Morphology of an early Oligocene beaver *Propalaeocastor irtyshensis* and the status of the genus *Propalaeocastor* (#10309)

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Morphology of an early Oligocene beaver *Propalaeocastor irtyshensis* and the status of the genus *Propalaeocastor*

Lüzhou Li, Qiang Li, Xiaoyu Lu, Xijun Ni

The early to late Oligocene *Propalaeocastor* Borissoglebskaya, 1967 is the most basal beaver genus from Eurasia. Although many species of this genus have been named, these species are exceptionally based on very fragmentary specimens. *Propalaeocastor irtyshensis* from the early Oligocene Irtysh River Formation in northwestern Xinjiang, China is one of the earliest-known members of *Propalaeocastor*. This species is based on a single maxillary fragment. Based on newly discovered specimens from the Irtysh River Formation, we revised the diagnosis of *P. irtyshensis* and the genus *Propalaeocastor*. *P. irtyshensis* possesses a mosaic pattern of plesiomorphic and apomorphic features. The dental morphology of *P. irtyshensis* is very similar to other early castorids. The caudal palatine foramen of *P. irtyshensis* is situated in maxillary-palatine suture. This is a feature generally accept as diagnostic character for the castorids. On the other hand, *P. irtyshensis* has two upper premolars, a rudimentarily developed sciuromorphous zygomatic plate, and a relatively large protrogomorphous form infraorbital foramen. Some previous researches suggested that *Propalaeocastor* is a junior synonym of *Steneofiber* Geoffroy Saint-Hilaire, 1833. Our comparison and revise suggest that *Propalaeocastor* differs from *Steneofiber* and is a valid genus. We also suggest that *Agnotocastor aubekerovi* Lytschev, 1978, *A. readingi* Korth, 1988, and *A. devius* Lytschev and Shevyreva, 1994 should be referred to *Propalaeocastor*. *Propalaeocastor* and *Agnotocastor* are the two earliest of beavers, and they share some similarities such as persisting of P3 (or DP3), caudoventrally extending angle of the mandible and complicated tooth cusp and loph arranging pattern. *Propalaeocastor* possibly was originated in North America and immigrated to Eurasia in Early Oligocene.

Title:

Morphology of an early Oligocene beaver *Propalaeocastor irtyshensis* and the status of the genus *Propalaeocastor*

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ABSTRACT

The early to late Oligocene *Propalaeocastor* Borissoglebskaya, 1967 is the most basal beaver genus from Eurasia. Although many species of this genus have been named, these species are ~~exceptionally~~ based on very fragmentary specimens. *Propalaeocastor irtyshensis* from the early Oligocene Irtysh River Formation in northwestern Xinjiang, China is one of the earliest-known members of *Propalaeocastor*. This species is based on a single maxillary fragment. Based on newly discovered specimens from the Irtysh River Formation, we revise~~d~~ the diagnosis of *P. irtyshensis* and the genus *Propalaeocastor*. *P. irtyshensis* possesses a mosaic pattern of plesiomorphic and apomorphic features. The dental morphology of *P. irtyshensis* is very similar to other early castorids. The caudal palatine foramen of *P. irtyshensis* is situated in maxillary-palatine suture. This is a feature generally accept as diagnostic character for the castorids. On the other hand, *P. irtyshensis* has two upper premolars, a rudimentarily developed sciuromorphous zygomatic plate, and a relatively large protrogomorphous form infraorbital foramen. Some previous researches suggested that *Propalaeocastor* is a junior synonym of *Steneofiber* Geoffroy Saint-Hilaire, 1833. Our comparison and revise suggest that *Propalaeocastor* differs from *Steneofiber* and is a valid genus. We also suggest that *Agnotocastor aubekerovi* Lytschev, 1978, *A. readingi* Korth, 1988, and *A. devius* Lytschev and Shevyreva, 1994 should be referred to *Propalaeocastor*. *Propalaeocastor* and *Agnotocastor* are the two earliest ~~of~~ beavers, and they share some similarities such as persisting of P3 (or DP3), caudoventrally extending angle of the mandible and complicated tooth cusp and loph arranging pattern. *Propalaeocastor* possibly was originated in North America and immigrated to Eurasia in Early Oligocene.

INTRODUCTION

Beavers are medium to large body-sized semi-aquatic or burrowing rodents. Extant beavers include one genus and two species (*Castor fiber* and *C. canadensis*). Fossil beavers are much more diverse, including at least twenty five genera and more than one hundred species (McKenna & Bell, 1997; https://www.paleobiodb.org/). It is generally accepted that all beavers ~~consist of~~ a monophyletic family: Castoridae (McKenna & Bell, 1997; Helgen, 2005). Castoridae is closely related to the extinct family Eutypomyidae, and the two families are usually referred to the superfamily Castoroidea (Simpson, 1945; Wood, 1955, 1965; Hugueney, 1999; Flynn & Jacobs, 2008). Within crown rodents, phylogenetic analyses based on molecular data and/or morphological data usually support the sister-group relationship between the castorids and the geomyoids (a superfamily of rodent that contains the pocket gophers, the kangaroo rats and mice (Adkins et al., 2001; Adkins, Walton & Honeycutt, 2003; Douady et al., 2000; Fabre et al., 2012; Huchon et al., 2002; Montgelard et al., 2002; Murphy et al., 2001).

Beavers probably originated in the late Eocene of North America. The earliest-known castorids fossil, *Agnotocastor galushai*, was discovered from the South Fork of Lone Tree Gulch of Wyoming, with an age of middle to late Chadronian of North American Land-Mammalian Ages (NALMA) and approximately 36.6 Ma (Emry, 1972; Flynn & Jacobs, 2008). The dental and cranial morphology of *Agnotocastor* shares many similarities with the eutypomid *Eutypomys* (Wilson, 1949a; Wood, 1965; Wahlert, 1977; Xu, 1995, 1996; Flynn & Jacobs, 2008). Castorids dispersed into Asia probably during the Early Oligocene (Lytschev, 1978; Lytschev & Shevyreva, 1994; Xu, 1995; McKenna & Bell, 1997). The earliest-known beavers outside of the North America belong to the genus *Propalaeocastor* Borissoglebskaya, 1967, which occurred from the early to late Oligocene of Eurasia (Misonne, 1957; Borisoglebskaya, 1967; Lytschev, 1970; Kretzoi, 1974; Bendukidze, 1993; Lytschev & Shevyreva, 1994; Wu et al., 2004; Bendukidze et al., 2009). The species of *Propalaeocastor* are all represented by isolated teeth and/or jaw fragments. The handful dental specimens of *Propalaeocastor* exhibit a pattern resembling both *Agnotocastor* and *Eutypomys*. Because of their rarity, the generic diagnoses for *Propalaeocastor*, *Agnotocator* and *Eutypomys* have not been well defined. For instance, one of the *Propalaeocastor* species (*P. kumbulakensis* Lytschev, 1970) was even considered ~~as~~ a member of *Eutypomys* (Xu, 1996). *Propalaeocastor irtyshensis* Wu et al., 2004 was discovered from the early Oligocene at the XJ200203 locality in Burqin County in northwestern Xinjiang, China. Previously only upper dentition was known. Here we report new *Propalaeocastor* specimens discovered from the Irtysh River Formation at a new locality close to the type locality of *P. irtyshensis*. Those newly collected specimens make *P. irtyshensis* the best-known species of *Propalaeocastor*. Base on those new specimens we are able to emend the diagnosis of *Propalaeocastor*.

GEOLOGIC SETTING

~~The~~ Cenozoic sediments are widely exposed in the drainage area of the Irtysh (=Ertix) River in Burqin-Jeminay region in northwestern Xinjiang of China (Figs. 1A & B). The holotype of *Propalaeocastor irtyshensis* was discovered from the lower portion of the early Oligocene Irtysh River Formation at the XJ200203 locality in the Burqin-Jeminay region (Fig. 1B). The new specimens of *P. irtyshensis* reported here were discovered from a new fossiliferous locality of the lower Irtysh River Formation about 50 km southwest to the XJ200203 locality. The Irtysh River Formation is a set of fluviolacustrine mudstone, siltstone, sandstone and thick conglomerate. The fossiliferous layer of the Irtysh River formation is dated as 32.0 Ma (Sun et al., 2014). Same fossiliferous layer at the XJ200203 locality can be traced to the new locality despite ~~of~~ long distance between the two localities. This fossiliferous layer at the new fossil locality is an ~~about~~ 5-meter thick bed of grey greenish and light brown-reddish mudstone with rich calcareous nodules (Fig. 1C). The new *P. irtyshensis* remains include a fragmentary maxilla, several incomplete jaws and isolated cheek teeth. The mammals associated with these new beaver fossils include *Cricetops dormitor*, *Parasminthus tangingoli*, *Cyclomylus lohensis*, and *Prosciurus* sp. All of those mammals are typical early Oligocene fossils and also present at the XJ200203 locality.

MATERIALS, METHODS AND ABBREVIATIONS

The new materials include a broken maxilla preserving P4-M1, two isolated upper cheek teeth and three mandibular fragments. The holotype of *Propalaeocastor irtyshensis* (IVPP V 13690) is re-described. All fossils are housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing. The specimens are CT-scanned using the 225kv Micro-CT at the Key Laboratory of Vertebrate Evolution and Human Origins, Chinese academy of Sciences. Segmentation and 3D virtual reconstruction are made by following the standard procedure introduced by Ni et al. (Ni, Flynn & Wyss, 2012). Specimens are measured by using Olympus SZX7 microscope and mandibles by vernier caliper both with a precision of 0.01 mm. The dental terminology (Fig. 2) is adapted from Stirton (1935), Hugueney (1975, 1999), Lopatin (2003), and Wu et al. (2004). Postfixes flexus/flexid, fossette/fossettid and stria/striid are used for descri~~pting~~ the valleys between two lophs/lophids or between two cusps. Flexus ~~are~~ flexid are used when the valleys are open to the tooth sides, usually in ~~the freshly worn~~ specimens. Stria and striid ~~are~~ refer~~red~~ to the notches in buccal or lingual view. These notches are the buccal or lingual openings of the valleys. As ~~the~~ tooth wear deepens, the flexus or flexid will be gradually closed near the tooth sides. These closed flexus or flexids are called fossettes or fossettids. Paraflexid and metaflexid were often used for the mesial and distal flexids respectively (Stirton, 1935; Hugueney, 1975, 1999; Wu et al., 2004). Here we followed Lopatin (2003) by using metaflexid for the mesial flexid and entoflexid for the distal flexid. We use premetafossettid instead of proparafossettid (Hugueney, 1999) or parafossettid (Lopatin, 2003) to describe the small fossa enclosed between anterolophid and mesial metalophulid.

Abbreviations: **CSC**, Chadron State College; **FAM**, Frick American Mammals, Department of Vertebrate Paleontology, the American Museum of Natural History; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; **UCM**, University of Colorado Museum; **XJ**, prefix to Xijiang, field localities of the IVPP.

Systematic paleontology

Order Rodentia, Bowdich, 1821

Family Castoridae Hemprich, 1920

Genus *Propalaeocastor* Borissoglebskaya, 1967

Synonym. *Asteneofiber* Kretzoi, 1974: p.427.

Type Species. *Propalaeocastor kazachstanicus* (including *P. habilis*) Borissoglebskaya, 1967.

Included Species. *P. butselensis* (Misonne, 1957), *P. kumbulakensis* (Lytschev, 1970) (including *Capatanca schokensis* and *Capacikala sajakensis* in Bendukidze, 1993), *P. aubekerovi* (Lytschev, 1978), *P. redingi* (Korth, 1988), *P. shevyrevae* (Lytshev & Shevyreva, 1994), *P.* sp. aff. *P. shevyrevae* (Lytshev & Shevyreva, 1994), *P. zaissanensis* (Lytshev & Shevyreva, 1994), *P. devius* (Lytschev & Shevyreva, 1994 (Lytschev & Shevyreva 1994)), and *P. irtyshensis* Wu et al., 2004.

Distribution. Early to Late Oligocene, Eurasia; Early Oligocene, North America.

Emended Diagnosis. A small-sized castorid. Dental formula: 1/1, 0/0, 2/1, 3/3. Sciuromorphous skull with a large infraorbital foramen. Sciurognathous lower jaw. Digastric eminence present in some advanced species. Mandibular angular processs extending caudoventrally. Lower incisor enamel surface smooth, mediolaterally convex, and lacking enamel ornamentation. Lower incisor root terminating in a lateral capsule. Wide space present between lower tooth row and vertical ramus. Cheek teeth brachydont or mesodont. Upper tooth crown lingual side higher than buccal side. Lower tooth crown buccal side higher than lingual side. Upper cheek tooth crown nearly quadrate. P4 slightly larger than M1 and M2. M3 being the smallest. Upper cheek teeth presenting five lophs and six flexures or fossae. Premesoflexus and postmesoflexus always present. p4 mesiodistally elongated. Lower molar crown rectangular. p4 larger than molars. m3 being the narrowest. p4 having five lophids and six flexids or fossettids. Lower molars having four lophids and five flexids or fossettids. Postmesoflexid always present. No cement.

Propalaeocastor irtyshensis Wu et al., 2004

(Figs. 3-6; Tables 1 & 2)

Holotype. IVPP V 13690, a right maxillary fragment preserving P4–M3. Locality XJ200203, northwest of Burqin, Xinjiang. The Irtysh Formation, Early Oligocene.

Referred specimens. IVPP V 23138.1, a right maxillary fragment preserving P4-M1, IVPP V 23138.2, an isolated left P4, and IVPP V 23138.3, an isolated left M1, probably belong to the same individual; IVPP V 23139, a right ~~mandibular~~ fragment preserving p4-m3; IVPP V 23140, a right ~~mandibular~~ fragment preserving p4-m1; IVPP V 23141, a right ~~mandibular~~ fragment preserving p4.

Loalities and Horizon. Northeast of Jeminay County, Junggar Basin, Xinjiang (Fig. 1B). Irtysh River Formation, early Oligocene.

Emended Diagnosis. P3 present. Infraorbital foramen and canal large and round. Differing from *P. kazachstanicus* in having posteroventrally extending angular process of the ~~mandible;~~ ~~higher~~ mandibular depth beneath p4, complete entoloph and open postmesoflexus on P4, two premesofossettids and more transverse mesoflexid on lower cheek teeth, and in lacking digastric eminence. Different from *P. butselensis* in having more complicated septa or spurs in buccal premesoflexus, metaflexus and premesofossettid, more distally extending mesoflexus. Different from *P. kumbulakensis* in having smaller size, lower tooth crown, less distally extend~~ing~~ mesoflexus, closed postmesoflexus on P4, and two premesoflexids on p4. Differing from *P. zaissanensis* in having separated hypoflexus and mesoflexus on M3. Differing from *P. aubekerovi* by lacking digastric eminence and having higher mandibular depth beneath p4. Different from *P. reading* in having more transversely expanded m1 and m2. Differing from *P. devius* in having larger size, ~~higher~~ mandibular ~~height~~ beneath the p4, and more caudoventrally extending angular process of the mandible. Differing from *P. shevyrevae* in having lower tooth crown, less folded inner surface of enamel islets, and in lacking premetafossettid and having double premesofossettids on p4, and less elongated m3 with single entofossettid.

Measurements. See Tables 1 & 2.

Description. The two maxillary fragments (V 13690, holotype and V 23138.1) preserve a part of the palatine process, a part of the alveolar process, and a part of the zygomatic process. The alveolar process forms the tooth sockets and holds the teeth. The dorsal side of the alveolar process is flat and smooth. It does not show any bulges for the expansion of the tooth roots. On its dorsal-medial side above the M2, it presents the opening of the caudal palatine foramen, which leads to two canals running in the maxillary-palatine suture (Figs. 3A1-2). The preserved palatine process is very small. On V 13690, only the major palatine foramen is well preserved. It is an oval and oblique opening situated between M1 and M2 in the suture between the palatine process of the maxilla and the palatine bone (Figs. 4A1-2). On V 23138.1, the broken surface shows that ~~the major and minor palatine foramens~~ lead to a short canal and meet at the ~~caudal~~ palatine foramen (Fig. 3A1). The preserved zygomatic process of the maxilla is small. It extends dorsolaterally from at the level of the mesial root of P4. The mesial surface of the zygomatic process is a slopping plate, indicating that a narrow zygomatic plate probably is present (Figs. 4A1-2). No masseteric tubercle for the superficial masseter is present on the root of the zygomatic process. Dorsal to the zygomatic process, a round and smooth surface indicates that the infraorbital foramen is large and round, and the infraorbital canal is very short (Figs. 4A3, B2). Dorsoventrally, the infraorbital foramen and infraorbital canal are at the level of the tooth roots, a situation as in extant protrogomorphous and sciuromorphous rodents.

On both V 13690 and V 23138.1, there is a small semi-cylindrical depression mesial to the mesial root of P4 (Figs. 4A1-2 & B1). This depression indicates the presence of a small single-rooted P3. On the mesial surface of the P4, no obvious contacting facet is present. It is probably because the crown of P3 ~~is~~ very small and low, and has no contact with P4.

The lingual side of the upper cheek tooth crown is slightly higher than the buccal side (Figs. 3, 4B1; Table 1). From the mesial to the distal of the tooth row, the tooth size decreases gradually. The lingual tooth cusps, namely protocone and hypocone, distolingually expanded and form two fold-like structures on each tooth. The buccal cusps (paracone and metacone) are small, round and not expanded.

The P4 (Figs. 3A, B; Fig. 4A1) is the largest of the upper cheek teeth. Its occlusal surface has an inverted trapezoid outline with its mesial side wider than its distal side. The tooth can roughly divided into four regions: the protocone region on the mesiolingual side, the paracone region on the mesiobuccal side, the hypocone region on the distolingual side and the metacone region on the distobuccal side. The lingual sides of the protocone region and hypocone region are separated by the deep and mesiobuccally directed hypoflexus. The buccal sides of those two regions are connected by the strong and oblique entoloph. Paracone region is separated from the metacone region by the deep mesoflexus. Within the protocone region, the protocone is the dominant cusp. Its distolingual side is expanded and forms a fold-like structure. The buccal side of the cusp has two arms, the mesial protocone arm and the distal protocone arm, which merge with anteroloph and entoloph respectively. The anterocone is a very small cusp. It is well delimited as a small node situated mesial to the paracone on a slightly worn specimens (V 23138.1-2). In the moderately worn specimen (V 13690), the anterocone is merged with the anteroloph. In the paracone region, it includes the paracone and two protolophules. The lingual side of the paracone smoothly extends into the mesial protolophule. In the less worn specimen (V 23138.1), the lingual end of the mesial protolophule does not join the protocone and is separated from the latter by a shallow groove. In the slightly more deeply worn specimens (V 13690, V 23138.2), the lingual end of the mesial protolophule connects the mesial arm of protocone. The distal protolophule is a long and curved crest. Its buccal end extends to the distal side of the paracone (V 23138.1-2) or merges with postparacrista (V 13690). Its lingual end connects the entoloph in two speciemens (V 23138.1-2), but is separated from the entoloph in the holotype (V 13690). On

V13690, an extra fold is present at the distolingual side of distal protolophule. Mesocone and mesoloph are absent. Three small fossae are present in the paracone region: including paraflexus, lingual premesofossette and buccal premesofossette. Paraflexus is enclosed by anteroloph and mesial protolophule. Lingual premesoflexus is enclosed by mesial and distal protolophules. Buccal premesoflexus is enclosed by distal protolphule and postparacrista. In the hypocone region, the hypocone forms a fold, which is smaller than the protocone. The mesial and distal arms of hypocone are smoothly merged with the entoloph and the posteroloph respectively. The metacone region normally develops three ridges. The shortest ridge is the mesial metalophule, a ridge mesiobuccally extending towards the distal protolophule. The longest ridge is the medial metalophule, which transversely connects the metacone and hypocone. Distal to the metalophule is a long ridge referred as distal metalophule here. This ridge distobuccally ~~extends~~ and always connects the posteroloph via a short and thin ridge. The postmesoflexus, which lies between the medial metalophule and distal metalophule, is always buccally open. The metaflexus lying in between the distal metalophule and posteroloph is divided into two or three fossae by small ridges. From the lateral view, the tooth has 3 deep grooves, which are collectively called lateral strias. From the mesial to the distal, the three lateral strias are named as the parastria, the mesostria and the metastria. From the lingual view, the only deep groove generated by the hyoflexus is the hypostria. The hypostria is the longest. It extends nearly two third of the crown height. The mesostria is the second deepest groove that reaches about a half of the crown height. The parastria and the opening of postmesoflexus are very short. P4 has a strong lingual root and two slim buccal roots.

The M1 (Figs. 3A, C; Fig. 4A1) has a more rectangular crown than the P4, but both teeth have very similar cusp-ridge pattern. The width of M1 is larger than the length. In the paracone region, it presents two protolophules. The paraflexus and the groove between the mesial and distal protolophules are worn into four enamel islets. The mesoflexus is a straight groove in the V 23138.1 and V 23138.2. In the slightly more deeply worn specimen (V 13690) the groove is divided into two parts by a longitudinal ridge. In the metacone region, ~~it develops~~ three or four ridges. The grooves between those ridges are divided into three or four fossae. As in the P4, the lingual side of M1 has one deep groove (hypostria), and the buccal side of M1 has one (mesostria) or two (mesostria and metastria) shallow grooves on moderately worn specimens (V 23138.1, .3) and lacks groove on deeply worn specimen (V 13690). The M1 also has three roots.

The M2 (Fig. 4A1) is very similar to the M1 in both size and cusp-ridge pattern. In its paracone region, there are two protolophules, two opened grooves and one enclosed enamel islet. The mesial groove is the long and narrow paraflexus. The distal groove is the premesoflexus. A short ridge divided the premesoflexus into an open groove on the buccal side and a small enamel islet on the lingual side. The mesoflexus is a long and curved groove separating the paracone region and the metacone region. In the metacone region, there are also two metalophules. The mesial metalophule has an indentation at its middle part. This indentation joins the postmesofossette with the fossa between the metalophules. The distal metalophule is a complete ridge that connects the metacone and hypocone. From the distolingual part of the distal metalophule, it develops a short spur protruding into the metaflexus. The posteroloph is a strong ridge as a buccal extension of the distal arm of the hypocone. The development of the stria~~s~~ on the lingual and buccal side of M2 is identical to those in M1 of the same dentition (V 13690).

M3 (Fig. 4A1) has a narrower distal edge than in the M1-2. The hypocone of M3 is relatively small ~~that~~ the posteroloph is reduced. The paracone region is almost identical as those in M1 and M2, while the metacone region is proportionally smaller.

The newly collected specimens include three ~~mandibular~~ fragments (Fig. 5). Two of the three specimens preserve most of the horizontal ramus and a portion of the vertical ramus (V 23139 and V 23141). The other specimen preserves only a small part of the horizontal ramus (V 23140). The horizontal ramus of the ~~mandible~~ can further be divided into two parts: the part that bears the incisor and the part that bears the premolar and molars. The part that bears the incisor contains a long incisor alveolus, which runs beneath the premolar and molars and extends distally and buccally to a point lateral and above the leve~~r~~ of tooth crown. The part that bears the premolar and molars contains eleven alveoli for the roots of the lower cheek teeth (Figs. 6A2, C2). Its lingual side ~~is~~ bulge~~d~~ ~~for the~~ expansion of the tooth roots ~~and~~ forms the alveolar juga. The buccal surface of the body of the mandible is smooth. A large and round mental foramen is present at a place ventral to the p4 (Figs. 5A3, B3, C3). On the mesiolingual surface of the horizontal ramus of the mandible, an oval rugose region mesioventral to the alveolus of p4 is identified as the caudoventral expansion of the mandibular symphysis (Figs. 5A1, C1). Ventral to this rugose region, no digastric eminence is present. On the ventral portion of the lingual side of the mandible, there are many nutrient foramina. A small portion of the angular process of the mandible is preserved in two specimens~~. It shows a~~ caudoventral ~~extension direction.~~ On the lingual side of the vertical ramus, the medial pterygoid muscle fossa is very deep. On the buccal surface of the vertical ramus, the masseteric fossa is well defined by the masseteric crest. The dorsal and ventral branches of masseteric crest are convergent nearly at a right angle, and extend to a point ventral to the m1. The coronoid crest of the vertical ramus arises ~~from the~~ lateral ~~side~~ of the m1~~. Lateral to the coronoid crest~~, it ~~presents~~ a bulge that contains the most distal extension of the incisor root. On the medial side of the cor~~ac~~oid process, there is a well-developed ridge (Figs. 5A2, C2). This ridge probably marks the inferior limit for the lateral pterygoid muscle. The space between the tooth row and the vertical ramus is broad.

The lower incisor is only preserved in one specimen (V 23141). The cross-section of this lower incisor is in a rounded triangular shape. The pulp cavity is large and round. The enamel band of the incisor is smooth and buccoventrally convex (Fig. 6D).

The buccal ~~crown~~ sides of the lower cheek t~~ee~~th are slightly higher than the lingual ~~crown~~ side (Table 1). From p4 to m3, the sizes are gradually reduced. On all the check teeth, the protoconid and hypoconid are large and mesiobuccally protruding. The metaconid and entoconid are all relatively small and round.

All the three mandibles preserve the fourth premolar (Figs. 5-6). The crown of the p4 (Figs. 5A2, B2, C2) has a trapezoid outline with its mesial side narrower than its distal side. The hypoflexid and mesoflxid (=mesofossettid) form a waist that divides the tooth crown into mesial and distal lobes. The protoconid, the anterolophid and the mesial part of the ectolophid are merged into a strong curved loph that forms the buccal margin of mesial lobe. The metaconid, lingual part of the metalophulid, the metastylid and the metastylid crest are fused into another curved loph that forms the lingual margin of the mesial lobe. In less worn individual (V 23139, 23140), the cusps and ridges in the mesial lobe enclose three fossae (Figs. 5A2, B2). In deeply worn individual (V 23141), only one fossa is left (Fig. 5C2). The metaflexid (=metafossettid), which is enclosed between the anterolophid and metalophulid, is a long and curved fossa. A spur derived from the anterolophid extends into the metafossettid. Between the metalophulid and the metastylid crest, two fossae are present, namely the buccal premesofossettid and the lingual premesofossettid (Figs. 5A2, B2). The distal side of the lingual premesofossettid is open in one specimen (Fig. 5B2). The two fossae ~~are~~ disappear~~ed~~ in the heavily worn specimen (V 23141, Fig. 5C2). The mesoflexid is a long and deep groove~~. It~~ extends transversely across more than half of the crown width. The hypoflexid on the buccal tooth side has a broad opening. It extends distolingually to the mesiolingual side of the hypoconid. The hypoflexid and mesoflexid are separated by the ectolophid. The ectolophid also connects the mesial and distal lobes. The distal lobe is formed by the hypoconid, entoconid and the ridges and arms associated with those two cusps. The hypoconid is very large and forms the buccal half of the distal lobe. The posterolophid, the entoconid, the hypolophulids and the distal part of ectolophid form the lingual half of the distal lobe. The mesial hypolophulid and the small postmesofossettid are present in the less worn specimen (Figs. 5B2). The entoflexid is present as long groove between the distal hypolophulid and posterolophid. Complicated enamel folds developed from the hypolophulid and posterolophid protrude into the entoflexid. In deeply worn specimen (V 23141), these folds connect to each other and divide the entoflexid into 3 enamel islets. Two broad roots are present on p4 (Figs. 6A2, B2, C2).

The m1 (Figs. 5A2, B2) is preserved on two specimens (V 23139, V 23140). Both of them are heavily worn. The m1 has a rectangular crown, with its width larger than its length. As in the p4, the conspicuously deep mesoflexid and hypoflexid form a waist and divide the tooth into mesial and distal lobes. The protoconid, metaconid and the ridges associated with the mesial lobe tend to merge together. One or two enamel islets are enclosed in the mesial lobe. It is hard to deduce whether they homologize with the metafossettid or with the premesofossettid. The mesoflexid is lingually open on V 23140 but closed on V 23139. The hypoflexid of m1 is narrower than that of the p4. The distal lobe of m1 is slightly broader than the mesial lobe. In the slightly worn specimen (V 23140), a small enamel islet is identified as the postmesofossettid. A transverse curved groove is the entoflexid. In the heavily worn specimen (V 23139), the hypoconid, the entoconid, the hypolophulids, and the posterolophid completely merge. The tooth has three roots, including two slim mesial roots and one broad distal root (Figs. 6A2, B2, C2).

Only one specimen (V 23139) preserves m2 and m3. The m2 (Fig. 5A2) is very similar to the m1. A shallow oval fossa in the middle of mesial lobe can be identified as the metaflexid. The mesoflexid between the mesial lobe and distal lobe is lingually closed. In the distal lobe, the transverse fossa is identified as the entoflexid. As in m1, m2 also has two slim mesial roots and one broad distal (Figs. 6A2, C2).

The m3 (Fig. 5A2) is very similar to m1 and m2, but is slightly longer and narrower. Its mesial lobe has two fossae. The large buccal one is identified as the metaflexid. The tiny lingual fossa is identified as the premesofossettid. As in m2, the mesoflexid is lingually closed. In the distal lobe, the large and oblique entoflexid is preserved. The tooth has three roots as ~~those of~~ m1 and m2 (Fig. 6C2).

Comparisons. *Propalaeocastor* is very similar to *Steneofiber* (Lytschev, 1970; Lytschev & Shevyreva, 1994; Lopatin, 2003, 2004; Bendukidze et al., 2009). Wu et al. (2004) listed seven characters shared by the two genera. The new Jeminay specimens reported here show that *Propalaeocastor* differs from *Steneofiber* (Stefen, 1997) by presenting larger P4 and p4 relative to the molars, mesiodistally more elongated P4 and p4, relatively wider molars, and more complicated ridge-fossa pattern. In *Propalaeocastor*, the metalophules on the upper teeth and the hypolophulids on the lower teeth are divided to two or three branches. The upper teeth and the lower teeth usually have premesofossette and postmesofossette, and premesofossettid and postmesofossettid respectively. The mesoflexus and mesoflexid are more transversely orientated. In the narrower flexures and fossae of *Propalaeocastor*, it usually develops many crenulated enamel folds from the adjacent lophs or ridges. In a sharp contrast, *Steneofiber* has relatively simpler and less crenulated ridge-fossa pattern.

Propalaeocastor shares many similarities with *Agnotocstor*. The North American late Eocene *Agnotocstor* is widely regarded as the oldest castorid genus (Korth, 1994; Xu, 1995, 1996; Flynn & Jacobs, 2008). *Agnotocastor* includes six species. Four of them, namely the type species *A. praetereadens*, *A. coloradensis*, *A. galushai* and *A. readingi*, are from North American. Two species, *A. aubekerovi* and *A. devius*, are from Kazakhstan (Stirton, 1935; Wilson, 1949b; Emry, 1972; Lytshev, 1978; Korth, 1988; Lytschev & Shevyreva, 1994). *A. readingi*, *A. aubekerovi* and *A. devius* include on[illegible]wer jaw fragments and lower teeth. These three species all have a distinct postmesofossettid on their lower cheek teeth. This is the diagnostic feature of *Propalaeocastor*. Furthermore, these three species are distinguished from the genotype *A. praetereadens*, *A. coloradensis* and *A. galushai* by having a less developed metastylid crest (Hugueney, 1975; Wu et al., 2004), separated mesoflexid and entoflexid, and more transverse entoflexid. Here we transfer *A. readingi*, *A. aubekerovi* and *A. devius* to the genus *Propalaeocastor*.

The genotype *Propaleocastor kazachstanicus* was discovered from Kyzylkak, Dzhezkazgan and Kazakhstan (Borissoglebskaya, 1967). *P. irtyshensis* has a relatively deeper ~~mandible~~ beneath the p4 than in *P. kazachstanicus* (Table 2). Caudoventral to the mandibular symphysis, a small digastric eminence is present in *P. kazachstanicus*, but not in *P. irtyshensis*. The angular process in *P. irtyshensis* is more caudoventrally direct~~ing~~, while in *P. kazachstanicus* the angular process is more caudally direct~~ing~~. *P. irtyshensis* has more transverse mesoflexids on lower cheek teeth than those in *P. kazachstanicus*. Lytschev & Shevyreva (1994) referred nine isolate cheek teeth discovered from Maylibay of Zaissan Basin to *P. kazachstanicus* (fig 2 in Lytschev & Shevyreva, 1994). These teeth differ from *P. irtyshensis* by having more distally extending mesoflexus on M1/2, and narrower crown and having only one premesofossettid on p4.

Compared to *P. butselensis* from the Hoogbustsel-Hoeleden of Belgium (Misonne, 1957), *P. irtyshensis* has more complicated dental structure. The premesofossette, metaflexus and premesofossettid in *P. irtyshensis* are usually divided by extra septa or spurs. The mesoflexus in

P. irtyshensis is more distally extending, while in *P. butselensis* is nearly transverse. "*Steneofiber* cf. *S. butselensis*" from the Buran Svita of Podorozhnik, locality K15, south of Lake Zaissan (Emry et al., 1998) was regarded as also a member of *Propalaeocastor* by Wu et al. (2004). These specimens are very similar to *P. irtyshensis*. They have slightly smaller tooth size and relatively narrower m1-2 than *P. irtyshensis*.

P. kumbulakensis was discovered from the Kumbulak cliffs, and loc. Altyn Schokysu, loc. Akotau, and loc. Sayaken near the Aral Sea (Lytschev, 1970; Bendukidze et al., 2009). It is much large more robust than *P. irtyshensis*. The upper teeth of *P. kumbulakensis* have premesofossette, postmesofossette and double metalophules. The lower teeth have the postmesofossettid and double hypolophulids. These features are similar to those in *P. irtyshensis*. Similar to *P. irtyshensis*, *P. kumbulakensis* does not have a digastric eminence, and its angular process of the mandibles extends caudoventrally. The p4 of *P. kumbulakensis* has a single premesofossettid, and a large open flexure merged by mesoflexid and metaflexid. The hypoflexid in *P. kumbulakensis* is very deep and extends lingually on p4-m1. The postmesofossettid is absent on the p4, but is present on the m1 of *P. kumbulakensis*. The tooth crown of m1 in *P. irtyshensis* is mesial-distally more compressed and buccal-lingually wider than those of *P. kumbulakensis*.

Compared to *P. aubekerovi* from Tort-Molla, Ulutau, Dzhezkazgan Province in Kazakhstan (Lytshev, 1978), *P. irtyshensis* is different by lacking the digastric eminence and presenting much thicker mandibular depth beneath p4 (Table 2).

P. readingi from the Orella Member of Brule Formation of Dawes County, Nebraska, America (Korth, 1988) is similar to *P. irtyshensis* in size, and both species are similar in dental and mandibular morphology. *P. irtyshensis* differs from *P. readingi* in having more transversely expanded m1 and m2. Given the very wide geographic separation, the similarity shared by *P. readingi* and *P. irtyshensis* is remarkable.

Compared to *P. irtyshensis*, *P. shevyrevae* from Talagay of Zaissan Basin (Lytshev & Shevyreva, 1994) has relatively lower tooth crown, less folded inner surface of enamel islets, smaller p4 with more rounded protoconid and less projected hypoconid. The lower cheek teeth of *P. shevyrevae* have a premetafossettid and a single premesofossettid. The m3 is more elongated and has two metafossettids. *P.* aff. *shevyrevae* from Podorozhnik and Novei Podorozhnik of the Zaissan Basin (Lytshev & Shevyreva, 1994) is similar to *P. irtyshensis* in overall size. The P4 of *P.* aff. *shevyrevae* is slightly larger and slenderer than that of *P. irtyshensis*. It differs from *P. irtyshensis* in having more tortuous enamel folds protruding into the fossae on upper teeth, and having one premesofossettid on p4.

P. zaissanensis from Talagay of Zaissan Basin (Lytschev & Shevyreva, 1994) is very close to *P. irtyshensis* in both tooth size and morphology. *P. zaissanensis* differs from *P. irtyshensis* in having a relatively narrow p4, and a hypoflexus transversely confluent with the mesoflexus on M3.

P. devius from Maylibay of Zaissan Basin (Lytschev & Shevyreva, 1994) differs from *P. irtyshensis* in having smaller tooth size, shallower mandibular depth beneath the p4, and more caudodorsally extending angular process of the mandible.

Steneofiber aff. *dehmi* from the early Oligocene Saint-Martin-de-Castillon of France

(Hugueney, 1975) was treated as a member of *Propalaeocastor* by Wu et al. (2004). As in other *Propalaeocastor*, *P. dehmi* has premesofossettes and postmesofossettes on upper cheek teeth, and postmesofossettid on lower cheek teeth. It is larger than *P. irtyshensis*. The mesoflexus on upper cheek teeth are more distally extend~~ing~~. The lower cheek teeth in *P. dehmi* ~~is~~ slender than those in *P. irtyshensis*, and have the metastylid crest.

DISCUSSION

The genus *Propalaeocastor* was established by Borissoglebskaya (1967) based on the specimens from the Early Oligocene of Kyzylkak, Dzhezkazgan, Kazakhstan. The validity of this genus was debatable. Lytschev and Shevyreva (1994), and Lopatin (2003, 2004) considered *Propalaeocastor* as a junior synonym of *Steneofiber* Geoffroy Saint-Hilaire, 1833. Some other researchers suggested that *Propalaeocastor* is different from *Steneofiber* and is a valid genus. (McKenna & Bell, 1997; Korth, 2001; Wu et al., 2004). Kreztozi (1974) referred "*Steneofiber*" *butselensis* Misonne, 1957 to a new genus "*Asteneofiber*". However, the validity of *Asteneofiber* was not widely recognized. Some researchers considered "*Asteneofiber*" as the junior synonym of *Steneofiber* (McKenna & Bell, 1997; Korth, 2001), while Wu et al. (2004) regarded "*Asteneofiber*" as a junior synonym of *Propalaeocastor*. Based on the new specimens of *Propalaeocastor irtyshensis*, we are able to make a thorough ~~revise on~~ *Propalaeocastor*. Our new results indicate that *Propalaeocastor* is a valid genus and different from *Steneofiber*. Detailed comparison also supports sinking *Asteneofiber* into *Propalaeocastor*.

Besides the type species *Propalaeocastor kazakhstanicus*, Borissoglebskaya (1967) also named *P. habilis* in the same paper. In their study of beaver remains from Maylibay of Zaissan (or Zaysan) Basin, Kazakhstan, Lytschev & Shevyreva (1994) synonymized *P. habilis* with *P. kazakhstanicus* and reported another three species: *P. shevyrevae*, *P.* aff. *shevyrevae* and *P. zaissanensis*. Wu et al. (2004) recognized *P. butselensis*, *P. shevyrevae*, *P.* sp. aff. *P. shevyrevae*, *P. zaissanensis*, *P. kazakhstanicus*, and named the species *P. irtyshensis*. Recently, Bendukidze et al. (2009) transferred another two species "*Capatanca schokensis*" Bendukidze, 1993 and "*Steneofiber*" *kumbulakensis* Lytschev, 1970 to *Propalaeocastor*. Bendukidze et al. (2009, p.350) also suggested that "*Capatanca schokensis*" and "*Capacikala sajakensis*" are synonymous. Lopatin (2003) reasonably suggested that "*Capacikala sajakensis*" is the junior synonym of "*Steneofiber*" *kumbulakensis*. "*Steneofiber*" *kumbulakensis*, "*Capatanca schokensis*" and "*Capacikala sajakensis*" overlap in tooth size and are almost identical in dental morphology. We suggest that "*Capatanca schokensis*" and "*Capacikala sajakensis*" should all be sunk into "*Steneofiber*" *kumbulakensis*, and should all be referred to *Propalaeocastor*. As mentioned above, "*Agnotocastor*" *aubekerovi* Lytschev, 1978, "*Agnotocastor*" *readingi* Korth, 1988 and "*Agnotocastor*" *devius* Lytschev and Shevyreva, 1994 share many mandibular and dental similarities with *P. irtyshensis*, and therefore should all be assigned to *Propalaeocastor*. In summar~~izing~~, the genus *Propalaeocastor* include *P. kazakhstanicus* Borissoglebskaya, 1967, *P. butselensis* (Misonne, 1957), *P. kumbulakensis* (Lytschev, 1970), *P. aubekerovi* (Lytschev, 1978), *P. readingi* (Korth, 1988), *P. shevyrevae* (Lytschev & Shevyreva, 1994), *P.* sp. aff. *P. shevyrevae* (Lytschev & Shevyreva, 1994), *P. zaissanensis* (Lytschev & Shevyreva, 1994), *P.*

devius (Lytschev & Shevyreva, 1994) and *P. irtyshensis* Wu et al., 2004.

Korth (1994) and Flynn & Jacobs (2008) enumerated many features of Castoridae that are different from Eutypomidae, such as the small and mediolaterally compressed infraorbital foramen, the long infraorbital canals, the ~~caudal~~ palatine foramen located in the maxillary-palatine suture, distinctive chin process (symphyseal flange, or mandibular eminence), base of lower incisor terminating in a lateral bulbous expansion etc. Xu (1996) once defined the castorids as "the rodents that have sciuromorphous masseter arrangement on the skull and a derived mandible here termed the beaver-pattern mandible." His "beaver-pattern mandible" is referred to a mandible presenting "digastric eminence" and "the angle extending up posteriorly". Eutypomyidae is characterized by presenting a narrow zygomatic plate, a large and round infraorbital foramen, a short infraorbital canal, two upper premolars, and a lower jaw lacking the digastric eminence and having a caudoventrally extending angular process (e.g., Wahlert, 1977; Korth, 1994).

The new *Propalaeocastor irtyshensis* specimens reported here show that this rodent possesses a mosaic pattern of plesiomorphic and apomorphic features. The dental morphology of *P. irtyshensis* is very similar to other early castorids. The ~~caudal~~ palatine foramen of *P. irtyshensis* is situated in maxillary-palatine suture. This is a feature generally accept as being diagnostic for the castorids (Korth, 1994, p.137). On the other hand, *P. irtyshensis* also possesses some features shared with eutypomyids. The upper dentation of *P. irtyshensis* has two premolars. Among castorids, it is known that two upper premolars are present in *P. devius* (Lytschev & Shevyreva, 1994), and some North American early castorids, such as *Agnotocastor*, *Neatocastor* and *Oligotheriomys* of North America (Flynn & Jacobs, 2008). The zygomatic process of maxilla of *P. irtyshensis* displays a conspicuous mesiodorsaly-distoventraly oblique surface, indicating that a sciuromorphous zygomatic plate probably is present (Figs. 4A1-2). Medial to the zygomatic plate and dorsal to the zygomatic root of the maxilla, it presents a smooth and round surface. This surface indicates that the infraorbital foramen is large and round, and the infraorbital canal is short. That rudimentarily developed sciuromorphous zygomatic plate coupled with a protrogomorphous form of infraorbital foramen and canal is probably a plesiomorphic feature for all castorids. Although it is impossible to deduce whether the medial masseter muscle extends to the rostral region through the large infraorbital foramen in *Propalaeocastor*, it is reasonable to believe that the sciuromorphous zygomatic and infraorbital foramen morphology must be convergently evolved in crown castorids and sciurimorphs.

Xu (1996) argued that *Propalaeocastor kumbulakensis* should be assigned to the eutypomid genus *Eutypomys* because the lower jaw of *P. kumbulakensis* does not have a digastric eminence, and its angular process extends caudoventrally. We reexamined the mandibular specimens of *Propalaeocastor* and found that the digastric eminence is variably present in different species. In *P. kumbulakensis*, *P. irtyshensis*, *P. readingi* and *P. devius*, the digastric eminence is absent, while in some other species, such as *P. aubekerovi* and *P. kazachstanicus* it is well-developed. In *P. irtyshensis*, the articular facet of the mandibular symphysis has a large expansion beneath the genial fossa. The presence of this enlargement strengthens the mandibular symphysis. In all the castorids with genial region preserved, the articular facet of the mandibular symphysis ~~all~~ has this ventral expansion. When the digastric eminence is present, the articular facet always extends onto it. The so-called digastric eminence probably is a part of articular expansion related to the strengthening of the mandibular symphysis, not just provide the arising places for the digastric muscles. In that sense, the expansion of the articular facet of the mandibular symphysis, rather than the presence of digastric eminence, should be regarded as a synapmorphy of castorids. As far as the angular process of mandible, it is also variably present in different species of *Propalaeocastor* and other basal castorids. In some species preserving that part, such as *P. kumbulakensis*, *P. irtyshensis*, *P. aubekerovi*, the angular process of the mandible extends caudoventrally, but in some other species, such as *P. devius* and *P. kazachstanicus*, the angular process shows a tendency of caudodorsal extension (Fig. 7). It is likely that the direction of the angular process is related with the development of the medial pterygoid muscle and does not have particular significance for phylogeny.

Propalaeocastor shares many features with the oldest-known beaver *Agnotocastor*, such as persistence of P3, angular process of the mandible extending caudoventrally and complicate dental pattern. These features are likely plesiomorphic for castorids, because they are also present in the eutypomids, which are widely considered as the sister group of castorids. *Agnotocastor* probably represents the most basal castorid. Its appearance in the late Eocene of North America marks the origin of Castoridae (Fig. 7). Slightly younger *Propalaeocastor* dispersed to Eurasia ~~probably~~ during the Eocene-Oligocene transition and survived to the end of Oligocene (Fig. 7).

ACKNOWLEDGMENTS

We thank the field participants in the Jeminay and Burqin regions of Xinjiang, especially to Mr. Shaoguang Zhang and the local drivers Messrs. Ming Hao, Hongwei Li and Jianxun Yan. We would like to express our gratitude to Mr. Yongchun Yang for his enthusiastic favors in our fieldworks. Many thanks are also due to Mr. Yemao Hou for the computed tomography.

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1

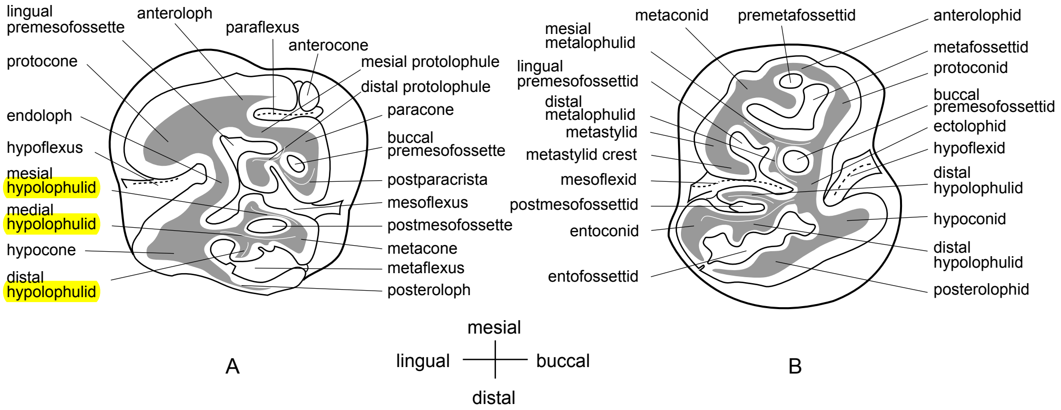
Jeminay and Burqin *Propalaeocastor irtyshensis* fossil localities in the Irtysh River drainage area in northwestern Xinjiang, China (modified from Stidham & Ni, 2014)

A. Map showing the location of the *P. irtyshensis* localities in the Irtysh River region within China adjacent to several other countries; B. Detailed map showing the border region between Xinjiang and Kazakhstan and the localities of *P. irtyshensis*; C. Panoramic view of the fossiliferous profile of the Irtysh River Formation that produced the additional material of *P. irtyshensis*

Figure 2(on next page)

Terminology of the fourth premolars of *Propalaeocastor*. (modified from Stirton, 1935; Hugueney, 1975, 1999; Lopatin, 2003 and Wu et al., 2004)

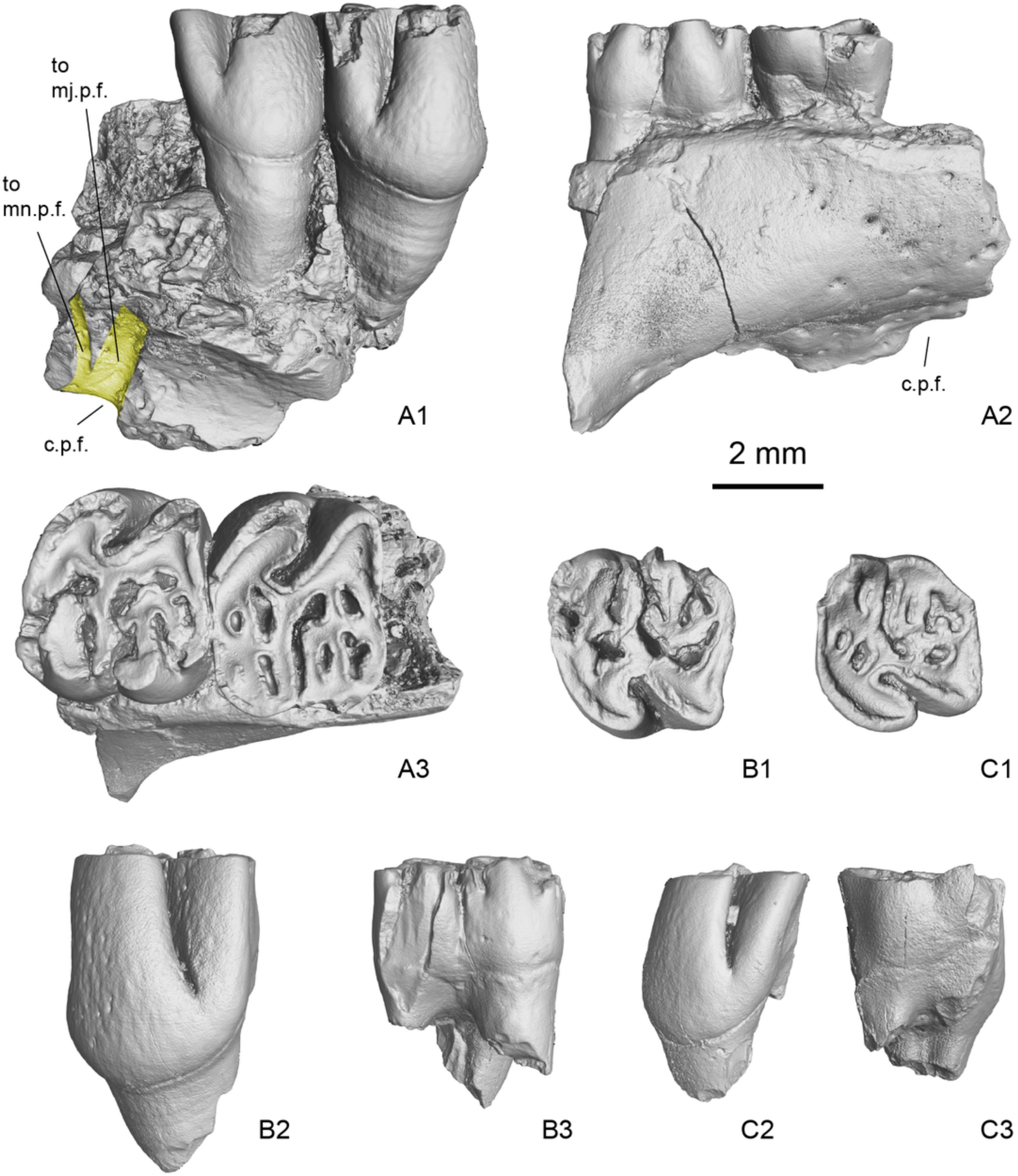
A. left P4; B. left p4. Entofossettid = entoflexid = entostriid; hypoflexid = hypostriid; hypoflexus = hypostria; mesoflexid = mesofossettid; mesoflexus = mesofossette = mesostria; metaflexid = metafossettid; metaflexus = metafossette = metastria; paraflexus = parafossette = parastria; premesoflexid = premesofossettid; premesofossette = premesoflexus = premesostria, postmesofossette = postmesoflexus; postmesofossettid =postmesoflexid


lingual premesofossette
anteroloph
paraflexus
anterocone
protocone
mesial protolophule
distal protolophule
paracone
endoloph
buccal premesofossette
hypoflexus
mesial hypolophulid
postparacrista
mesoflexus
medial hypolophulid
postmesofossette
hypocone
metacone
metaflexus
distal hypolophulid
posteroloph
A
metaconid
premetafossettid
anterolophid
mesial metalophulid
metafossettid
lingual premesofossettid
protoconid
distal metalophulid
buccal premesofossettid
metastylid
ectolophid
metastylid crest
hypoflexid
mesoflexid
distal hypolophulid
postmesofossettid
hypoconid
entoconid
distal hypolophulid
entofossettid
posterolophid
B
mesial
lingual
buccal
distal

3

Maxilla and isolated upper cheek teeth referred to *Propalaeocastor irtyshensis* from Jeminay area, northwestern Xinjiang, China.

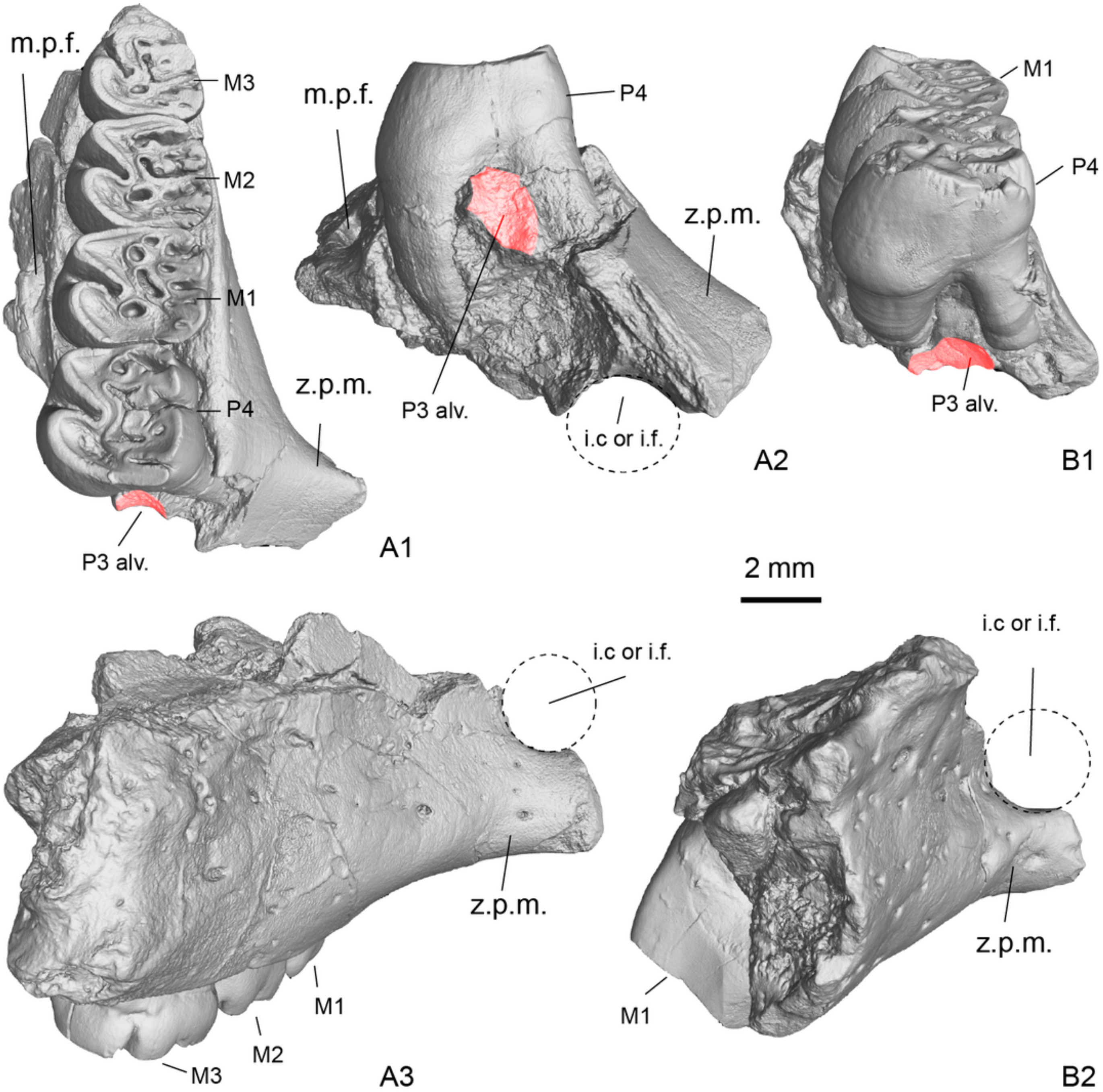
Yellow shadow showing the divergence of palatine nerve. A. broken maxilla with right P4-M1 (IVPP V 23138.1); B. left P4 (IVPP V 23138.2); C. left M1 (IVPP V 23138.3). 1. lingual; 2. occlusal; 3. buccal. c.p.f. caudal palatine foramen; mj.p.f. major palatine foramen; mn.p.f. minor palatine foramen. All in same scale.


to
mj.p.f.
to
mn.p.f.
c.p.f.
A1
c.p.f.
A2
2 mm
A3
B1
C1
B2
B3
C2
C3

4

3D virtual reconstruction of the maxillae of *Propalaeocastor irtyshensis* by the X-ray computed tomography.

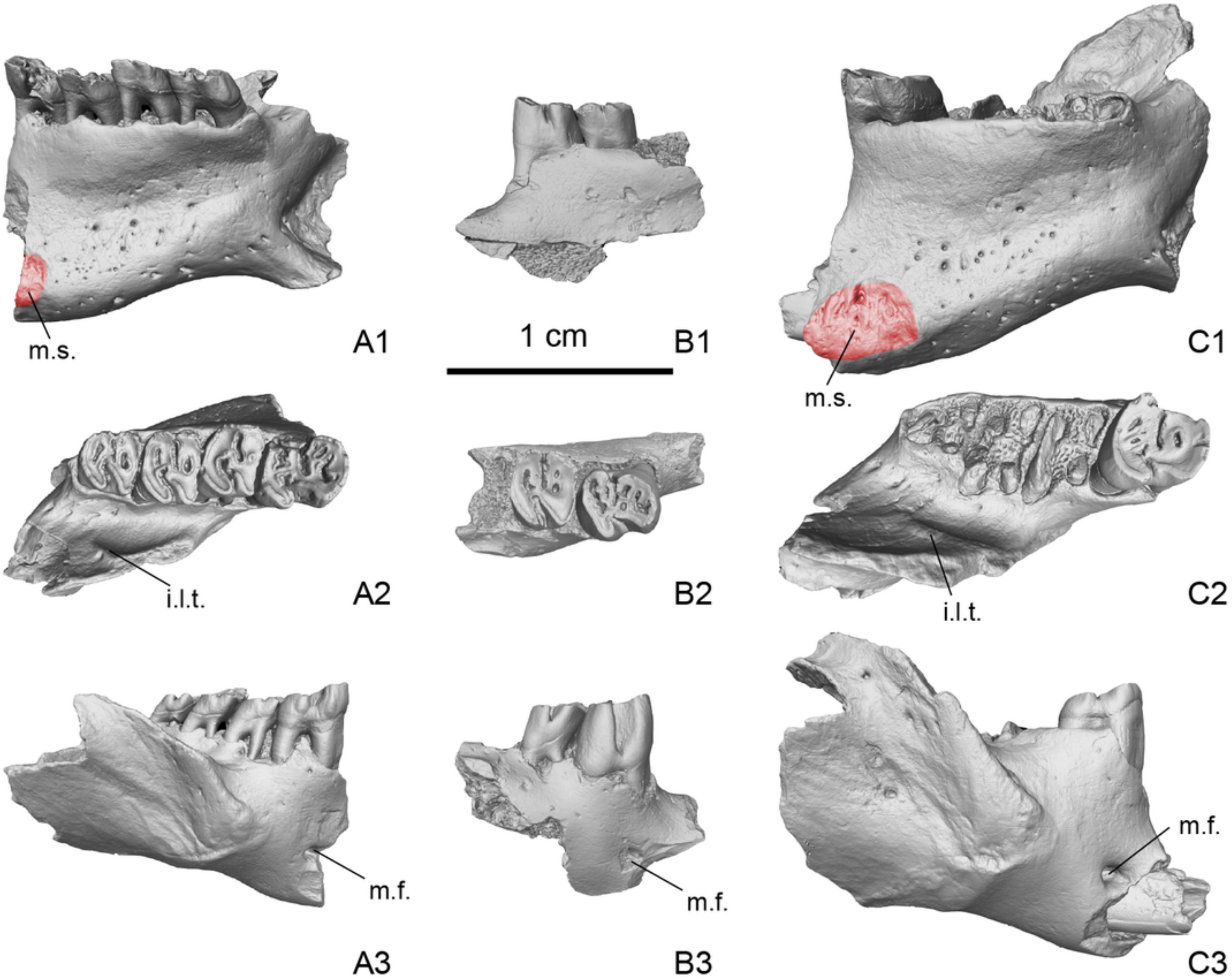
Red shadow showing a residual P3 alveolus mesial to the mesial roots of P4; dashed cycle displaying a relative large and round infraorbital canal (or foramen) dorsal to the zygomatic arch root preserved in both holotype of Burqin (A1-3: IVPP V 13690) and additional specimen of Jeminay (B1 and 2: IVPP V 23138.1). alv. alveolus; i.c. infraorbital canal; i.f. infraorbital foramen; m.p.f. major palatine foramen; z.p.m. zygomatic process of maxilla


m.p.f.
M3
M2
M1
P4
z.p.m.
P3 alv.
A1
m.p.f.
P4
z.p.m.
P3 alv.
i.c or i.f.
A2
M1
P4
P3 alv.
B1
2 mm
i.c or i.f.
z.p.m.
M1
M2
M3
A3
i.c or i.f.
z.p.m.
M1
B2

5

Fragmentary mandibles of *Propalaeocastor irtyshensis* from Jeminay, Xinjiang.

Red shadow displaying articular facet of mandibular symphysis. A. fragmentary right mandible with broken p4-m3 (IVPP V 23139); B. broken right mandible with p4-m1 (IVPP V 23140); C. broken right mandible with p4 (IVPP V 23141). m.s. mandibular symphsis; m.f. mental foramen; i.l.t. inferior limit of temporalis. 1. lingual; 2. occlusal; 3. buccal. All in same scale.



6

Transverse and sagittal sections of mandibles and transverse section of lower incisor of *Propalaeocastor irtyshensis* of Jeminay, Xinjiang.

Showing convex enamel surface of lower incisor, permanent fourth premolar and root number of lower cheek teeth (P4:M1:M2:M3=2:3:3:3). A. fragmentary right mandible with p4 (IVPP V 23141); B. broken right mandible with p4-m1 (IVPP V 23140); C. fragmentary right mandible with p4-m3 (IVPP V 23139). D. lower incisor (IVPP V 231411). 1. sagittal section; 2. transverse section

**Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*

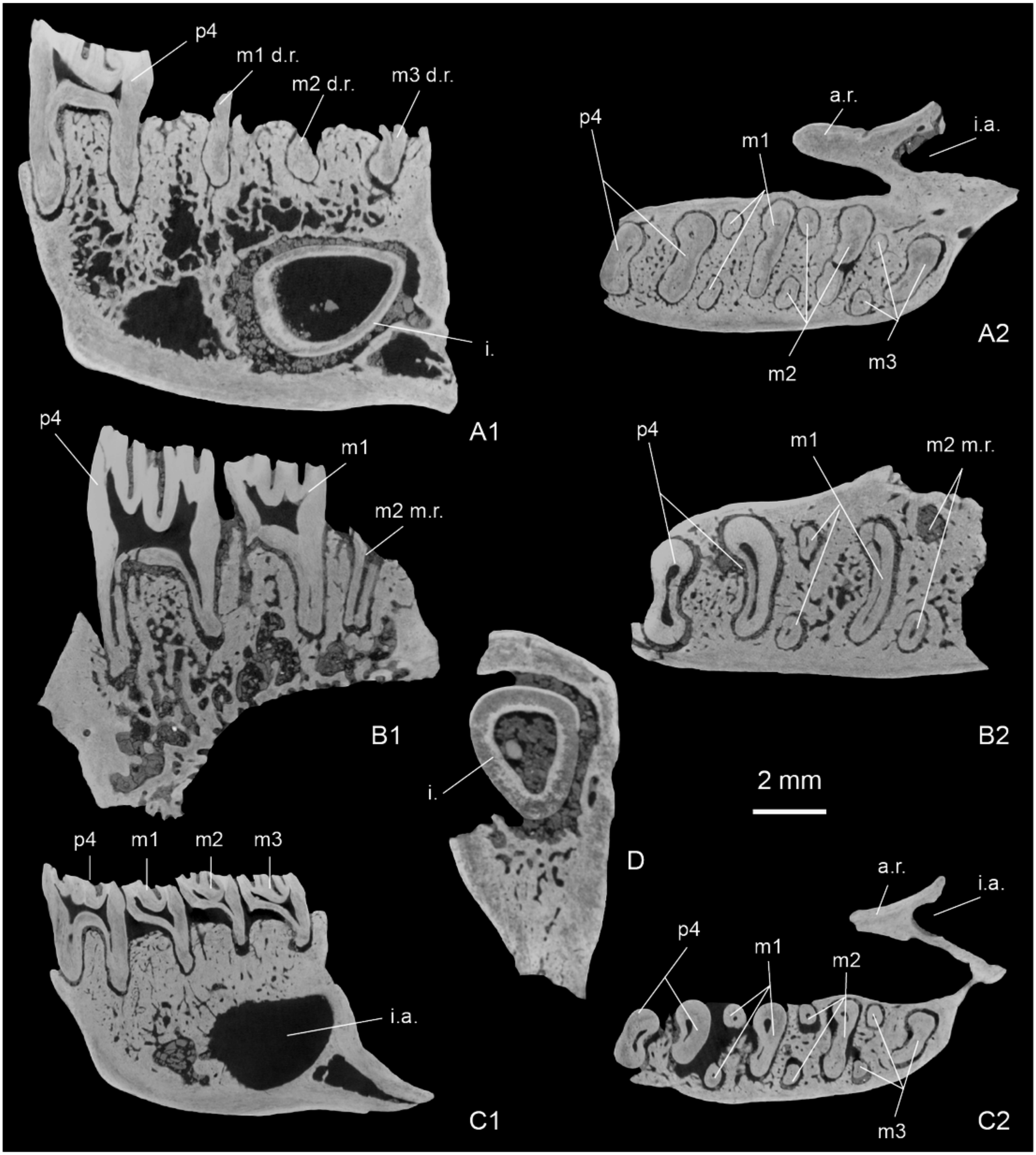

p4
m1 d.r.
m2 d.r.
m3 d.r.
i.
A1
a.r.
i.a.
p4
m1
m2
m3
A2
p4
m1
m2 m.r.
B1
p4
m1
m2 m.r.
B2
i.
D
2 mm
p4
m1
m2
m3
i.a.
C1
a.r.
i.a.
p4
m1
m2
m3
C2

Figure 7(on next page)

Temporal ranges and comparisons of mandibles and dental patterns of *Agnotocastor* of North America and *Propalaeocastor* of North America and Asia.

Displaying the developments of digastric eminence and angular process of the mandible extending orientations of their mandibles and similarities of dental constructions. Arrow showing a suggestion of Asian *Propalaeocastor* possibly radiated rapidly in the Early Oligocene soon after its migration from North America. Asterisk showing the genotypes of *Agnotocastor* and *Propalaeocastor*. Except for the figures of *Propalaeocastor irtyshensis* (mandible, IVPP V 23141; dentition, IVPP V 23139), the illustrations in right column are facsimiles of their original figures (Wilson, 1949; Borissoglebskaya, 1967; Lytschev, 1970; Emry, 1972; Lytschev, 1978; Korth, 1988; Lytschev & Shevyreva, 1994). Abbreviations used in left column are biochrons of North American Land-Mammal Ages (NALMA): Ch-1=Early Chadronian; Ch2-3=Middle Chadronian; Ch4=Late Chadronian; Or1-Or4=Orellan; Wh1-Wh2=Whitneyan (see Flynn & Jacobs, 2008). Mandibles and lower dentitions are in same scales, respectively

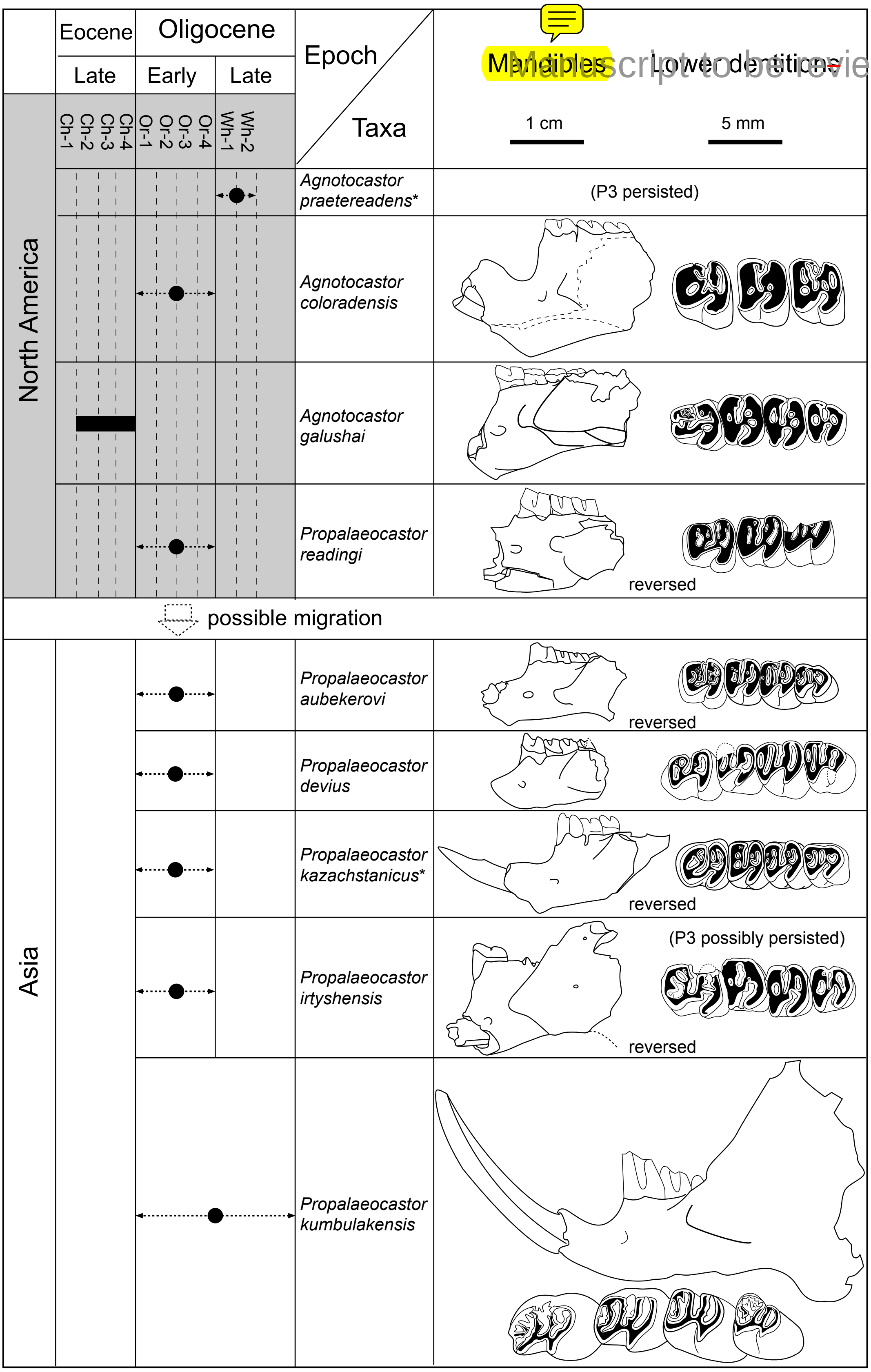

Eocene
Oligocene
Late
Early
Late
Epoch
Taxa
Mandibles
Lower dentitions
1 cm
5 mm
North America
Ch-1
Ch-2
Ch-3
Ch-4
Or-1
Or-2
Or-3
Or-4
Wh-1
Wh-2
Agnotocastor praetereadens*
(P3 persisted)
Agnotocastor coloradensis
Agnotocastor galushai
Propalaeocastor readingi
reversed
possible migration
Asia
Propalaeocastor aubekerovi
reversed
Propalaeocastor devius
Propalaeocastor kazachstanicus*
reversed
Propalaeocastor irtyshensis
(P3 possibly persisted)
reversed
Propalaeocastor kumbulakensis

Table 1(on next page)

Measurements (in mm) of cheek teeth of *Propalaeocastor irtyshensis* from Jeminay, Xinjiang (L., length; W., width)

Inventory numbers	Tooth	Surface L.×W.	Base L.×W.	Buccal ~~L.×W~~.	Lingual ~~L.×W.~~	Mesostria(id) Height	Hypostria(id) Height	Maximum height/ maximum length indices
V 23138.1	P4	3.53×3.47	3.63×4.67	2.09	3.49	0.49	1.37	0.96
V 23138.1	M1	3.15×3.79	3.15×4.81	1.56	2.43	-	0.84	0.77
V 23138.2	P4	3.46×3.48	3.66×4.38	1.97	3.91	0.92	1.74	1.06
V 23138.3	M1	3.04×3.16	3.27×3.69	1.87	3.38	-	1.64	1.03
V 23139	p4	3.79×3.29	4.10×3.52	2.06	1.97	-	1.14	0.50
V 23139	m1	3.12×3.35	3.26×3.62	1.39	1.35	0.2	0.29	0.43
V 23139	m2	3.08×3.58	3.48×3.71	1.53	1.42	-	0.34	0.44
V 23139	m3	3.05×3.04	3.64×3.22	1.44	1.45	-	0.52	0.40
V 23140	p4	3.38×3.02	4.12×3.54	3.83	2.60	0.82	2.27	0.93
V 23140	m1	3.05×3.39	3.54×3.98	2.49	2.07	0.49	0.9	0.70
V 23141	p4	4.31×4.18	4.65×4.41	1.83	1.54	-	0.42	0.39

Table 2(on next page)

Measurements comparison of mandibles among *Propalaeocastor irtyshensis* and other taxa of *Propalaeocastor* and *Agnotocastor*

Asterisk numbers are re-measured from their originally illustrations i.e. Borissoglebskaya, 1967; Lytschev, 1970; Lytschev & Shevyreva, 1994

Taxa	Inventory numbers	Depth of jaw beneath middle of p4	p4-m3, mesiodistal length	p4-m2, mesiodistal length	p4-m1, mesiodistal length	p4, mesiodistal length
P. irtyshensis	V 23139	11.8	12.4	9.2	6.2	3.79-4.10
P. irtyshensis	V 23140	-	-	-	12.0	3.38-4.12
P. irtyshensis	V 23141	13.2	-	-	-	4.31-4.65
P. kazachstanicus	No. 2259-322	9.5*	-	8.4*	6.1*	3.5*
P. aubekerovi	M-2041/74	9.1	11.6	9.0	6.0-7.0	3.2-3.7
P. devius	No. 3463-4	7.0*	10.0*	7.7*	5.1*	3.2*
P. kumbulakensis	M-2020/66	11.4*	19.8*	16.1*	10.9*	6.3*
P. readingi	CSC 80-1	11.0	-	10.6		3.35
A. coloradensis	UCM 19809	14.6	-	11.9		4.1
A. galushai	FAM 79310	10.1	11.7	9.1	-	3.4