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## *Propalaeocastor* (Rodentia, Mammalia) from the Early Oligocene of Burqin Basin, Xinjiang

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### ABSTRACT

A new species of castorids, *Propalaeocastor irtyschensis*, n.sp., from the Burqin Basin of Xinjiang Uygur Autonomous Region, China, is described. The new species, represented by a right maxilla with well-preserved P4–M3, is the earliest and northernmost occurrence of castorids in China. It is characterized mainly by the cheek tooth crown being higher than that of *P. butselensis* but lower than that of *Steneofiber* aff. *dehmi* (probably a new species of *Propalaeocastor*), and by lingual confluence of the mesoflexus to the lingual fossette of the pre-mesoflexus. Comparison with known species previously assigned to *Steneofiber* from Europe and Kazakhstan leads to the conclusion that the early Oligocene forms previously assigned to the genus, such as “*S. butselensis*” and “*S. kazachstanicus*”, differ significantly from those represented by *S. eseri* from the Late Oligocene and Early Miocene of Europe. We consider *Propalaeocastor* a valid genus, provide an emended diagnosis for it, and discuss its evolutionary trend in relation to *Steneofiber*. Preliminary analysis of Burqin fauna suggests an age of early Early Oligocene. Faunal transformations across the Eocene–Oligocene boundary in the Burqin region are comparable to those of Europe and the Mongolian Plateau and suggest linkage of faunal turnovers and global climate changes.

### INTRODUCTION

The beavers are represented by two living species of a single genus, *Castor fiber* and *C. canadensis*, which are members of the family Castoridae and distributed in Eurasia and North America, respectively (Nowak, 1999). Fossil species of castorids are exten-

sive in Eurasia and North America (Stirton, 1935; Korth, 2001) and date back to the latest Eocene (McKenna and Bell, 1997). *Steneofiber*, known from Europe and Asia, is one of the earliest castorids. This genus is considered either a member of Castoroidinae (McKenna and Bell, 1997) or a member of Castorinae (Korth, 2001). According to

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Korth (2001), the early Oligocene *Steneofiber* is the earliest castorine in Europe and has unspecialized cheek teeth in which flexi are closed to form fossettes at relatively early stages of wear. Species of *Steneofiber* are well studied in Europe since Stirton's work (1935), but are less so for those more recently found in Asia. Several species referred to *Steneofiber* are known from the Oligocene of Kazakhstan in Central Asia and are represented by fragmentary specimens (Lytshev, 1970, 1978; Lytshev and Shevyreva, 1994; Emry et al., 1998).

Taxonomy of *Steneofiber* has been unstable and confusing. Most notable is the proposal of *Asteneofiber* Kretzoi (1974: 426–427), a genus based on *S. butselensis*, which has not been recognized until recently (Hugueney and Escuillié, 1995, 1996; Hugueney, 1999). In other studies *Asteneofiber* is usually synonymized with *Steneofiber* (McKenna and Bell, 1997), a view probably followed by Korth (2001), who did not recognize the name of *Asteneofiber*.

Another relevant genus is *Propalaeocastor* Borissoglebskaya, 1967. The type species *P. kazakhstanicus* is from the Early Oligocene of Central Kazakhstan. The genus was later synonymized to *Steneofiber* (Lytshev and Shevyreva, 1994). Recently, Korth (2001) resumed the name *Propalaeocastor* and placed it, together with *Anchitheriomys* and *Oligotheriomys*, to Tribe Anchitheriomyini under the subfamily Agnotocastorinae.

We report here a new early Oligocene species, *Propalaeocastor irtyshensis*, which is the earliest and northernmost occurrence of castorids in China. The new species is represented by a right maxilla with well-preserved P4–M3 discovered during the field season of 2002. The specimen was found at the 115.5 m horizon of the section on the northern bank of the Irtysh River near Burqin City, Xinjiang. This level is 26 m above the Late Eocene locality (XJ1999027 = 99027 in our previous publication) in the same section that has been reported elsewhere (Ye et al., 2002). Screenwashing of sediments from the castorid bed generated isolated teeth representing 14 additional rodent species. The assemblage of small mammals suggests an age of early Early Oligocene.

We compare the new species with those

previously referred to *Steneofiber* and discuss the taxonomic validities of *Propalaeocastor* and *Steneofiber*. We also examine the composition of *Propalaeocastor*, the relationships between *Propalaeocastor* and *Steneofiber*, and the biostratigraphic and biogeographic implications of the new species and its associated fauna.

The terminology used for the upper cheek teeth of the early castorids is adapted from Hugueney (1975, 1999) and Lytshev and Shevyreva (1994), and is illustrated in figure 1. Measurements are made under the Wild M7A stereomicroscope, with each tooth dimension measured twice from opposite sides; the average values of measurements are presented in table 1.

## SYSTEMATIC PALEONTOLOGY

CASTORIDAE HEMPRICH, 1920

CASTORINAE HEMPRICH, 1920

*Propalaeocastor* Borissoglebskaya, 1967

SYNONYM: *Asteneofiber* Kretzoi, 1974: 427.

TYPE SPECIES: *Propalaeocastor kazakhstanicus* Borissoglebskaya, 1967.

TYPE LOCALITY AND AGE: Kyzylkak, 70 km southwest to City Dzhezkazgan in central Kazakhstan, Early Oligocene.

EMENDED DIAGNOSIS: Primitive, small castorids with brachyodont to mesodont cheek teeth having folded enamel but lacking cement filling; P3 absent; P4 subquadrate; cheek teeth decreasing in size posteriorly; in addition to the five main lophes (anteroloph, protoloph, mesoloph, metaloph, and posteroloph), the metastyle crest, protolophule I and II, and metalophule I and II also present (figs. 1, 3); the paraflexus, mesoflexus, metaflexus, hypoflexus, premesoflexus (or fossette), and postmesoflexus (or fossette) developed; the protolophule II dividing the premesoflexus into the labial flexus (or fossette) and lingual fossette; the short paraflexus about one-third to one-half of the tooth crown width and positioned anterior to the hypoflexus; the hypoflexus about two-fifths of the tooth crown width with its labial end being opposite to the lingual fossette of the premesoflexus; lower teeth having five main lophids (anterolophid, metalophid, mesolo-

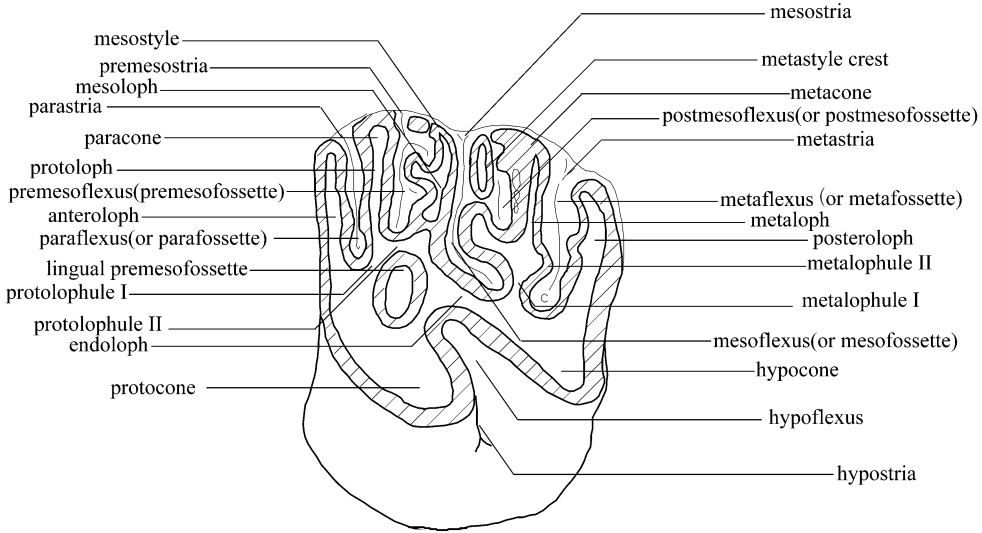


Fig. 1. Terminology of the upper cheek tooth of *Propalaeocastor*.

phid, hypolophid, and posterolophid), a metastylid crest, and an endostylid crest; the preparafossettid, premesofossettid, and postmesofossettid present in addition to the paraflexid, mesoflexid, metaflexid, and hypoflexid; all main lophs and lophids on the cheek teeth transversely or nearly transversely extended.

**INCLUDED SPECIES:** *Propalaeocastor butselensis* (Misonne, 1957), *P. shevyrevae* (Lytshev and Shevyreva, 1994), *P. aff. shevyrevae* (Lytshev and Shevyreva, 1994), *P. zaisanensis* (Lytshev and Shevyreva, 1994), and *P. irtyshensis*, n.sp. *Steneofiber aff. dehmi* Freudenberg, 1941 is probably a species of *Propalaeocastor* (see below).

**GEOLOGICAL RANGE:** Early Oligocene.

***Propalaeocastor irtyshensis*, new species**

Figures 1–4, table 1

**HOLOTYPE:** A right maxilla with P4–M3, IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences) V13690.

**TYPE LOCALITY AND AGE:** Locality XJ200203 (=200203 [Ye et al., 2002], 47°50.454'N, 86°40.883'E), 20 km northwest to Burqin City, Xinjiang. Early Oligocene.

**ETYMOLOGY:** After the name of the Irtysh River.

**DIAGNOSIS:** Brachyodont *Propalaeocastor*

with size and dental morphology similar to those of *Propalaeocastor butselensis*. Differing from *Propalaeocastor butselensis* in having higher tooth crown, much longer mesoflexus that bends posteriorly, more developed anteroloph, posteroloph, metastyle crest, and paraflexus, more folded enamel, and the lingual end of the mesoflexus connected the lingual premesofossette. Differing from “*Steneofiber aff. dehmi*” in having lower tooth crown, smaller size, shorter mesoflexus and more transversely extended main lophs and flexus. Differing from *P. kazakhstanicus*, *P. shevyrevae*, and *P. aff. shevyrevae* mainly in having lower tooth crown. In contrast, *P. kazakhstanicus* possesses longer and anteroposteriorly more stretched mesoflexus; *P. shevyrevae* has a postmesofossette on the P4 and closed metaflexus to form fossette at all stages of wear on M1–2; *P. aff. shevyrevae* has the mesoflexus being confluent with the labial premesofossette and has a postmesofossette on P4 and the labially always closed paraflexus on M1–2.

**DESCRIPTION**

The root of the zygomatic arch is preserved on the fragmentary maxilla and is anterolateral to the P4. A distinct posterior palatine foramen is medial to the position between M1 and M2 at the maxillary–palatine

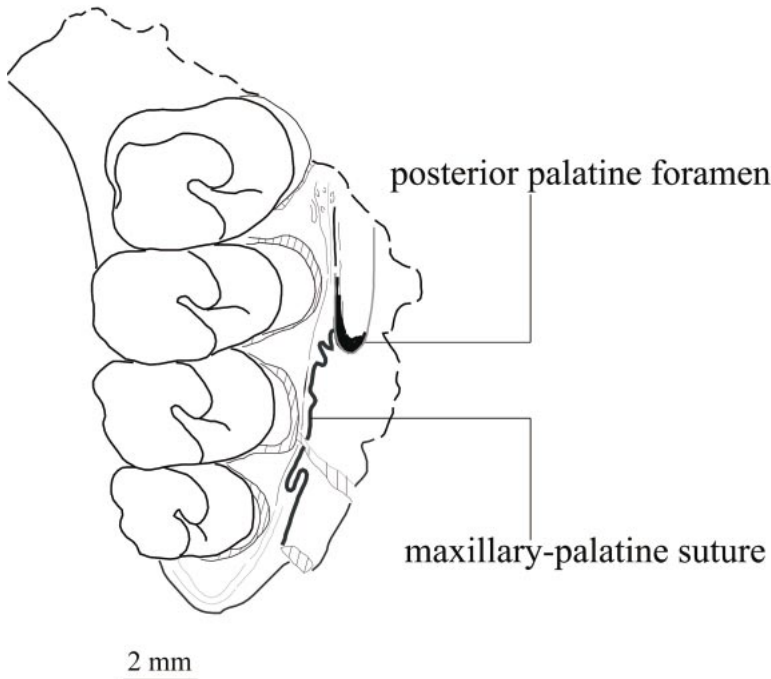


Fig. 2. Sketch showing the maxillary-palatine suture, the posterior palatine foramen, and the groove leading anteriorly from the foramen on the palate of *Propalaeocastor irtyszensis*, n.sp. (IVPP V13690).

suture on the palate. A groove leads anteriorly from the foramen.

Measurements of individual tooth are presented in table 1. The total length of P4-M3 is 11.75 mm along the occlusal surface or 12.15 mm along the crown base. The teeth are moderately or slightly worn so that all lophs and fossettes are clear. Cheek teeth are brachydont with the lingual side being higher than the labial. The length of each tooth is greater than its lingual crown height (the teeth are only lightly or at the most moderately worn). The occlusal surface of the cheek tooth is slightly arched, with the labial side being more ventral. The enamel-dentine boundary is distinct on all teeth. All cheek teeth are wider than long. Cheek tooth enamel is folded. The enamel folds are more complicated on the labial half than the lingual side of the tooth, whereas the enamel around the protocone and hypocone is much thicker than that distributed on the labial half of the tooth. Cement filling is absent.

Four main striae are present on each upper cheek tooth: parastria, mesostria, metastria, and hypoostria. The hypoostria, mesostria, and

metastria are distinctly present on all four cheek teeth. The hypoostria is the deepest stria, and deepest on P4, about three-fourths of the crown height, while it is about a half of the crown height on the other teeth. The mesostria is also deepest on P4, around a half the labial crown height; it is most shallow on M1, about one-fifth of the crown height. The metastria is deepest on M3, about three-fifths of the crown height and decreased in depth from M2 to P4. The parastria is the shallowest stria; it is deepest on P4 and absent on M1 and M3. In addition, a shallow "premesostria" is present on M2 and M3. The measurements of each stria are presented in table 1.

Although broken, the preserved maxilla shows no sign of P3. There is no contact facet on the anterior surface of P4. In addition, unlike molars in which the enamel along the anterior edge thins at the area contacting the anterior tooth, the enamel along the anterior edge of P4 is thick and even. Thus, we consider that the individual does not have a P3 in life.

P4 is subquadrate, molariform, and the

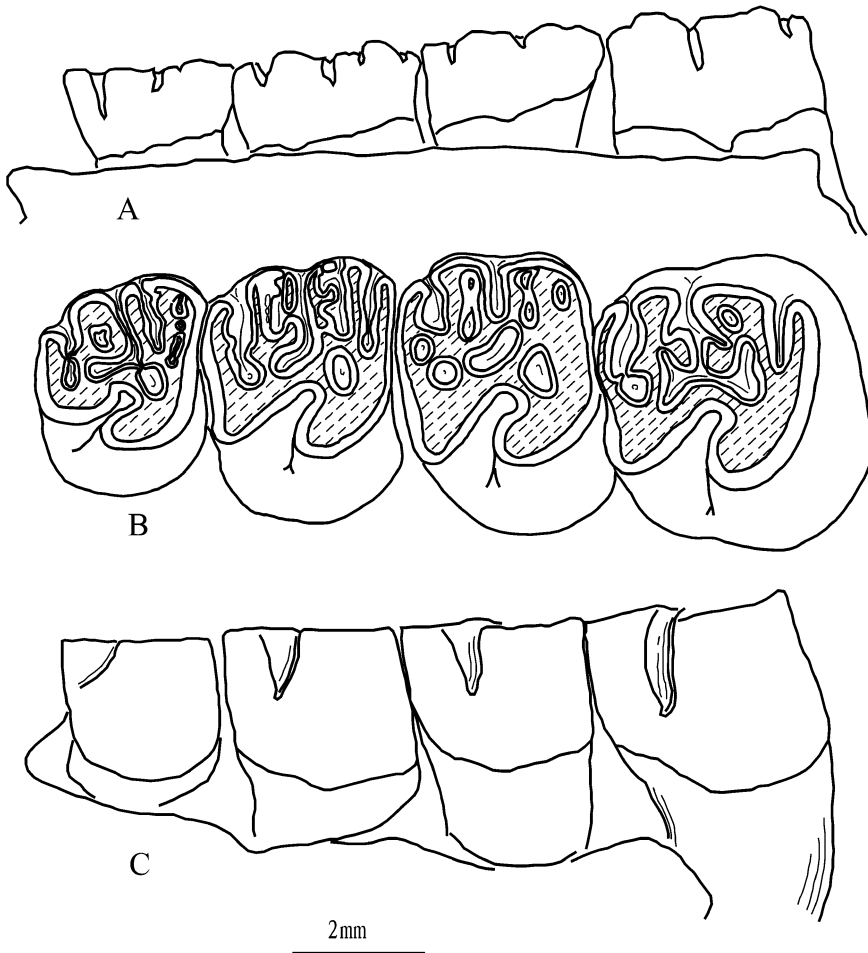


Fig. 3. Line drawing of right P4–M3 of *Propalaeocastor irtyshensis*, n.sp. (IVPP V13690). **A**, Labial view; **B**, occlusal view; **C**, lingual view.

largest cheek tooth. It is supported by three thick roots: one lingual and two labial. As in molars, the P4 protocone is the largest cusp of the tooth and has a rounded lingual contour; its lingual side is the highest region of the tooth crown. In contrast, the hypocone is angular lingually. The protocone and hypocone are separated by a deep hypoflexus that extends anterolaterally. On the lingual surface the hypostria between the protocone and hypocone is about three-fourths of the crown height, the deepest of all cheek teeth. The protocone and hypocone are connected by a curved endoloph.

The transverse anteroloph and protoloph on P4 are complete and between them is a

narrow paraflexus which opens labially and extends about two-fifths of the crown surface width at the current stage of tooth wear. The paracone is located at the labial end of the protoloph and is confluent with the mesostyle through a strong crest that closes the premesoflexus labially. The protolophule I is connected lingually with the anterior arm of the protocone or the anteroloph. The protolophule II, which is more labial than in molars, connects the protoloph and mesoloph and thus separates the premesoflexus from the lingual premesoflexus. The labial premesoflexus is a circular, shallow lake, whereas the lingual premesoflexus is transversely elongate and very deep. Because the enamel

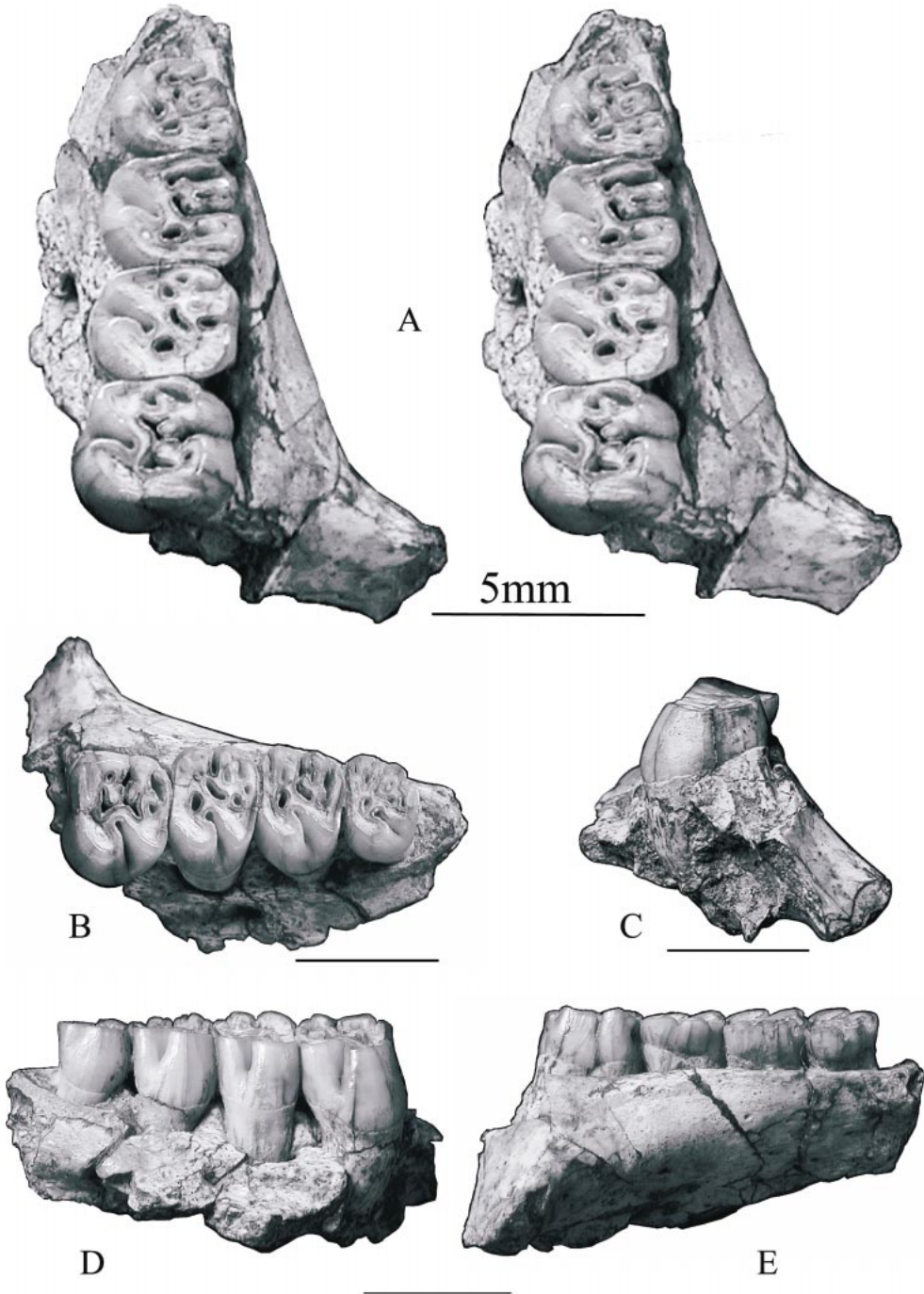


Fig. 4. Right upper jaw with P4–M3 (IVPP V13690) of *Propalaeocastor irtyshensis*, n.sp. **A**, Occlusal view of right P4–M3 (stereograph); **B**, occlusal view of right P4–M3 (inverse); **C**, anterior view of P4, showing unihypsodonty; **D**, lingual view; **E**, labial (buccal) view. All scale bars = 5 mm.

TABLE 1  
Measurements (in mm) of Upper Cheek Teeth of *Propalaeocastor irtyshensis*, n.sp. (IVPP V13690)

	P4	M1	M2	M3
Length x Width				
at surface	3.42 x 3.33	2.95 x 3.50	2.93 x 3.23	2.45 x 2.93
at base	3.62 x 4.74	2.95 x 4.50	2.93 x 4.30	2.45 x 3.62
Height				
labial	1.96	1.47	1.50	1.27
lingual	2.93	2.35	2.55	2.30
Parastria	0.38	—	0.175	—
Premesostria	—	—	0.175	0.16
Mesostria	0.88	0.22	0.38	0.28
Metastrria	0.05	0.28	0.35	0.75
Hypostrria	1.75	1.13	1.16	0.59 <sup>a</sup>
Maximum height/ maximum length indices	0.81	0.80	0.87	0.94

<sup>a</sup>Estimated.

ridge of the endoloph does not merge with that of the mesoloph, the lingual premesoflexus is therefore not closed, but has a narrow gap at its posterior side, confluent with the mesoflexus. There seems no sign of closing of the lingual premesoflexus with the increased wear of this tooth. This condition is similar to that of M3 but differs from M1 and M2 in which the mesoflexus and lingual premesoflexus are completely separated. The mesoflexus of P4 is deep and opens labially. On the labial side of the crown, the mesostria is about half of the crown height. The mid-portion of the mesoflexus is nearly closed by an enamel spike extending posterolingually from the mesoloph and an enamel loop growing out of the metaloph. The enamel loop originates at the same place as the metastyle crest would have joined, but it extends anteromedially rather than labially. The postmesoflexus is a small fold confluent with the mesoflexus. The metalophule I and metaloph form a continuous, transverse crest extending from the hypocone to the metacone. The metalophule II extends from the metaloph posteriorly to join the posteroloph and divides the metaflexus into a lingual, circular fossette and a labial, elongate fossette. The metalophule II is notched so that the lingual and labial portions of the metaflexus are partially confluent. The posteroloph joins the

metacone to close the metaflexus labially; a shallow metastrria is present at the joint.

The molars decrease in size posteriorly. M1 is the most worn cheek tooth and has the lowest crown but highest root exposed on the lingual side. It is shorter but wider than P4 and differs from P4 in several aspects. The paraflexus is a small, enclosed fossette at the anterolabial corner. The premesofossette is narrow and transverse, and is labially enclosed. The lingual premesofossette is complete and deep. The mesoloph is as narrow as the metastyle crest, lies within the anterior half of the tooth, and completely joins the endoloph. The mesoflexus is divided by a ridge that connects the mesoloph and the metastyle crest into a lingual, kidney-shaped fossette and a labial, transverse trench that partially opens labially. The metastyle crest and metaloph are complete and nearly parallel; they confine respectively a narrow postmesoflexus anteriorly and posteriorly. In addition to the metalophule II, there is another lophule, here not termed, that connects the metaloph and the posteroloph. Thus there are two lingual metafossettes on M1.

Probably because of the lower degree of wear, M2 differs from M1 in having a transversely longer paraflexus and premesoflexus and more labially open mesoflexus and metaflexus. However, other differences of struc-

tures are not wear related, including an incomplete metastyle crest, an incomplete metalophule II, and a continuous mesoflexus (lack of the ridge connecting the metastyle crest and mesoloph).

M3 differs from M1 and M2 mainly in being reduced posteriorly, with a rounded posterior contour. Unlike M1 and M2, the lingual side of the hypocone is rounded, rather than angular. The paraflexus becomes beaded fossettes. The mesoflexus is L-shaped, with the turning apex narrowly confluent with the lingual premesofossette. The postmesofossette is complete and circular. The metalophule II is incomplete. The metaflexus is about a half of the tooth width and is more open than that of M1 and M2. The hypoflexus is somewhat constricted at its midpoint.

### COMPARISONS

Korth (2001) has recently divided Castoridae into four families, Agnotocastorinae, Palaeocastorinae, Castoroidinae, and Castorinae, and placed *Steneofiber* in Castorinae. According to Korth (2001), Agnotocastorinae possesses several primitive characters, such as presence of P3 or dP3, P4 subequal in size to molars, the posterior palatine foramen within the palatine bone, and smooth palatal surface. In contrast, Castorinae, Castoroidinae, and Palaeocastorinae share the derived conditions of these features, including loss of dP3 and P3, P4 the largest upper cheek tooth, the posterior palatine foramina within the palatine-maxillary suture, and the palatal surface grooved. The new species we described here has all the derived conditions. Although McKenna and Bell (1997, electronic version) place *Steneofiber* in Castoroidinae and Korth (2001) distinguishes the three non-agnotocastorine subfamilies based on postcranial characters, we consider *Propalaeocastor irtyshensis* to belong to Castorinae for the following reasons: (1) *Steneofiber* is probably derived from "*Asteneofiber*" *butselensis* (Hugueney, 1999), (2) *Asteneofiber* is here considered synonymous with *Propalaeocastor*, and (3) Xu (1995) suggested that *Steneofiber* should be placed in Castorinae because *Steneofiber* and *Castor* were shown to form a clade in his phylogenetic analysis. Among early castorines, *Propalaeocastor ir-*

*tyshensis* is most similar to those from Europe and Kazakhstan that have usually been referred to *Steneofiber*, such as *P. butselensis* (= *Steneofiber butselensis*; see below for discussion) from the earliest Oligocene (MP21) of Belgium, *P. kazakhstanicus* (= *S. kazakhstanicus*), *P. shevyrevae* (= *S. shevyrevae*), *P. aff. shevyrevae* (= *S. aff. shevyrevae*), and *P. zaissanensis* (= *S. zaissanensis*) from the Early Oligocene of Kazakhstan. These species share the following characters: (1) The cheek teeth are brachyodont to mesodont. (2) In addition to the five main lophs (anteroloph, protoloph, mesoloph, metaloph, and posteroloph), minor ridges are also present, including the metastyle crest, protolophule I and II, and metalophule I and II. (3) All main lophs and the metastyle crest extend transversely. (4) The paraflexus is transversely short. (5) The premesoflexus is divided into the labial premesoflexus (or premesofossette) and the lingual premesofossette. (6) The labial end of the hypoflexus is opposite to the lingual premesofossette. (7) The tooth enamel is folded. Given these similarities, our comparison will focus on the species of *Propalaeocastor* and those we consider to be *Steneofiber*, including *S. kumbulakensis*, *S. dehmi*, and *S. eseri*.

Based on the study by Hugueney (1975) and our observation on a cast of *Propalaeocastor butselensis* (a fragmentary right maxilla with worn M1–M2, a courtesy from Wang Ban-Yue) from the earliest Oligocene of Hoogbutsel of Belgium, it is clear that *P. irtyshensis* is comparable to *P. butselensis* in size. The measurements of the cast are: M1, 3.08 × 3.62, 4.50 (length × width at the crown surface, width at the crown base); labial height 1.12; lingual height 2.00; the index of maximum height/maximum length 0.65; M2, 2.90 × 3.23, 3.96; labial height 1.17; lingual height 1.86; index of maximum height/maximum length 0.64. *P. irtyshensis* differs from *P. butselensis* in having higher tooth crown, much longer mesoflexus that bends posteriorly, more developed anteroloph, posteroloph, metastyle crest, and paraflexus, more folded enamel, and the lingual end of the mesoflexus confluent with the lingual premesofossette. Although M1 and M2 on the cast of *P. butselensis* are worn at a greater degree than those of *P. irtyshensis*,



the mesostria extends to the half way point of the crown height and the metastria is almost absent. In contrast, the mesostria is short and the metastria on molars of *P. irtyshensis* is well developed.

*Propalaeocastor kazachstanicus* from Zaissan Basin and Central Kazakhstan is also similar to *P. irtyshensis* in size, but has higher tooth crown. The maximum height/maximum length indices of moderately worn cheek teeth of *P. kazachstanicus* are M1/2: 1.46, M3: 1.20 (Lytshev and Shevyreva, 1994: 85), which are apparently greater than those of *P. irtyshensis* (P4: 0.81; M1/2: 0.80–0.87; M3: 0.94). Moreover, the mesoflexus of *P. kazachstanicus* is longer and anteroposteriorly more stretched; the parastria, mesostria, and metastria either disappear or are shallow. On moderately worn cheek teeth of *P. irtyshensis*, however, the mesoflexus is shorter and the mesostria, metastria, and sometimes parastria remain open.

Compared to *P. irtyshensis*, *P. shevyrevae* from Talagay of Zaissan Basin also has greater maximum height/maximum length indices: P4: 0.81–0.92; M1/2: 1.21–1.32 (Lytshev and Shevyreva, 1994: 91). P4 of *P. shevyrevae* possesses a postmesofossette and the metaflexus on M1 and M2 is closed to form a fossette at all stages of wear. In contrast, the metaflexus remains open labially as the metastria with various depths on the molars and the postmesofossette is absent on P4 of *P. irtyshensis*.

*Propalaeocastor* aff. *shevyrevae* from Podorozhnik and Novei Podorozhnik of the Zaissan Basin is similar to *P. irtyshensis* in size, but differs from the latter in having higher tooth crown. The maximum height/maximum length index of *P. aff. shevyrevae* is 1.04 for nearly unworn P4, 1.00 for moderately worn P4, and 1.53 for moderately worn M1/M2. On the P4 of *P. aff. shevyrevae* the mesoflexus is confluent with the labial premesofossette, the postmesofossette present, and the metastria absent. The paraflexus on M1/M2 is always closed labially. On the P4 of *P. irtyshensis* the mesoflexus is confluent with the lingual premesofossette, the postmesofossette is absent, and the metastria, although shallow, is present. The metastria on the M1–M3 of *P. irtyshensis* is

well developed and the paraflexus opens labially on the less worn P4 and M2.

The *Propalaeocastor zaissanensis* from Talagay of Zaissan Basin is represented by one moderately worn P4, two deeply worn M1 and/or M2, and one moderately worn M3. The description, figures, and measurements provided by Lytshev and Shevyreva (1994: figs. 5, 6; tables 1, 4) show that *P. zaissanensis* is similar to *P. irtyshensis* in size and crown height. Its maximum height/maximum length index is 0.88 for P4 and 0.92 for M3. In addition, the two species are similar in some dental morphology, including the shape of the mesoflexus and hypoflexus, the depth of mesostria and hypostria, the position of the mesoflexus, hypoflexus, premesofossette, and postmesoflexus, the depth of the hypostria, and the relative position of the two fossettes of the mesoflexus on worn M1/2. Moreover, on M3 of both species the mesoflexus is confluent with the lingual premesofossette and a postmesofossette is present. *P. zaissanensis* differs from *P. irtyshensis* in the following aspects: The premesoflexus on worn P4 of *P. zaissanensis* is displayed as two isolated circles whereas the lingual premesoflexus is connected with the mesoflexus on P4 of *P. irtyshensis*; the lingual premesoflexus on the P4 of *P. irtyshensis* does not seem to become an isolated lake after further wear, as it is on M1 and M2. In *P. zaissanensis* the labial premesofossette and lingual metafossette on P4 are larger; the hypoflexus on M1 and M2 is longer, and the M3 hypoflexus is confluent with the mesoflexus (Lytshev and Shevyreva, 1994: fig. 6). The absence of the postmesofossette on M1 and M2 of *P. zaissanensis* probably resulted from deep wear of the teeth.

Recently, “*Steneofiber* cf. *S. butselensis*” was reported from the Buran Svita of Podorozhnik, locality K15, south of Lake Zaissan (Emry et al., 1998: 307, fig. 8I–K). This occurrence is represented by a right P4, a right p4, and a left m1/2. Judging from the figures (no description is provided in the original study), we think those specimens belong to *Propalaeocastor* for the reason given above, and may belong to *P. aff. shevyrevae* from the same locality (Lytshev and Shevyreva, 1994). These teeth appear more derived than

those of *P. butselensis* because the metastyle crest is better developed and the mesoloph is complete on P4.

*P. irtyshensis* is also similar to the Early Oligocene "*Steneofiber* aff. *dehmi*" from Saint-Martin-de-Castillon of France (Hugueney, 1975; MP24) in dental pattern. In both species the metastyle crest is present, the premesoflexus is divided into the labial premesoflexus (or fossette) and lingual premesofossette by the protolophule II, the labial end of the hypoflexus is opposite to the lingual premesofossette, and finally the tooth enamel is folded. However "*S.* aff. *dehmi*" differs from *P. irtyshensis* in having higher tooth crown (based on Hugueney's [1975] figures; height measurements were not provided), larger size, longer mesoflexus, and main lophs and flexus extended slightly posterolingually. Given its similarities to the species of the Early Oligocene forms, "*Steneofiber* aff. *dehmi*" may prove to be another species of *Propalaeocastor*, but we choose not to synonymize it in this study.

Among the species of *Propalaeocastor*, it is difficult to make a thorough comparison between *P. irtyshensis* and *P. zaisanensis* and, to some degree, the other species from Kazakhstan because of the originally variable dental morphology of castorids and the isolated teeth with various degrees of wear. Nonetheless, the differences that we recognized above are sufficient to justify the establishment of the new species.

The Late Oligocene *Steneofiber kumbulakensis* from Agypse of the Aral region differs from *P. irtyshensis* in being larger and having higher tooth crown (Lytshev, 1970: table 1; the maximum length/maximum height indices are 1.25 for P4, 1.32 for M1, 1.36 for M2, and 1.22 for M3), longer paraflexus (about two-thirds of the tooth width on all upper cheek teeth), longer mesoflexus which curves backwards and joins to the metaflexus on P4 to form a U shape, and more folded enamel. More importantly, *Steneofiber kumbulakensis* lacks the lingual premesofossette, the labial end of the hypoflexus is opposite to the lingual end of the paraflexus, and lophs extend obliquely.

*Steneofiber dehmi* was based on a juvenile mandible with dentition and two other isolated lower cheek teeth from Gaimersheim

(MP29, Late Oligocene) of Germany (Freudenberg, 1941); therefore it is difficult to compare the type specimens with that of *P. irtyshensis*. Specimens of *S. dehmi* are now discovered from several Late Oligocene localities of Germany, Switzerland (Engesser et al., 1984, 1993), France, and Turkey (Ünay, 1989). Hugueney (1975) noted that unworn M1–2 and M3 of *S. dehmi* from Heute-Provence retain double connections of the protoloph and metaloph with lingual cusps. It implies that primitive characters remain only on unworn teeth. However the upper and lower cheek teeth rows from Mine de Rochette of Switzerland (Engesser et al., 1984: 14, fig. 5) display a larger size, higher crown, and simpler dental pattern in which the metastyle crest, the premesoflexus, and the postmesoflexus are absent, the paraflexus and the hypoflexus are longer, the labial end of the hypoflexus is opposite to the lingual end of the paraflexus, and the main lophs extend more obliquely.

*Steneofiber eseri* (Von Meyer, 1846) from the Early Miocene (MN2) of Örlinger Tal near Ulm in Germany is the type species of the genus. In McKenna and Bell (1997, electronic version) a note, based on Stirton (1935), indicates that the type species of *Steneofiber* is *S. castorinus* Pomel, 1846, from Aquitanian Saint-Gerand le Puy. According to Stefen (1997: 5) and Hugueney (1999: 284), however, Pomel's paper appeared in 1847 and *S. eseri* has priority over *S. castorinus*. In addition to the type specimens, Hugueney (1975) and Stefen (1997) made further investigations of *Steneofiber eseri* from Poncenat and Örlinger Tal, respectively. Based on their work, we found that the dental pattern of lightly worn upper cheek teeth of *S. eseri* is similar to that of *P. irtyshensis* in having five main lophs, a vestigial metastyle crest, a premesofossette, and a postmesofossette. In *S. eseri*, however, the protoloph and mesoloph merge into one, and the metastyle crest, premesofossette, and postmesofossette disappear soon after wear of the tooth so that the cheek tooth has only four lophs. *S. eseri* differs from *P. irtyshensis* considerably in having a much larger size, much higher tooth crown, and longer paraflexus. In addition, the labial end of the hypoflexus in *S. eseri* is opposite to the lingual end of the paraflexus,

protoloph and metaloph are not doubled, the lingual premesofossette is absent, and lophs extend medioposteriorly.

## DISCUSSION

### TAXONOMY OF *PROPALAEOCASTOR*

The earliest known castorine of Europe is *Steneofiber butselensis* from the earliest Oligocene (MP21) of Hoogbutsel-Hoeleden of Belgium (Misonne, 1957). Realizing differences between *S. butselensis* and other species of the genus, Ginsburg (1971: 2161) pointed out that “le *Steneofiber butselensis* du Sannoisien de Hoogbutsel en Belgique ne nous paraît pas appartenir à ce genre”, but he did not rename the taxon. Kretzoi (1974: 426–427) proposed *Asteneofiber butselensis* to replace “*S. butselensis*” and assigned “*S. butselensis*” as the type species of *Asteneofiber*. Kretzoi provided some diagnostic characters to distinguish *A. butselensis* from other taxa of Castorinae, such as smaller size, lower tooth crown, and complex dental pattern resembling that of Theridomyinae. Unaware of Kretzoi’s work, Huguene (1975) continued to use *Steneofiber butselensis* as a valid taxon in her study on material from Hoogbutsel-Hoeleden. She considered that the specimens of *S. eseri* from Saint-Martin-de-Castillon suggested affinity of *S. butselensis* with the *S. eseri* lineage, but agreed with Ginsburg (1971) that *S. butselensis* could be placed in a different genus. *A. butselensis*, as recognized by Kretzoi (1974), gains support in some recent investigations (Huguene and Escuillie, 1995, 1996; Huguene, 1999). Other opinions, however, exist. McKenna and Bell (1997: 129) synonymized *Asteneofiber* with *Steneofiber*. Korth (2001) did not mention *Asteneofiber* in discussion on castorines. Xu (1995) even synonymized *S. butselensis* with *S. castorinus*.

Meanwhile, however, Borissoglebskaya (1967) named a new genus and species *Propalaeocastor kazachstanicus* based on a fragmentary lower jaw with p4 in alveolus and m1–m3 (the type specimen) and some referred specimens (four fragmentary lower jaw, two upper and five lower isolated molars) from the Early Oligocene of Kyzylkak, Turgaysk depression, Kazakhstan. The second species included in the genus is *P. ha-*

*bilis* from Lake Chelkar-Tenize of the same depression (Borissoglebskaya, 1967). In their study of specimens from Maylibay of Zaisan Basin, Lytshev and Shevyreva (1994) synonymized *P. habilis* with *P. kazachstanicus*. Moreover, these authors recognized, as already noticed by Huguene (1975), the similarity between *P. kazachstanicus* and *Steneofiber butselensis* and went further to assign *Propalaeocastor kazachstanicus* to *Steneofiber*.

Having compared known species previously assigned to *Steneofiber*, we come to the conclusion that the Early Oligocene forms represented by “*Steneofiber butselensis*” show significant differences from those represented by *S. eseri* from the Late Oligocene and Early Miocene. As discussed above, dental features and crown heights can distinguish the two groups, which probably represent different evolutionary stages. We consider the Early Oligocene species should be placed in a separate genus. In such a case, *Propalaeocastor* has the priority over *Asteneofiber* as the genus name, even though *P. butselensis* was based on better material and more adequately described and figured (Misonne, 1957; Huguene, 1975) and still provides the morphological basis of the genus for comparisons with other early Oligocene species.

### RELATIONSHIPS OF *PROPALAEOCASTOR* AND *STENEOFIBER*

In the study on Oligocene castorids of Europe Huguene (1975) described “*Steneofiber*” *butselensis* from Hoogbutsel-Hoeleden (MP 21), *S. aff. dehmi* from Saint-Martin-de-Castillon (MP 24), and *S. dehmi* from Gaimersheim (MP 29), and discussed their affinities and evolution tendency. Huguene (1975: 802) summarized that the teeth with simplified and oblique lophs characterizing the Aquitanian *S. eseri* are probably evolved from the more primitive pentalophodont dental pattern of “*S.*” *butselensis* and that the dental structure of the Early Miocene *S. eseri* has already developed in the Late Oligocene *S. dehmi*. Huguene (1999: 285) recognized *Asteneofiber* as a valid genus and mentioned that “*S. eseri* seems to derive in situ from the Oligocene *S. dehmi* Freudenberg, 1941

which displays nearly the same dental pattern but is smaller; this form derives itself from the more complicated *Asteneofiber butselensis* (Misonne, 1957) from MP21 (misprinted as MP20 in Hugueney, 1999), the first castorid to be mentioned in Europe at the very beginning of the Oligocene." Given that *Asteneofiber* is a junior synonym of *Propalaeocastor*, the evolutionary stages of these castorids proposed by Hugueney (1999) can be restated as from *P. butselensis* at the beginning of Early Oligocene (MP 21), to "*S. aff. dehmi*" in late Early Oligocene (MP 24), to *Steneofiber dehmi* in Late Oligocene (MP 29), and finally to *S. eseri* in Early Miocene (MN 2). Although vestigial, some primitive features, such as the division of the premesoflexus and the opposition of the labial end of the hypoflexus to the lingual premesofossette, are still present on unworn or lightly worn upper cheek teeth of species of *Steneofiber* including *S. dehmi* and *S. eseri*. *Steneofiber* certainly displays more derived features than does *Propalaeocastor*. These include larger size, higher tooth crown, oblique extensions of main dental lophs, upper cheek teeth with four principal lophs (owing to the merging of the protoloph and mesoloph, weakness or absence of the metastyle crest), absence of the premesoflexus (or fossette) and postmesoflexus, longer paraflexus, opposition of the labial end of the hypoflexus to the lingual end of the paraflexus on upper cheek teeth, and weakness or absence of the lower cheek tooth metastylid crest, endostylid crest, preparafossettid, and pre- and postmesofossettid.

As we recognize here, species of *Steneofiber* include *S. dehmi*, *S. eseri*, and *S. depereti* of Europe and *S. kumbulakensis* of Kazakhstan. The geological distributions of this genus range from Late Oligocene to Early Miocene. Species of *Propalaeocastor*, as we consider here, are only found in the Early Oligocene.

Hugueney (1975) thought that the Early Oligocene castorid *Agnotocastor* from North America, *Steneofiber* (partly = *Propalaeocastor* in our usage) from Europe, and *Propalaeocastor* from Asia belong to different lineages. When additional and better material was found from Kazakhstan, however, Lytshnev and Shevyreva (1994) synonymized *Pro-*

*palaeocastor* with *Steneofiber*. Based on our analyses, those species should be assigned to *Propalaeocastor*, including *P. kazachstanicus*, *P. shevyrevae*, *P. aff. shevyrevae*, and *P. zaissanensis*. *P. irtyshensis* is morphologically intermediate between European *P. butselensis* and "*Steneofiber aff. dehmi*", and is also similar to Asian species, particularly *P. zaissanensis*, as we compared above. The similarities shared by these Early Oligocene Asian and European castorids indicate that they belong to one lineage.

#### RELATIONSHIP OF *PROPALAEOCASTOR* TO AGNOTOCASTORINAE

As we mentioned above, Korth (2001) assigned *Propalaeocastor* to tribe Anchitheriomiyini under the subfamily Agnotocastorinae. However the maxilla of *P. irtyshensis* from Burqin shows characteristic features of castorines: absence of P3, P4 being the largest cheek tooth, posterior palatine foramina within the palatine-maxillary suture, and the grooved palatal surface. We consider therefore that *Propalaeocastor* should be assigned to Castorinae, not to Agnotocastorinae.

Xu (1995: 15) also excluded *Propalaeocastor* from Castoridae in a phylogenetic analysis of the family because he considered that the mandibles of this genus "do not show a digastric eminence." However, we believe that the eminence is clearly present on the specimen figured by Borissoglebskaya (1967: 131, fig. 1). Thus, there seems no evidence to exclude *Propalaeocastor* from Castoridae.

#### AGE IMPLICATIONS

Small mammals associated with *Propalaeocastor irtyshensis* from locality XJ200203 of Burqin include (preliminary list): *Palaeoscaptor cf. acridens*, *Tupaiodon cf. morrisoni*, *Desmatolagus aff. vetustus*, *Prosciurus? sp.*, *Karakoromys decessus*, *Cyclomylus lohensis*, *Cricetops dormitor*, *Eucricetodon asiaticus*, *E. caducus*, *Ulaancricetodon cf. badamae*, *Parasminthus aff. tangingoli*, *P. aff. asiae-centralis*, *Tatalsminthus*, n.sp., and Sciuridae gen. et sp. indet.

Among these taxa Matthew and Granger (1923, 1924) already described *Palaeoscaptor acridens*, *Tupaiodon morrisoni*, *Karakoro-*

*mys decessus*, *Cricetops dormitor*, *Eucricetodon asiaticus* from Hsanda Gol Formation of Central Mongolia. Höck et al. (1999) made a multidisciplinary study of the Hsanda Gol and Loh Formations in the area of Valley of Lakes of Central Mongolia. Seven informal biozones were established throughout the Hsanda Gol and Loh Formations based on the newly, sequentially collected rodents. Among the rodents, *Cyclomytus*, *Karakoromys decessus*, *Cricetops dormitor*, *Eucricetodon asiaticus*, and *E. caducus* found in Biozones A and B are present in the Burqin fauna. These taxa, with the exception of *Cyclomytus*, are restricted only in Biozones A and B. Recently Erbajeva and Daxner-Höck (2001) reported *Desmatolagus* cf. *D. vetustus* from Biozone A, and Daxner-Höck (2000, 2001) described a new cricetid, *Ulaancricetodon badamae*, from Biozones A and B and a new zapodid, *Tatalsminthus khandae*, from Biozone A. We noticed that *Tataromys* is absent in both Biozone A and XJ200203 Burqin fauna, which occurs in the Hsanda Gol Formation in Biozone B and younger biozones. *Desmatolagus vetustus*, a Late Eocene taxon originally from Ulan Gochu of China (Burke, 1941), is absent in Biozone B. *Parasminthus* aff. *tangingoli* and *P.* aff. *asiae-centralis* in Burqin fauna are distinctly more primitive than *Parasminthus tangingoli* and *P. asiae-centralis* from Taben Buluk, respectively. Comparing these species collectively, the Burqin fauna is best correlative to Biozone A of Hsanda Gol Formation. According to Höck et al. (1999), Biozone A is below the basalt I that is dated 31.5 Ma.

Although *Propalaeocastor irtyshensis* appears more derived than European *P. butselensis* of the earliest Oligocene and slightly more primitive than “*Steneofiber* aff. *dehmi*”, this alone does not necessarily indicate that *P. irtyshensis* must be younger than *P. butselensis* in age. *Propalaeocastor zaissanensis*, which is most comparable to *P. irtyshensis* among Asian species of *Propalaeocastor*, is from the Buran Svita of Zaissan Basin. According to Lytshev and Shevyreva (1994) and Shevyreva (1994), the associated fauna of *Propalaeocastor* in Zaissan Basin consists of *Cyclomytus mashkovae* (= *C. lohensis*; Wang, 2001), *Beatomys gloriadei* (= *Tsaganomys altaicus*; Wang, 2001), *Crice-*

*tops collator* (= *C. dormitor*; McKenna et al., 1996), *Leidymys asybaevi*, *Woodomys dimetron* (= *Karakoromys decessus*; Wang, 1997b), *Muratkhanomys velivolus* (= *Tataromys sigmodon*; Wang, 1997b), *M. kulgayniae* (= *Tataromys plicidens*; Wang, 1997b), *M. djanarae*, *Roborovskia collega* (= *Tataromys plicidens*; Wang, 1997b), *Tataromys raeda* and *T. boreas* (= *Tataromys sigmodon*; Wang, 1997b). Buran fauna appears younger than Burqin fauna in age because of the occurrence of *Tataromys* that is more derived than *Karakoromys*.

The faunal sequence of Chinese Early Oligocene consists of Kekeamu (Wang, 1991), early Wulanbulage, and late Wulanbulage faunas ranging from the earliest to latest (Wang, 1992, 1997a). The early Wulanbulage fauna is characterized by the appearance of *Cyclomytus*, *Parasminthus tangingoli*, while the late Wulanbulage fauna is characterized by the appearance of *Tsaganomys*, *Cricetops*, *Eomys*, *Tataromys*, *Bounomys*, and *Sinolagomys*. *Cyclomytus* and *Cricetops* became extinct in Asia by the end of Early Oligocene (Wang, 1997a, 1997b, 2001). The absence of *Tataromys*, *Tsaganomys*, *Eomys*, *Bounomys*, and *Sinolagomys*, and the presence of *Tupaiaodon*, *Desmatolagus* cf. *vetustus*, *Prosciurus?* sp., *Karakoromys decessus*, *Eucricetodon asiaticus*, and *E. caducus* in Burqin fauna suggested an age equivalent to the early Wulanbulage fauna or to Kekeamu fauna, which is currently considered the earliest Oligocene in China (Wang, 1991).

To sum up, the Burqin fauna is correlative to Biozone A in the Hsanda Gol Formation of Mongolia and to the early Wulanbulage or Kekeamu faunas of China, but is older than the Buran fauna of Kazakhstan. It is probably early Early Oligocene and is older than 31.5 Ma.

#### BIOGEOGRAPHIC IMPLICATIONS

Many lines of evidence have pointed to a global cool-off through the Eocene–Oligocene boundary about 33.5 m.y. ago (Prothero and Berggren, 1992), which is the greatest climate shift of the Cenozoic Era, characterized by a 13°C drop in mean annual temperature and vegetation changes from Eocene warm, dense forests to Oligocene cold, open

grasslands (Prothero and Heaton, 1996). In Asia, a prominent change of terrestrial faunas has been recognized and named as the Mongolian Remodelling (Meng and McKenna, 1998), which is characterized by the shift from Eocene perissodactyl-dominant faunas to Oligocene rodent-lagomorph dominant faunas. In Europe, a large-scale faunal restructuring, the *Grande Coupure*, is present across the Eocene–Oligocene boundary, roughly corresponding the global cool-off (Stehlin, 1909; Lopez and Thaler, 1974; Russell et al., 1982; Hooker, 1992; Legendre and Hartenberger, 1992). Both events were believed linked with the global climate change across the Eocene–Oligocene boundary (Meng and McKenna, 1998).

The faunas discovered from Burqin and Zaissan basins also reflect such faunal turnovers. The Late Eocene faunas were dominant with large perissodactyls, whereas the early Oligocene faunas are rich in small rodents and lagomorphs (Emry et al., 1998; Ye et al., 2002). Given their geographic locations, the similar Eocene–Oligocene faunal structures in Burqin and Zaissan basins support the proposal that the European *Grande Coupure* and Asian Mongolian Remodelling are related and probably linked to the same global cooling event across the Eocene–Oligocene boundary (Meng and McKenna, 1998).

A specific issue is the direction of dispersal for early castorids during this period of time. Because the Asian *Propalaeocastor*, including *P. irtyschensis*, is more derived than European *P. butselensis*, one may infer that the Asian castorids were immigrants from Europe. However, as has been recognized in many studies that most of the European Oligocene taxa after the *Grande Coupure* were immigrants from Asia or from North America via Asia (Stehlin, 1909; Savage and Russell, 1983), it is probable that the European castorids are among the immigrants from Asia after the *Grande Coupure*. The earliest record of castorids, noted as *Castoridae* indet. (McKenna and Bell, 1997, notes in the electronic version; personal commun. with Shevyreva, 1981), is from the Kusto Svita, Zaissan Basin. The Kusto Svita is correlative to the Late Eocene Mongolian Ergilianian (Emry et al., 1998). We are not aware of a

formal description of the Kusto castorid, but if confirmed, that record adds to the evidence for dispersal of Asian castorids to Europe.

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