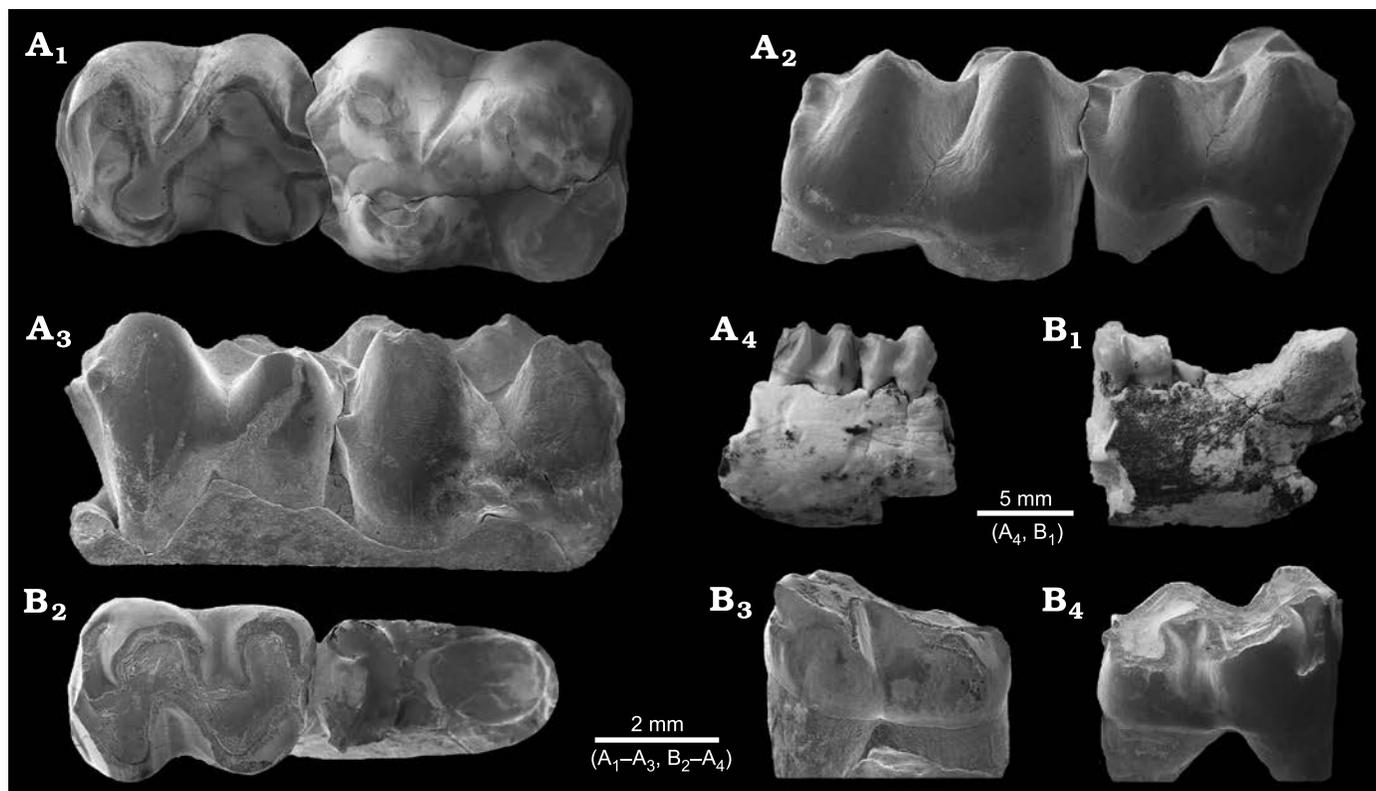
Fig. 1. The middle Eocene "condylarth" mammal *Hyopsodus arshantensis* sp. nov. (A) and *Hyopsodus* sp. (B) from the Arshanto Formation of the Erlian Basin, Inner Mongolia, China. **A**. IVPP V 28282 from Chaganboerhe, m1–m2 in occlusal (A_1), buccal (A_2), and lingual (A_3) views; mandible in buccal view (A_4). **B**. IVPP V 28283 from Huheboerhe, mandible in buccal view (B_1); m2 and m3 root in occlusal (B_2), buccal (B_3), and lingual (B_4) views.

Differential diagnosis.—Differs from other species of *Hyopsodus* by the combination of following characters of m1–m2: a moderate degree of lophodonty, a relatively longer trigonid without a paraconid, a moderately obliquely aligned protolophid, an angle between the cristid obliqua and posthypocristid slightly greater than 90°, a midline position of the hypoconulid on m2, a relatively larger entoconid, and absence of the cingulids on the buccal and lingual sides. Further differs from contemporaneous Bridgerian species of *Hyopsodus* in having a generally larger size and in lacking a variably developed metastylid. Further differs from *H. marshi* by a generally less robust appearance. Differs from *Asiohyopsodus confuciusi* in having more lophodont molar crowns, a more obliquely aligned protolophid, a more lingually directed cristid obliqua, a more distinct posthypocristid and postentocristid, a larger entoconid on m1–m2, and absence of the paraconid on m1.

Material.—Holotype only.

Description.—m1: The tooth is moderately worn and rectangular in outline with the talonid slightly wider than the trigonid (Table 1). The protoconid and metaconid are conical and obliquely arranged. The protolophid is shallowly notched, joining the posterior walls of the protoconid and metaconid. The paralophid descends from the protoconid anteriorly more than lingually, and then extends lingually to the anterobuccal base of the metaconid. The paraconid is absent, and the trigonid is relatively open and expanded rather than being anteroposteriorly compressed. The hypoconid is as high as the protoconid, extending the cristid obliqua anterolingually to the posterobuccal wall of the metaconid. The posthypocristid, which joins the hypoconid and hypoconulid, is posterolingually extended, and forms an angle of slightly less than 90° with the cristid obliqua at current wear stage. As a result, the hypoconid exhibits a selenodont

Table 1. Measurements (in mm) of lower molars for some species of *Hyopsodus* from the Eocene of China. Abbreviations: ?, missing data; a, approximate; AW, anterior width; L, length; PW, posterior width.

Species	m1			m2			m3		
	L	AW	PW	L	AW	PW	L	AW	PW
Hyopsodus arshantensis sp. nov.	4.05	3.10	3.08	4.60	3.60	3.38	?	?	?
Hyopsodus sp. (IVPP V 28283)	?	?	?	4.10	3.20	2.90	4.05a	2.12a	?
Hyopsodus fangxianensis (IVPP V 12005)	4.10	3.20	3.45	4.41	3.80	3.50	4.00	3.10	2.25
Hyopsodus turpanensis (IVPP V 4355)	3.15	2.41	2.45	3.30	3.00	2.85	4.00	2.70	2.20
Hyopsodus huashigouensis (IVPP V 7921)	?	?	?	4.12	3.20	2.80a	?	?	?

appearance. The hypoconulid is deeply worn and relatively small, and is positioned closer to the entoconid than to the hypoconid. The entoconid is conical, obliquely arranged relative to the hypoconid, and relatively isolated with a narrow postentocristid joining the hypoconulid. A weak cingulid is present along the anterior border, and the posterior cingulid rises up to form the hypoconulid, with the buccal side of the hypoconulid much more distinct than the lingual one.

m2: The tooth is slightly worn and rectangular in outline with the talonid slightly narrower than the trigonid. The m2 is larger than m1, but is similar to the latter in morphology. The m2 mainly differs from m1 in that: (i) the buccal wall of the hypoconid is lingually slanted, with the angle between the cristid obliqua and posthypocristid becoming narrower during wear, with the current slightly wear stage associated to an angle slightly greater than 90°; (ii) the hypoconulid is positioned near the midline of the talonid; and (iii) the postentocristid is more distinct, joining the entoconid and hypoconulid.

Stratigraphic and geographic range.—Type locality and horizon only.

Hyopsodus sp.
Fig. 1B.

Material.—IVPP V 28283, a left mandible with a heavily worn m2 and roots of m3 from the upper level of the lower part of the Arshanto Formation (AS-2), Huheboerhe, Erlian Basin, Inner Mongolia, China.

Description.—The m2 is about 11% smaller than that of *Hyopsodus arshantensis* sp. nov. (IVPP V 28282) in longitudinal dimensions (Table 1). It differs from *H. arshantensis* sp. nov. in having a more lingually extended paralophid, and the angle between the cristid obliqua and the posthypocristid is slightly less than 90°. Only the roots of m3 are preserved on the specimen. The m3 was almost as long as m2, but it appears to have been narrower than the latter. The cross section of the anterior root is an anteroposteriorly compressed oval, and that of the posterior one is an elongated ellipsoid.

Discussion

Comparison with North American *Hyopsodus*.—*Hyopsodus* was first described by Leidy (1870), and is among the earliest fossil mammal genera to be named from the Eocene of North America (Gazin 1968). The following comprehensive studies of *Hyopsodus* include those by Osborn (1902), Loomis (1905), and Matthew (1909, 1915). Gazin (1968) thoroughly reviewed the North American record of *Hyopsodus* and recognized 12 species as valid, including five species from the Wasatchian, five species from the Bridgerian, and two species from the Uintan. However, the taxonomy and validity of some species remain unclear with ongoing debates. Gingerich (1974) recognized 10 species of

Hyopsodus from the Wasatchian and studied their changes in size, but Archibald (1998) considered those fossils to represent eight species. West (1979) reported only three species of *Hyopsodus* from the Bridger Formation, in contrast to the five species from the Bridgerian proposed by Gazin (1968). In terms of Uintan *Hyopsodus*, Krishtalka (1979) considered *H. fastigatus* as a junior synonym of *H. uintensis*, and erected a new species *H. sholemi*. By contrast, Storer (1984) considered *H. fastigatus* to be a valid species. Redline (1997) identified two anagenetically evolving "species lineages" of *Hyopsodus* from the Wasatchian and early Bridgerian: *H. paulus* and *H. powellianus*, which are divided into successive, informal segments. For the purposes of our work here, we mainly follow the taxonomy of *Hyopsodus* species utilized in Archibald's (1998) brief revision of the genus (Fig. 2). In general, the morphology of the new Chinese fossil material is intermediate between that of the Wasatchian and Uintan species of *Hyopsodus*, being most comparable with those from the Bridgerian.

The size of *H. arshantensis* sp. nov. falls within the ranges of those of *H. wortmani* (m2 length 3.8–4.6 mm) and *H. miticulus* (m2 length 3.8–5.0 mm) from the early Wasatchian to the middle Bridgerian, but *H. arshantensis* sp. nov. is smaller than *H. powellianus* (= *H. browni* and *H. jacksoni*; m2 length 4.9–6.2 mm) and *H. walcottianus* (m2 length 6.4–6.5 mm) from the middle Wasatchian to the middle Bridgerian (Figs. 2, 3) (Gazin 1968; Redline 1997; Archibald 1998; Tong and Wang 2006). *Hyopsodus arshantensis* sp. nov. is generally larger than other species of Wasatchian *Hyopsodus*, including *H. loomisi* (m2 length 3.5–4.0 mm), *H. minor* (m2 length 3.0–3.8 mm), *H. latidens*, and *H. mentalis* (Gazin 1968; Redline 1997; Archibald 1998). The m1–m2 of *H. arshantensis* sp. nov. differ from those of Wasatchian *Hyopsodus* in having more lophodont molar crowns, a relatively longer and more expanded trigonid, a shallower notch of the protolophid, an angle slightly greater than 90° between the cristid obliqua and posthypocristid, and a smaller hypoconulid. Moreover, some Wasatchian species further differ from *H. arshantensis* sp. nov. in having a paralophid rising up lingually to form a small paraconid (positioned high on the anterior slope of the metaconid on m1 and/or m2), a small entostylid anterior to the entoconid (Gazin 1968), and a distinct cingulid at the base of the ectoflexid.

Four species of *Hyopsodus* have been named from the Uintan to the Chadronian NALMA (Fig. 2). *Hyopsodus lovei* is known from the earliest Uintan (Flynn 1991), *H. uintensis* from the Uintan and early Chadronian (Osborn 1902; Krishtalka 1979; Archibald 1998), *H. fastigatus* from the late Uintan (Storer 1984), and *H. sholemi* from the Duchesnean (Krishtalka 1979). It is necessary to mention that the species *H. paulus*, *H. despiciens*, and *H. lepidus*, which occur mostly in the Bridgerian, are also known from the early Uintan (Archibald 1998; Murphey and Kelly 2017). The size of *H. arshantensis* sp. nov. is similar to that of *H. uintensis* (m1 length 4.1 mm; Osborn, 1902), but *H. arshantensis* sp. nov. is smaller than *H. lovei* (m2 length 4.76–5.17 mm;
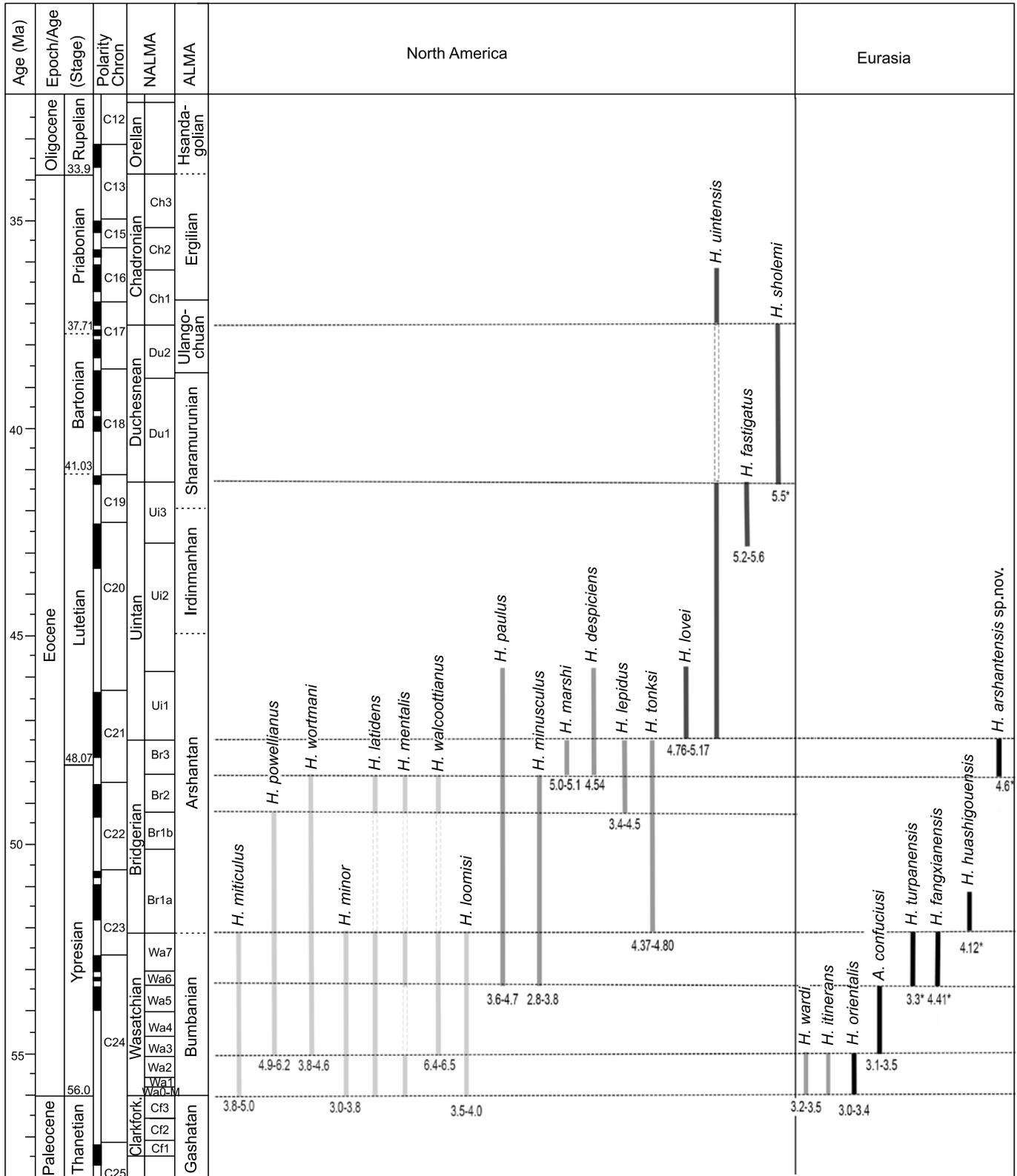
Fig. 2. Temporal distributions of species of *Hyopsodus* and *Asiohyopsodus* from North America and Eurasia based on Archibald (1998) and Tong and Wang (2006). The left column shows the correlation between NALMAs and ALMAs modified from Speijer et al. (2020) and Wang et al. (2019b). The numbers below the vertical bars indicate the range or the mean value for lower molar m2 length in millimeters. Numbers with an asterisk mean that the measurement is taken from a single specimen. The traditional Wasatchian, Bridgerian, and Uintan species of *Hyopsodus* are discriminated by different grey shading. Abbreviations: *A.*, *Asiohyopsodus*; ALMA, Asian Land Mammal Age; Clarkfork., Clarkforkian; *H.*, *Hyopsodus*; NALMA, North American Land Mammal Age.
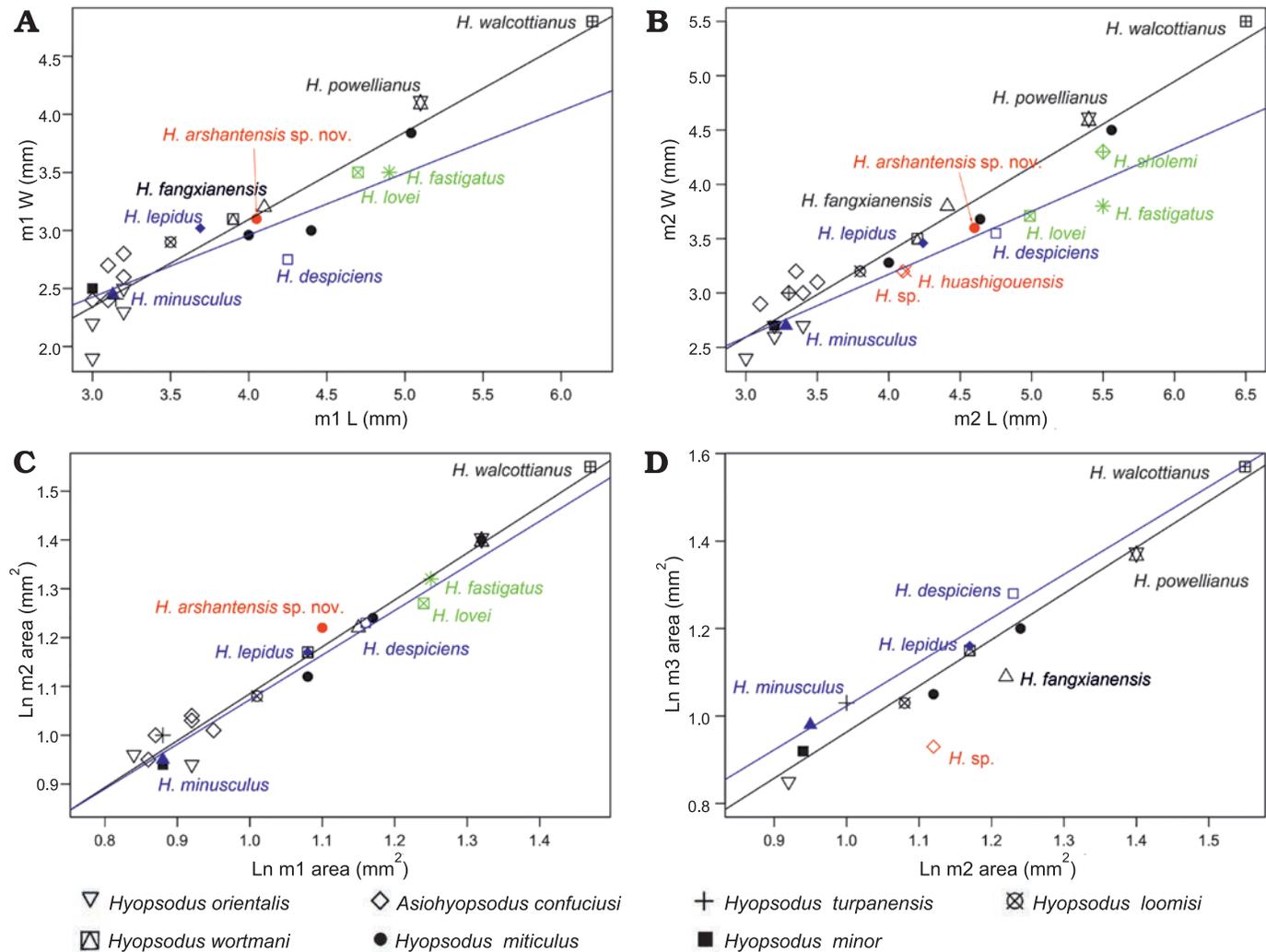
Fig. 3. Scatter plots of lower molar m1–m2 width (W) versus length (L), and size proportions of *Hyopsodus* and *Asiohyopsodus*. m1 (**A**) and m2 (**B**) width versus length, and regression lines for width as a function of length in species of *Hyopsodus* and *Asiohyopsodus*. Size proportions of m2 versus m1 (**C**) and m3 versus m2 (**D**), and regression lines for tooth size as a function of its preceding tooth size in species of *Hyopsodus* and *Asiohyopsodus*. Black symbols and lines, Wasatchian, blue symbols and lines, Bridgerian, red symbols represents the middle Eocene *Hyopsodus* from China, and the green symbols represent the Uintan *Hyopsodus* from North America. Abbreviation: *H.*, *Hyopsodus*. (Raw data: SOM, the Supplementary Online Material available at http://app.pan.pl/SOM/app66-Bai_etal_SOM.pdf).

Flynn 1991), *H. fastigatus* (m2 length 5.2–5.6 mm; Storer 1984) and *H. sholemi* (m2 length 5.5 mm; Krishtalka 1979) (Fig. 3). The m1–m2 of typical Uintan *Hyopsodus* differ from the new species in the presence of the following derived features: a greater degree of lophodonty with a more crescentic protoconid and hypoconid; a more obliquely oriented trigonid; and a greatly enlarged and more isolated entoconid (Krishtalka 1979; Storer 1984; Flynn 1991). The m1–m2 of typical Uintan *Hyopsodus* differ further from *H. arshantensis* sp. nov. in having a hypoconulid placed close to the entoconid, and a metastylid positioned on the posterior slope of the metaconid (Russell and Wickenden 1933; Flynn 1991). The m1–m2 of *H. arshantensis* sp. nov. share some similarities with that of typical Uintan *Hyopsodus* in having a reduced hypoconulid and a relatively longer trigonid on m2. The p4–m3 of *H. fastigatus* and *H. sholemi* are also characterized by being more hypsodont (Storer 1984).

Gazin (1968) considered five species of *Hyopsodus* to be valid and present mainly during the Bridgerian, including *H. paulus* from the late Wasatchian to early Uintan, *H. minusculus* from the late Wasatchian to middle Bridgerian, *H. lepidus* from the middle Bridgerian to early Uintan, *H. marshi* from the late Bridgerian, and *H. despiciens* from the late Bridgerian to early Uintan (Archibald 1998; Tong and Wang 2006; Murphey and Kelly 2017). However, West (1979) recognized only three species of *Hyopsodus* from the Bridgerian, and proposed both *H. marshi* and *H. despiciens* as junior synonyms of *H. paulus*. By contrast, *H. marshi* and *H. despiciens* still are considered as valid by some authors (Archibald 1998; Tsukui 2016; Murphey and Kelly 2017), and this viewpoint is followed here (Fig. 2). The species of Bridgerian *Hyopsodus* can be differentiated mainly on the basis of their relative sizes and stratigraphic distributions (Storer 1984), or by their cingulids (Tsukui 2016). *Hyopsodus*

arshantensis sp. nov. is similar in size to *H. paulus* (m2 length 3.6–4.7 mm; Gazin 1968), *H. despiciens* (mean of m2 length 4.54 mm; Gazin 1968), and *H. tonksi* (m2 length 4.37–4.80 mm; Eaton, 1982), smaller than *H. marshi* (m2 length 5.0–5.1 mm; Gazin 1968), larger than *H. minusculus* (m2 length 2.8–3.8 mm; Storer 1984), and *H. lepidus* (m2 length 3.4–4.5 mm, mean 4.24 mm; Storer 1984) (Fig. 3). The m1–m2 of *H. arshantensis* sp. nov. are generally similar to those of Bridgerian *Hyopsodus* in lacking a paraconid and entostylid, and in having moderately lophodont molar crowns, a distinct entoconid, and a midline position of the hypoconulid. However, the Erlian Basin material differs from Bridgerian *Hyopsodus* in having a longer trigonid, and in lacking variably developed metastylid and cingulids on the buccal and lingual sides. *Hyopsodus arshantensis* sp. nov. further differs from *H. paulus* by a greater angle between the cristid obliqua and posthypocristid, and from *H. despiciens* and *H. lepidus* by a less posteriorly directed posthypocristid and a more distinct postentocristid joining the hypoconulid. The species *Hyopsodus tonksi* has many unique dental morphological features and its assignment within *Hyopsodus* is even controversial (Eaton 1982; Flynn 1991). Thus, in terms of size and morphology, *H. arshantensis* sp. nov. is most comparable to the late Bridgerian species of *Hyopsodus* (except for *H. tonksi*) with relatively larger sizes. However, *H. marshi* is known mainly from upper dentitions, which are characterized by a well-developed protocone on P2–P4, a hypocone as prominent as the protocone on M1–M2, and conical paracone and metacone on the upper molars (Osborn 1902). The morphology of the lower teeth in *H. marshi* was rarely mentioned and is likely indistinguishable from other Bridgerian species of *Hyopsodus*, which in turn differ from *H. arshantensis* sp. nov. as discussed above. *Hyopsodus marshi* probably further differs from *H. arshantensis* sp. nov. by a generally more robust appearance (Tsukui 2016). The discovery of the upper dentition of *H. arshantensis* sp. nov. in the future could provide more differential characters in comparison with Bridgerian *Hyopsodus*.

Comparison with Asian *Hyopsodus* and *Asiohyopsodus*.— Four species of *Hyopsodus* have been named from Asia, including *H. orientalis* (Dashzeveg 1977; Kondrashov and Agadjanian 1999; Hooker and Dashzeveg 2003), *H. turpanensis* (Zhai 1978; Tong 1989), and *H. fangxianensis* (Huang 1995) from the early Eocene, and *H. huashigouensis* (Tong 1989) from the middle Eocene (Fig. 2). Tong and Wang (2006) named a new genus and species, *Asiohyopsodus confuciusi*, from the early Eocene of the Wutu fauna (Shandong Province, China), and suggested that *H. orientalis* and the North American *H. loomisi* (McKenna 1960) are likely members of *Asiohyopsodus*. However, Rose et al. (2012) still considered the species *H. loomisi* more reasonably placed in *Hyopsodus* than in *Asiohyopsodus* and doubted the validity of *Asiohyopsodus*, because whether the relatively short and wide p3–p4 and reduced m3 in *Asiohyopsodus confuciusi* merit generic distinction from *Hyopsodus* needs fur-

ther comparison with larger samples. Moreover, Kondrashov and Lucas (2004) synonymized *H. turpanensis* and *H. fangxianensis* with *H. orientalis* and *H. huashigouensis*, respectively. The taxonomy of five species of *Hyopsodus* and *Asiohyopsodus* previously reported from Asia (Tong and Wang 2006) is followed here (Fig. 2).

Hyopsodus arshantensis sp. nov. is similar in size to *H. fangxianensis*, and larger than other previously described Asian species of *Hyopsodus* or *Asiohyopsodus* (Fig. 3, Table 1). The m1–m2 of the new material differ from those of *Asiohyopsodus confuciusi* and *H. orientalis* in having more lophodont crown morphology, more obliquely aligned protoconid and metaconid, and a more distinct posthypocristid and postentocristid, and in lacking a paraconid on m1. The m1–m2 of *Asiohyopsodus confuciusi* is further characterized by a midline direction of the cristid obliqua and a smaller entoconid. The m1–m2 of *H. orientalis* further differ from those of *H. arshantensis* sp. nov. in having a hypoconulid located close to the entoconid. However, the three species are similar in having a relatively longer trigonid, an obtuse angle between the cristid obliqua and posthypocristid (*H. orientalis* with an angle slightly less than 90°), and in lacking cingulids on the buccal and lingual sides on m1–m2.

Hyopsodus turpanensis is known from a left mandible with a broken p4 talonid and m1–m3 (Zhai 1978; Tong 1989; Fig. 4A). The m1 of the holotype is heavily worn, and the m2 is moderately worn. The m1–m2 of *H. arshantensis* sp. nov. differ mainly from those of *H. turpanensis* in having a longer trigonid and a midline position of the hypoconulid. They are similar in the shared absence of the paraconid and cingulids on the buccal and lingual sides of m1–m2, and in having the obliquely aligned trigonid on m1–m2. *Hyopsodus turpanensis* also has a single-rooted p2 (Fig. 4A$_5$, A$_6$), an elongated m3, and the hypoconulid and entoconid almost fused into a ridge with a posthypocristid joining the hypoconulid in a relatively low position. The fused hypoconulid and entoconid, which almost form a ridge, are also present on m3 of *H. wortmani* (IVPP FV 0416, cast of AMNH FM 4716).

Hyopsodus fangxianensis is known from a right mandible with m1–m3 (Huang 1995; Fig. 4B). The m1 is heavily worn, and the m2 is moderately worn. The m1–m2 of *H. arshantensis* sp. nov. is similar to that of *H. fangxianensis* in having a relatively long trigonid and a midline position of the hypoconulid. However, *H. fangxianensis* can be differentiated by its more lingually directed paralophid on m1–m2, distinct entostylid on the anterior slope of the entoconid, relatively wider m1 and m2, and more robust horizontal ramus of the mandible (Fig. 4B$_4$). The entostylid is also present in some Wasatchian *Hyopsodus* (Gazin 1968), such as the holotypes of *H.* "*simplex*" (as observed on IVPP FV 0418, cast of ACM 2290) and *H.* "*jacksoni*" (as observed on IVPP FV 0411, cast of ACM 3246).

Hyopsodus huashigouensis is known from a fragmentary right mandible with m2 (Tong 1989; Fig. 4C). The tooth is slightly worn with an incomplete entoconid. The m2 of
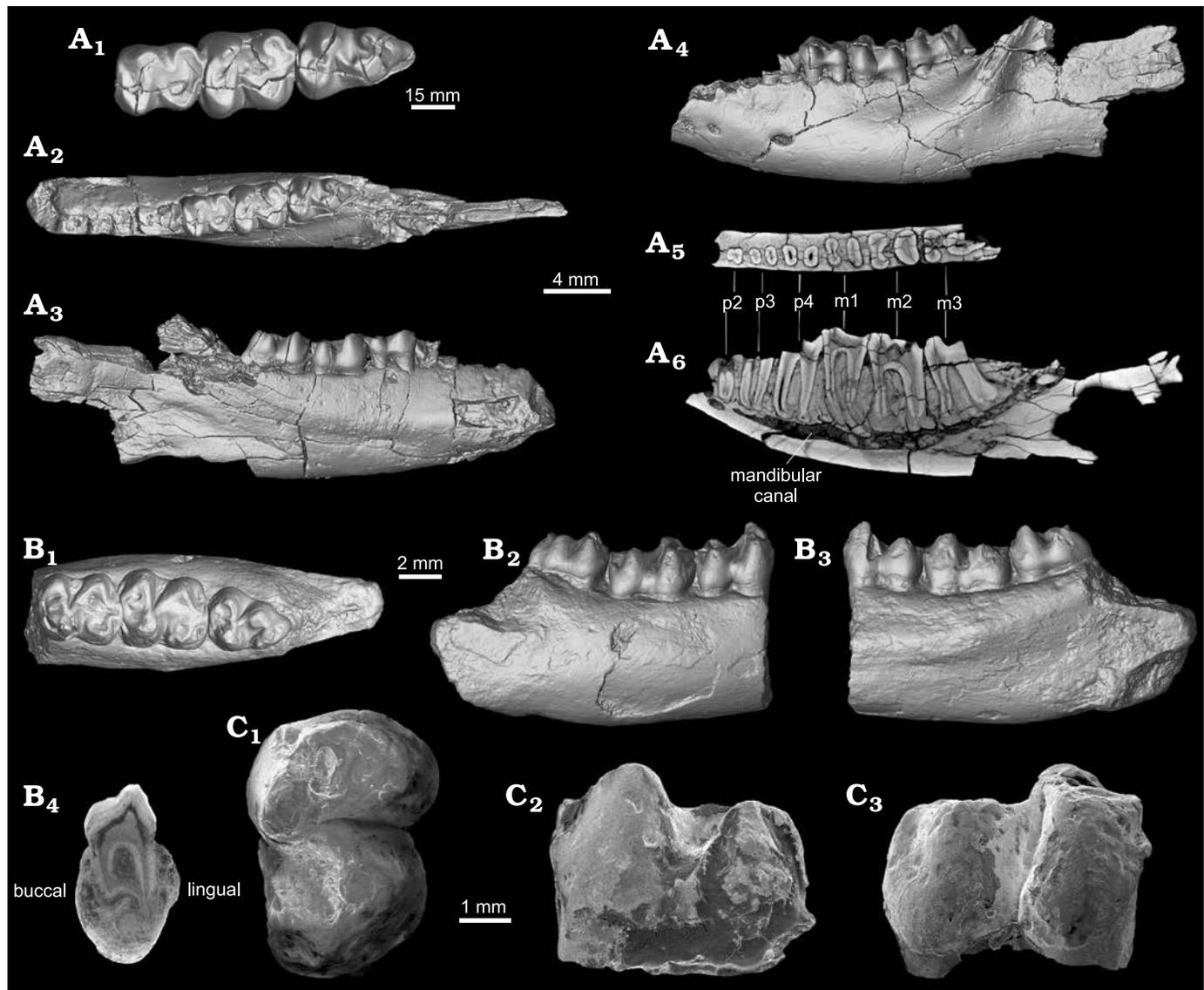
Fig. 4. Mandible fragments and teeth for several species of "condylarth" mammal *Hyopsodus* previously reported from China utilizing μ-CT scanning (A, B) and SEM images (C). **A**. *Hyopsodus turpanensis* Zhai, 1978 (IVPP V 4355) from the early Eocene Shisanjianfang Formation, Turpan Basin, Xinjiang, China. The left mandible with p2–p3 root, p4 talonid and m1–m3 in occlusal (A_1, A_2), lingual (A_3), and buccal (A_4) views, horizontal (A_5) and longitudinal (A_6) sections. **B**. *Hyopsodus fangxianensis* Huang, 1985 (IVPP V 12005) from the early Eocene Youping Formation, Fangxian, Hubei, China. The right mandible with m1–m3 in occlusal (B_1), buccal (B_2), and lingual (B_3) views; cross section at the level of m2 trigonid (B_4). **C**. *Hyopsodus huashigouensis* Tong, 1989 (IVPP V 7921) from the middle Eocene Üqbulak Formation, Junggar Basin, Xinjiang, China. The right m2 in occlusal (C_1), lingual (C_2), and buccal (C_3) views.

H. arshantensis sp. nov. is similar to that of *H. huashigouensis* in having a relatively long trigonid, an obtuse angle between the cristid obliqua and posthypocristid, a midline position of the hypoconulid with a small size, and in lacking the cingulids at the buccal and lingual bases. However, the m2 of *H. huashigouensis* is different from that of *H. arshantensis* sp. nov. in its smaller size, a slightly more lophodont crown, more distinct postentocristid, and absence of the posterior cingulid.

Comparison with European *Hyopsodus*.—Two species of *Hyopsodus* have been reported from the early Eocene of Europe: *Hyopsodus wardi* and *H. itinerans* (Godinot 1978;

Hooker 1979; Hooker and Dashzeveg 2003). Hooker and Dashzeveg (2003) considered *H. wardi* and *H. itinerans* as closely related to the North American *H. loomisi* and Asian *H. orientalis*, respectively. However, Tong and Wang (2006) suggested that the European species probably represent a unique group and could be treated as a new genus. The m1–m2 of *H. arshantensis* sp. nov. are different from those of *H. wardi* and *H. itinerans* in having a larger size, a more lophodont crown morphology, a longer trigonid without the paraconid, a more obliquely oriented trigonid, an obtuse angle between the cristid obliqua and posthypocristid, and a midline position of the hypoconulid. *Hyopsodus wardi* is further characterized by a prominent entostylid on the ante-

rior slope of m1–m2 entoconid, and a distinct cingulid at the base of the ectoflexid on m1–m2 (Hooker 1979).

Biostratigraphic implications.—Compared with North American Bridgerian *Hyopsodus* species, the relatively large size of *H. arshantensis* sp. nov. is close to that of species of *Hyopsodus* from the late Bridgerian (Archibald 1998). Although *H. despiciens*, *H. paulus*, and *H. lepidus* are not restricted in the late Bridgerian as is *H. marshi*, the specimens of Bridgerian *Hyopsodus* with relatively larger sizes likely evolved later in the Bridgerian (Fig. 2). Considering the similarities in size and morphology between *H. arshantensis* sp. nov. and the late Bridgerian species of *Hyopsodus*, the age of the middle part of the Arshanto Formation, where the holotype of *H. arshantensis* sp. nov. was collected, likely can be correlated to the late Bridgerian. In addition, the perissodactyl *Ephyrachyus woodi* from the upper part of the Arshanto Formation (AS-4) is similar to *Ephyrachyus implicatus* from the Washakie Formation in the Washakie Basin of Wyoming (Bai et al. 2020). Wood (1934) suggested that *E. implicatus* was probably unearthed from the late Bridgerian deposits, however, the species is actually distributed through Ui1b to Ui3 (Roehler 1973; Gunnell et al. 2009). Thus, the age of the upper part of the Arshanto Formation is most likely correlated to the early Uintan. Furthermore, the age of the Irdin Manhan Formation is intermediate between the late Bridgerian and late Uintan, as indicated by bearing helaletid *Desmatotherium mongoliensis* and *Paracolodon fissus*, the former being more derived than late Bridgerian *D. intermedius* and the latter being more primitive than late Uintan *Colodon*? *kayi*, *C.*? *woodi* (Bai et al. 2017). The early primate *Tarkops* from the Indin Manhan Formation was considered being relatively more primitive than *Tarka* from the Ui1b of the Tepee Trail Formations, East Fork Basin, Wyoming (Gunnell et al. 2009; Ni et al. 2010). Thus, these correlations would mean that the upper part of the Arshanto Formation was deposited in the time interval of the early Uintan, and may bracket the period equivalent to the Bridgerian/Uintan boundary (Fig. 2).

Hyopsodus huashigouensis was recorded from the bone bed A of the Üqbulak Formation, Üqbulak area of the Junggar Basin, Xinjiang, China and the Üqbulak Formation is considered equivalent to the Bridgerian (Tong 1989). Bone beds B and C of the Üqbulak Formation are correlated to the Arshantan and Irdinmanhan, respectively. Tong et al. (1990) later considered the entire Üqbulak Formation (bone beds A to C), as middle Eocene in age (Li 2018). Bone bed B of the Üqbulak Formation has produced specimens of *Mesonyx uqbulakensis*, also known from the base of the Arshanto Formation (Tong 1989; Jin 2012). That distribution suggests that the stratigraphically lower bone bed A is no younger than the early Arshantan, and that *H. huashigouensis* is somewhat older than *H. arshantensis* sp. nov..

The early Eocene *Hyopsodus turpanensis* from the Shisanjianfang Formation of the Turpan Basin, Xinjiang, China (Zhai 1978) and *H. fangxianensis* from the Youping Formation of Fangxian, Hubei Province, China (Huang 1995) are more derived than *H. orientalis* and *Asiohyopsodus confuciusi*. Those hypothesized relationships support the idea that the Shisanjianfang and Youping formations are equivalent to the *Heptodon* Interval Zone of the Bumbanian and can be correlated to the Lysitean and Lostcabinian subzones of the Wasatchian (Ting 1998). The Wutu fauna, which produced *Asiohyopsodus confuciusi*, is correlated to the *Homogalax* Interval Zone of the Bumbanian and correlated to the Graybullian subzone of the Wasatchian (Ting 1998). *Hyopsodus orientalis* from the Bumban fauna of Mongolia is correlated to the *Orientolophus* Interval Zone of the Bumbanian and to the Sandcouleean of the Wasatchian (Ting 1998).

Conclusions

The middle Eocene "condylarth" mammal *Hyopsodus arshantensis* sp. nov. from the middle part of the Arshanto Formation represents the first record of hyopsodontids from the Erlian Basin, Inner Mongolia, China. Its morphology is somewhat intermediate between Wasatchian and Uintan species of *Hyopsodus*, and is comparable to species of *Hyopsodus* from the Bridgerian. The relatively large size of *H. arshantensis* sp. nov. is close to the species of *Hyopsodus* from the late Bridgerian, suggesting that the middle part of the Arshanto Formation most likely can be correlated to the late Bridgerian. Thus, the Bridgerian/Uintan boundary could be correlated to a level lying in the upper part of the Arshanto Formation, rather than to the contact of the Arshanto and Irdinmanha formations. It is necessary to mention that the fauna from the upper part of the Arshanto Formation (AS-4 and AS-5) is somewhat different from those of the lower and middle parts of the Arshanto Formation (AS-1–3), and shows the first appearance of some new rodents and perissodactyls (Li and Meng 2015; Li 2016; Bai et al. 2018). The study of other fossil mammal groups (e.g., artiodactyls and deperetellids) from the Arshanto and Irdin Manhan formations are underway, and more evidence could point to the necessity of subdividing the Arshantan and/or redefining the Arshantan/Irdinmanhan boundary in future studies.

Acknowledgements

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