

The revision of the Early Miocene beavers (Castoridae, Rodentia, Mammalia) from the North Aral Region

Alexey V. Lopatin

ABSTRACT. The results of the revision of the Early Miocene beavers (Castoridae) from the Aral Svita of the Akespe and Altynshokysu localities (North Aral Region, Kazakhstan) show the presence of three species: *Steneofiber kumbulakensis* (Lytshev, 1970), *S. schokensis* (Bendukidze, 1993) and *Asiacastor* sp. The study of the dental morphology variability of *S. kumbulakensis* during the wear process suggests that *Capacikala sajakensis* Bendukidze, 1993 is the junior subjective synonymous of this species. *Capatanka schokensis* Bendukidze, 1993 is transferred to the genus *Steneofiber*.

KEY WORDS. *Steneofiber*, *Asiacastor*, Castoridae, Rodentia, Early Miocene, North Aral Region, Western Kazakhstan.

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Ревизия раннемиоценовых бобров (Castoridae, Rodentia, Mammalia) Северного Приаралья

А.В. Лопатин

РЕЗЮМЕ. В результате ревизии раннемиоценовых бобров (Castoridae) из аральской свиты местонахождений Акеспе и Алтыншоқысу (Северное Приаралье, Казахстан) установлено присутствие трех видов: *Steneofiber kumbulakensis* (Lytshev, 1970), *S. schokensis* (Bendukidze, 1993) и *Asiacastor* sp. Изучение изменчивости морфологии зубов *S. kumbulakensis* в процесс стирания показало, что *Capacikala sajakensis* Bendukidze, 1993 является младшим субъективным синонимом этого вида. *Capatanka schokensis* Bendukidze, 1993 отнесен к роду *Steneofiber*.

КЛЮЧЕВЫЕ СЛОВА: *Steneofiber*, *Asiacastor*, Castoridae, Rodentia, ранний миоцен, Северное Приаралье, Западный Казахстан.

Introduction

At present the families Aplodontidae, Sciuridae, Eomyidae, Zapodidae, Cricetidae, Tachyoryctoididae, Ctenodactylidae and Castoridae make up the rodent assemblage of the Early Miocene (~MN1) Aral Fauna of Western Kazakhstan, North Aral Region (Bendukidze, 1993, 1997; Lopatin, 1996, 1997, 1999, 2000). In quantity of remains, the beavers are dominated among large-sized rodents. Eight forms of Castoridae were described from the Aral Svita by previous investigators (Lytshev, 1970; Bendukidze, 1993): *Steneofiber kumbulakensis* (Lytshev, 1970), *Palaeocastor* sp., *Capatanka schokensis* Bendukidze, 1993, *Capatanka* aff. *schokensis*, *Capacikala sajakensis* Bendukidze, 1993, *Capacikala* aff. *sajakensis*, *Capacikala* cf. *sciuroides* (Matthew, 1907) and *Asiacastor* aff. *orientalis* Lytshev, 1987. The study of the new and large material, collected by the author in Altynshokysu and Akespe localities in 1991–1993, revealed the stages of the ontogenetic development of the occlusal surface structure in the most common Aralian castorid, *Steneofiber kumbulakensis*, and allowed to revise the taxa earlier described on this base.

The dental terminology follows Lytshev & Shevyreva (1994) (Fig. 1). The systematics of the beavers follows Korth (2002). The main material is housed in the collection of the Paleontological Institute of the Russian Academy of Sciences (PIN) in Moscow, Russia. Several samples were collected Dr. Th. Bolliger from Paleontological Institute of the University of Zurich (PIUZ) from Altynshokysu in 1994; they belong to the PIUZ collection.

Systematic Paleontology

Order Rodentia Bowdich, 1821

Family CASTORIDAE Hemprich, 1820

Subfamily Castorinae Hemprich, 1820

Genus *Steneofiber* Geoffroy, 1833

Steneofiber kumbulakensis (Lytshev, 1970) Figs. 1–3, 4A–M, 5.

Propalaeocastor kumbulakensis: Lytshev, 1970: 84, fig.1; 1987: 70, fig.1.

Steneofiber cf. *viciacensis*: Lytshev & Aubekerova, 1971: 14, fig.3.

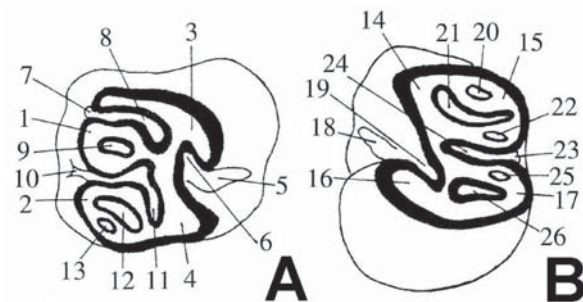


Figure 1. The dental structure of the Castoridae after the example of the middle worn premolars of *Steneofiber kumbulakensis* (Lytshev, 1970).

A — right P4; B — left p4. 1 — paracone, 2 — metacone, 3 — protocone, 4 — hypocone, 5 — hypostria, 6 — hypoflexus, 7 — anterostria, 8 — anteroflexus and anterofossette (parafossette by Huguene, 1999), 9 — parafossette (subparafossette by Huguene, 1999), 10 — mesostria, 11 — mesoflexus, 12 — postmesofossette, 13 — metafossette, 14 — protoconid, 15 — metaconid, 16 — hypoconid, 17 — entoconid, 18 — hypostriid, 19 — hypoflexid, 20 — parafossettid (parafossettid by Huguene, 1999), 21 — metafossettid (parafossettid by Huguene, 1999), 22 — premesofossettid, 23 — mesostriid, 24 — mesoflexid, 25 — postmesofossettid, 26 — entofossettid (metafossettid by Huguene, 1999).

Steneofiber aff. *kumbulakensis*: Bendukidze, 1993: 79, pl.23, fig.6; pl.24, figs.1–3.

Capacikala sajakensis: Bendukidze, 1993: 92, pl.27, figs.1, 2, 4.

Capacikala aff. *sajakensis*: Bendukidze, 1993: 94.

Holotype. Institute of Zoology of the Ministry of Education and Sciences of Republic of Kazakhstan, M-2020/66-Ar, fragmented skull with P4–M3 and p4–m3.

Referred material. A left dentary fragment with p4–m1 (PIN 210/767), and isolated M2 (PIN 210/768) and m2 (PIN 210/769) from Akespe; isolated m2 (PIN 4516/122) and m3 (PIN 4516/121) from Altynshokysu, bone-bearing level I; a right dentary fragment with m1–m2 (PIN 4516/320) and 38 isolated teeth and tooth fragments, eight P4 (PIN 4516/10–12, 307, 308, 315, 316, 339), sixth M1 (PIN 4516/24, 312, 313, 323, 330, 331), three M2 (PIN 4516/314, 317, 322), sixth M3 (4516/29, 310, 319, 332, 336, 337), four p4 (PIN 4516/23, 37, 38, 309), seven m1 (PIN 4516/39, 324, 326, 328, 329, 334, 338), four m2 (PIN 4516/301, 318, 326, 335) and one m3 (4516/333) from Altynshokysu, bone-bearing level IV.

Type locality. Kumbulak, North Aral Region, Kazakhstan.

Stratigraphic level. Aral Svita, Lower Miocene.

Description. Cheek teeth are relatively low crowned (mesodont), without cement. P4 has rectangular shape. The unworn occlusal surface is uneven, complex, with a great number of folds. There is one specimen exhibiting this wear stage (n=1; Fig. 4A). Hypostria ascends on the two thirds of the lingual crown height. Mesostria and anterostria extend dorsally across two thirds of the labial height and approximately one third of the anterolabial height, respectively. Hypoflexus is not very deep, directed sharply anteriorly. It communicates with point of connection of the anteroflexus and anterior arm of the mesoflexus (in anterolingual corner of the occlusal surface) by narrow groove. Posterior arm of the mesoflexus is sharply turned posteriorly. It is separated from the postmesofossette by very thin crest. There are two small fossettes between the posterior arm of mesoflexus

and the postmesofossette. Parafossette consists of three isolated fossettes. Metafossette region is located dorsally to the main plane of the occlusal surface. Metafossette is separated from the postmesofossette by a low crest. The walls of the folds are irregular in shape and plicated.

In the initial wear stage (n=2; Fig. 4B), the plane of occlusal surface of P4 is flat. The connection of anteroflexus and anterior arm of mesoflexus is preserved. Also, these folds are communicated with the end of hypoflexus. Posterior arm of the mesoflexus connects with a small rounded mark, which is located in the posterolingual corner of the occlusal surface. The heights of the flexi are approximately the same as those in unworn tooth. Occasionally, the metafossette is expressed by a small flexus with minute metastria. Parafossette consists of two or three small marks. The place of postmesofossette is occupied by three small oval or drop-shaped marks.

The little worn P4 (n=2; Fig. 4C) has well developed roots and it is characterized by relatively deep hypostria, which does not connect to the anteroflexus and posterior arm of mesoflexus. By a more prominent wear these two folds are connecting lingually. Anterostria is shortened. Posterior portion of mesoflexus adjoins (or associates) postmesofossette, or, correctly, the largest fossette consisting of it. There is one additional small mark between labial portion of mesoflexus and that of postmesofossette. Parafossette consists of two small marks. Metafossette is located slightly dorsally to the main plane of occlusal surface or at same level.

P4 in a middle wear stage (n=2; Figs. 2A, 4D, E) has a very small anterostria. Anteroflexus is compressed in the middle point and considerably enlarged lingually. Parafossette is a small mark with irregular shape. Anteroflexus and mesoflexus are dissociated, and mesoflexus has a small anterior process. Postmesofossette is separated from the mesoflexus, which is curved backward. Postmesofossette is expressed by a small oval mark, as well as the metafossette. In the next stage, hypoflexus became deeper and directed more posteriorly, anteroflexus divided in two parts, the lingual anterofossette and the labial anteroflexus, connecting with small anterostria, the anterior process of mesoflexus disappeared, and the parafossette became rounded. In this stage, hypostria extends across one fourth to half of the lingual crown height. The thickness of the enamel walls became increased. In heavily worn teeth (n=1), the enamel walls of fossettes are strongly elevated above the dentine field, and mesoflexus is closed and forms a mesofossette. A mark is detached from the posterior end of mesofossette. Moreover, the hypoflexus became closed.

The unworn M1 is similar to P4 (n=1). Hypoflexus is a little deepening into the occlusal surface. There are three distinct transverse fossettes in anterior lobe, i.e. wide anterofossette, relatively narrow parafossette, and small premesofossette. They are delimited by small uneven crests. An isolated longitudinal rounded fossette is located lingually. Lingual part of mesoflexus is

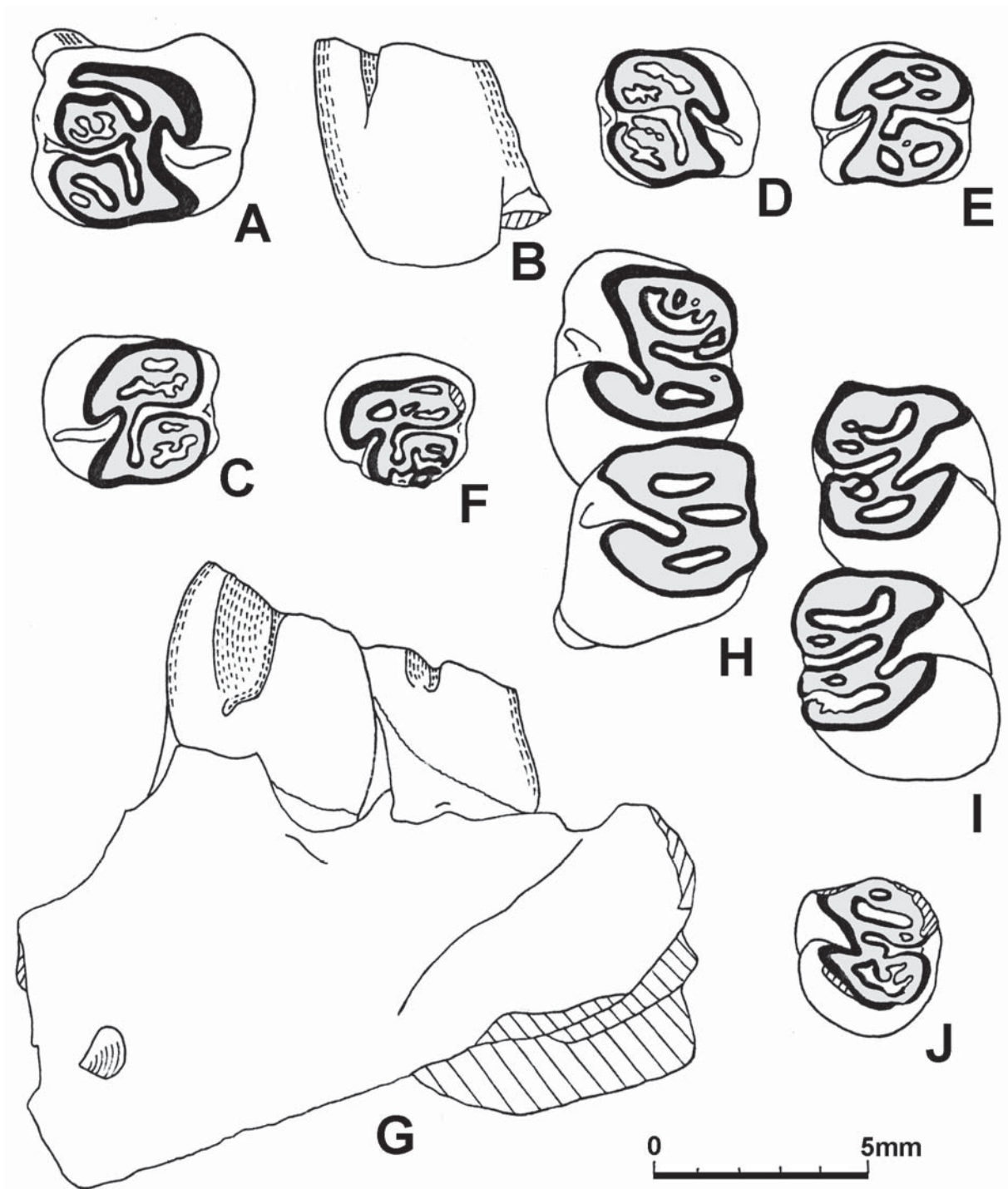


Figure 2. *Steneofiber kumbulakensis* (Lytshev, 1970). Kazakhstan, North Aral Region, Altynshokysu (A–D, F, I, J) and Akespe (E, G, H) localities; Aral Svita, Lower Miocene.

A, B — PIN 4516/11, right P4 (A — occlusal view, B — lingual view); C — PIN 4516/312, left M1; D — PIN 4516/322, right M2; E — PIN 210/768, left M2; F — PIN 4516/310, left M3; G, H — PIN 210/767, fragment of left lower jaw with p4–m1 (G — labial view, H — occlusal view of p4–m1); I — PIN 4516/320, right m1–m2; J — PIN 4516/333, left m3.

sharply turned posteriorly and almost reaches posterior margin of the occlusal surface. Posterior to mesoflexus, there are an isolated postmesofossette with weakly expressed exit, metafossette, which is curved posteriorly in lingual part, and an additional small mark in the most posterior position.

The little worn M1 ($n=2$; Figs. 2C, 4F) have deeper hypoflexus, shorter anterofossette, and merged parafofsette, postmesofossette, and anterolingual fossette. Posterior to mesoflexus, there are three successively located transverse long oval fossettes, namely, postmesofossette, and two-lobed metafossette (the lobes are joined or detached). In this stage, the walls of fossettes retain weak plications. Hypostria and mesostria extend across half of the lingual height and one third of the labial crown height, respectively. The middle worn M1 ($n=1$) retains the same structure pattern, but the lingual part of parafofsette became detached. In a heavy wear stage ($n=2$), posterior part of mesoflexus is detached, hypostria is shortened (it runs across $1/5$ lingual height), hypoflexus is very deep, and occlusal surface became more wide in outline.

The unworn M2 ($n=1$) is similar to M1 in structure. Anteroflexus has a weak expressed exit on anterolabial side. Lingual part of this fold is expressed by detached anterolingual fossette. Parafofsette is closed. Mesoflexus is sharply curved posteriorly. The extreme posterior part of this fold is the separate fossette. The long metafossette crosses obliquely the metacone and almost reaches the latter fossette. Hypostria extends across two thirds of the lingual height. Mesostria runs one third to half of the labial height. The exit of mesoflexus includes a weak developed exit of premesofossette. A small postmesofossette joins the mesoflexus posteriorly. In initial wear stage ($n=1$; Fig. 4G), the crests are flattened and fossettes have weakly crimped walls. Anterofossette joins the anterolingual fossette. Parafofsette is separated from the anterofossette by a distinct crest. Mesoflexus fuses its posterior lobe. Postmesofossette and metafossette are closed.

The little worn M2 ($n=1$; Figs. 2D, 4H) possess stout roots and united dentine field of the occlusal surface. Hypostria extends across one third to half of the lingual height, and mesostria runs one third of the labial height. The long anterofossette is formed. The lingual part of this valley is wide and it adjoins the end of hypoflexus. Postmesofossette, metafossette and mesoflexus are merged labially. M2 in a middle wear stage ($n=2$; Figs. 2E, 4I) is characterized by simplified structure of the occlusal surface. Anterofossette and metafossette are two-lobed. Posterior part of mesoflexus is detached. Parafofsette and postmesofossette are expressed by small lens-like marks.

M3 has rounded shape. Protocone protrudes more lingually than hypocone. The unworn tooth ($n=2$) has uneven folded pattern. Hypoflexus is little deepening into the occlusal surface. Anterofossette is isolated, and occasionally has a weakly expressed exit. The extreme lingual part of anterofossette is detached, and this

separated small fossette connects to parafofsette or lingual margin of mesoflexus. Near its labial end, parafofsette is divided by a very small transverse crest. The lingual part of the mesoflexus is sharply curved backward and occasionally connects to hypoflexus. Posterior to mesoflexus, there is a postmesofossette. Metaflexus has a weakly developed exit on the posterior side of the crown. This fold is oblique and placed markedly dorsally to the main plane of occlusal surface. It is separated from closely located labial part of postmesofossette by a small crest (Fig. 4J).

The little worn M3 ($n=2$) has a united dentine field. Anteroflexus is oval in shape and has a weakly developed exit expressing by a minute notch on the anterior side. Posterior to anteroflexus, there is parafofsette (or two twinned transverse fossettes). Lingually, a small triangle or oval detached fossette is located. The structure of mesoflexus, postmesofossette and metafossette follows by former stage. M3 in middle wear stage ($n=1$) shows the detachment of the wide posterior part of mesoflexus, the closed anteroflexus and metaflexus, and the fossettes decreasing in size.

The unworn p4 ($n=2$; Fig. 4K) has uneven folded pattern. In initial wear stage ($n=1$), the crests became flattened. Hypostriid extends across two thirds to three fourths of the labial height, and mesostriid extends across one third to half of the lingual crown height. In this stage, the main structural elements are hardly discernible because they are complied by the crimped and uneven enamel. However, an isolated fossettid in the anterolabial corner of occlusal surface, as well as a small parafofsettid, metafofsettid, premesofossettid having a minute exit into the mesostriid, mesoflexid, postmesofossettid, and wide entofossettid are observable. Apparently, in next wear stages the anterolabial isolated fossettid connects to the metafofsettid and the united metafofsettid is formed. The lingual part of entofossettid is detached and expressed by entoflexid.

The little worn p4 ($n=1$) has a united dentine field. Hypoflexid is deepening into the occlusal surface and adjoins the entofossettid. Entoflexid is detached, short and wide. The other structural elements are presented by a short transversely directed parafofsettid, long metafofsettid, short lens-like premesoflexid, mesoflexid, and drop-shaped small postmesofossettid. Metafofsettid is weakly oblique, with a wide labial part and curved lingual part. Premesoflexid has a very narrow and small exit. Mesoflexid is similar to metafofsettid in shape.

The middle worn p4 ($n=1$; Figs. 2H, 3B) is characterized by transformation of the parafofsettid, premesofossettid and postmesofossettid to three small marks. Moreover, the lingual part of mesoflexid became narrower, and entoflexid closed and forms the large entofossettid. Hypoflexid is strongly deepening into the occlusal surface and directed sharply posteriorly. Hypostriid extends across half labial height, and mesostriid extends across approximately one fifth of the lingual height of the crown.

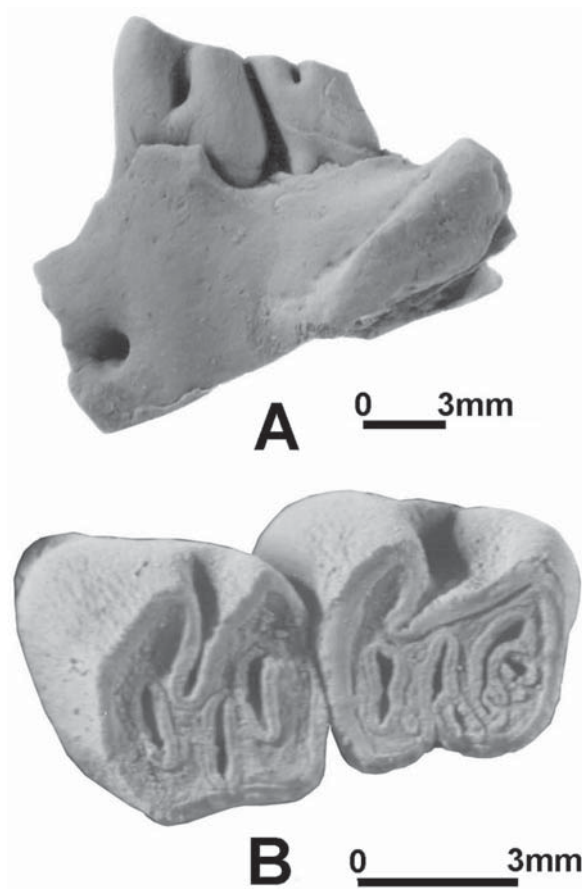


Figure 3. *Steneofiber kumbulakensis* (Lytshev, 1970), PIN 210/767, fragment of left lower jaw with p4–m1 (A — labial view, B — occlusal view of p4–m1). Kazakhstan, North Aral Region, Akеспе locality; Aral Svita, Lower Miocene.

The little worn m1 ($n=4$; Fig. 4L) is characterized by relatively deep hypoflexid. Parafofsettid is expressed by rounded mark in the middle line. Metafofsettid is sharply curved anteriorly. A small oval premesofossettid is located near the lingual margin of the occlusal surface. Mesoflexid is straight or slightly curved anteriorly. Posterior process of mesoflexid connects to a small postmesofossettid. Entoflexid has a narrow exit (occasionally, it is closed completely). As a rule, this fossette has a directed posteriorly process. Hypostriid and mesostriid are shallow; they extend across half of the labial height and one fifth of the lingual height, respectively.

In middle wear stage ($n=3$; Fig. 2I), parafofsettid is absent, entoflexid is closed and forms entofossettid, premesofossettid and postmesofossettid are decreased, hypoflexid is deeper. In heavy wear stage ($n=1$; Figs. 2H, 3B), the mesofossettid is formed. Only two fossettids are retained, the long oval metafofsettid (subequal to mesofossettid in transverse length), and entofossettid. Hypostriid extends across approximately one third of the labial height. In heaviest wear stage ($n=1$), the crown is worn at the root level. The occlusal surface

shows hypofossettid, short mesofossettid, and the rounded mark in the place of metafofsettid. Hypofossettid is directed posteriorly, but in the ending turns anteriorly.

The unworn m2 ($n=1$) possesses the slightly asymmetrical occlusal surface, because the posterior lobe is narrower than anterior one. Hypostriid is deep, extends across two thirds of the labial height. Mesostriid runs across one third of the lingual height. The occlusal surface is uneven, folded, and the discreet structural elements are hardly discernible.

The little worn m2 ($n=3$) has a wide parafofsettid with crimped walls. Metaflexid is very long, gently curved posteriorly, and wide lingually. Premesofossettid is reduced, occasionally united with mesoflexid. Mesoflexid is transversely elongated, has the crimped walls. Occasionally, this fold connects to smaller postmesofossettid posteriorly. Entoflexid is large, constricted in the middle or divided on lingual flexid and labial fossettid. Entofossettid is small. Entoflexid reaches the posterior end of hypoflexid. In a middle wear stage ($n=2$; Fig. 2I), parafofsettid, premesofossettid, and postmesofossettid disappear or are transformed to small marks, which are separated from mesoflexid. Metafofsettid is formed. Entoflexid retains very narrow exit or closed. Hypostriid extends across half of the labial height. Mesostriid extends across one fourth of the lingual height. Apparently, more advanced wear stages are similar to those of m1.

The little worn m3 ($n=3$) possesses the wide folds of mesoflexid and entoflexid, and small premesofossettid. In middle wear stage ($n=1$; Figs. 2J, 4M), m3 has the relatively shallow hypoflexid, small oval parafofsettid, anteriorly curved metafofsettid, superficial lingual mark of premesofossettid, mesoflexid having posterior process, and postmesofossettid mark joined with the enlarged entofossettid. Hypostriid extends across approximately half of the labial height, and mesostriid extends across near one fourth of the lingual height. Anterior lobe is wider than posterior one.

Measurements (all in mm). Length of p4–m1 (PIN 210/767) 7.7; length of m1–m2 (PIN 4516/320) 8.0. Measurements of isolated teeth see Tab. 1.

Comparison. *S. kumbulakensis* differs from *S. minimus* Filhol, 1891, *S. wenzensis* Sulimski, 1964, *S. butselensis* Misonne, 1957, and *S. dehmi* Freudenberg, 1941 in having postmesofossettid on p4–m2. Additionally, it differs from *S. minimus* and *S. wenzensis* in having anteroflexus and parafofsettid. Differs from *S. shevyrevae* Lytshev et Shevyreva, 1994 and *S. zaisanensis* Lytshev et Shevyreva, 1994 in having longer and crimped mesoflexus on P4, from *S. kazakhstanicus* (Borissoglebskaya, 1967) in being larger, from *S. depereti* Mayer, 1908, *S. anderssoni* (Schlosser, 1924), *S. broilii* (Teilhard de Chardin et Young, 1931), *S. jaegeri* (Kaup, 1832), *S. minutus* (Meyer, 1838), and *S. eseri* Meyer, 1846 in being smaller.

Remarks. The study of the ontogenetic variability of the dental structure in *S. kumbulakensis* shows the gradual simplification of the pattern of the occlusal surface during the wear process (Fig. 5). The structure

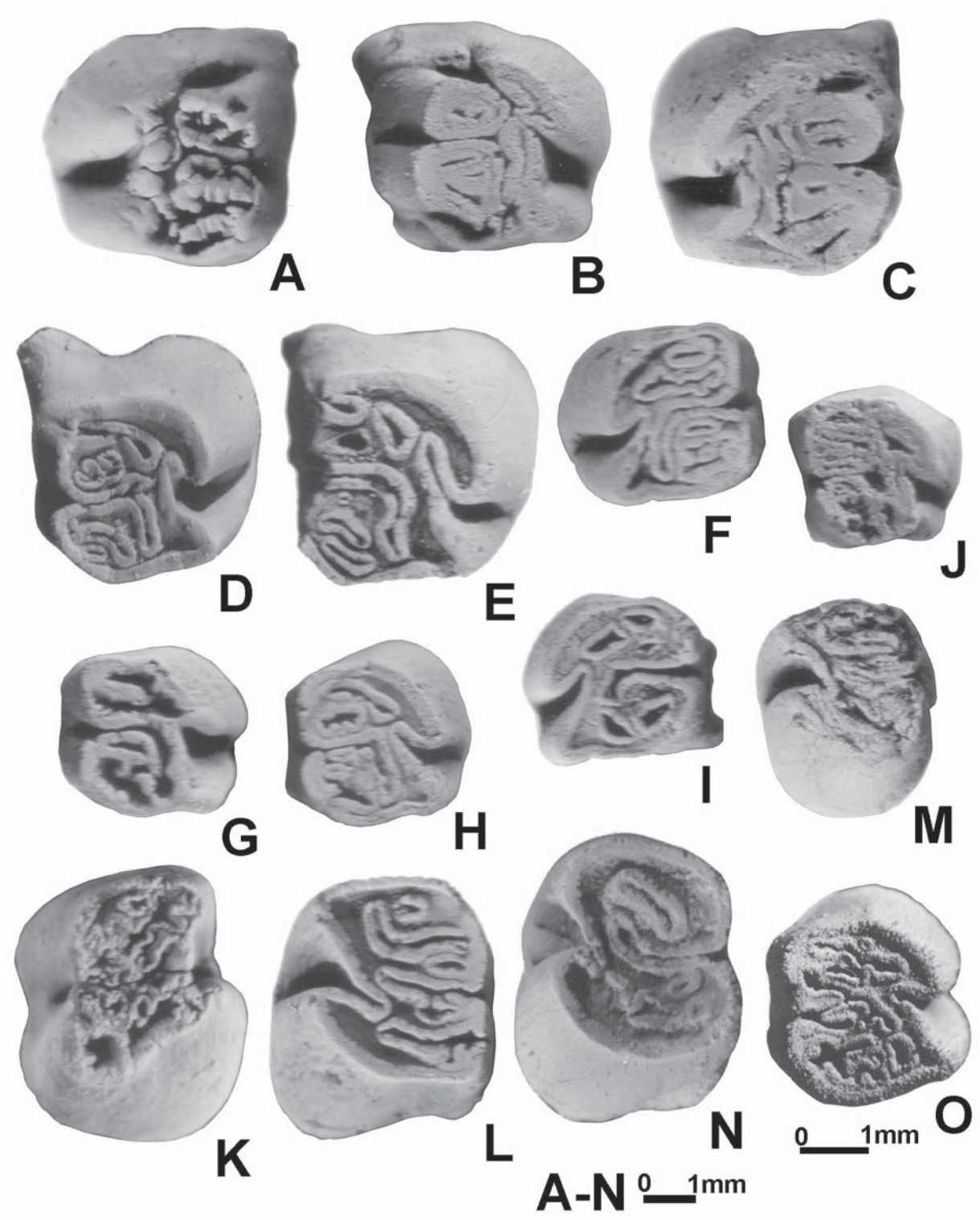


Figure 4. *Steneofiber kumbulakensis* (Lytshev, 1970) (A–M), *Steneofiber schokensis* (Bendukidze, 1993) (N) and *Asiacastor* sp. (O). Kazakhstan, North Aral Region, Altynshokysu (A–H, J–O) and Akespe (I) localities; Aral Svita, Lower Miocene. A — PIN 4516/10, left P4; B — PIN 4516/316, right P4; C — PIN 4516/308, left P4; D — PIN 4516/11, right P4; E — PIN 4516/12, right P4; F — PIN 4516/312, left M1; G — PIN 4516/314, right M2; H — PIN 4516/322, right M2; I — PIN 210/768, left M2; J — PIN 4516/332, right M3; K — PIN 4516/38, right p4; L — PIN 4516/329, left m1; M — PIN 4516/333, left m3; N — PIN 4516/321, left p4; O — PIN 4516/13, right M2.

Table 1. Measurements of isolated teeth (occlusal surfaces) in *Steneofiber kumbulakensis* (Lytshev, 1970). Kazakhstan, North Aral Region; Aral Svita, Lower Miocene.

Tooth	Length			Width		
	n	Limits	Average	n	Limits	Average
P4	6	3.7–4.2	4.0	5	2.7–3.5	3.1
M1	5	3.0–3.3	3.2	5	2.7–4.1	3.1
M2	3	2.9–3.2	3.0	3	2.3–3.0	2.6
M3	5	2.7–3.0	2.8	7	2.4–3.2	2.7
p4	4	3.7–4.0	3.9	5	2.9–3.6	3.2
m1	4	3.5–3.7	3.65	5	3.1–3.7	3.4
m2	6	3.0–3.7	3.3	6	2.7–3.4	3.05
m3	1	3.0	–	2	2.5–2.6	–

and size of p4–m1 in the holotype of *Capacikala sajakensis* Bendukidze, 1993 (Bendukidze, 1993: pl.27, figs.1, 2) does not differ from those of the heavily worn teeth of *S. kumbulakensis*, and their M1 are identical, too (Figs. 1–3, 4F, L, and 5). Therefore, species name *Capacikala sajakensis* should be considered as the junior subjective synonym of *S. kumbulakensis*.

Distribution. Kazakhstan; Early Miocene.

Steneofiber schokensis (Bendukidze, 1993)
Figs. 4N, 6A–D.

Palaeocastor sp.: Bendukidze, 1993: 84, pl.25, fig.8.

Capatanka schokensis: Bendukidze, 1993: 85, pl.26, figs.1–4.

Capatanka aff. *schokensis*: Bendukidze, 1993: 91.

Holotype. Institute of Paleobiology of the Academy of Sciences of Georgia, 15/48, dentary with incisor fragment and p4–m3.

Referred material. Two isolated premolars, fragmented P4 (PIN 4516/306) and p4 (PIN 4516/321), and four tooth fragments (two P4, one p4, and one m2, PIUZ) from bone-bearing level IV of Altynshokysu.

Type locality. Altynshokysu, North Aral Region, Kazakhstan.

Stratigraphic level. Aral Svita, Lower Miocene.

Description. The cheek teeth are relatively low crowned (mesodont), without cement in the flexi and flexids. P4 is a large, stout tooth. The crown is rounded-square in outline. There are three roots, a wide and strong lingual root and two small labial ones. The enamel walls of the crown and valleys are very thick. Hypostria extends across approximately half of the lingual crown height. Anterostria expressed by a small fold on the anterolabial side. Hypoflexus is directed sharply anteriorly. Anteroflexus is relatively small; its lingual part adjoins the rather large parafofsette. Parafofsette is rounded-triangle in shape with the posteriorly inclined lingual end, which closely approached the labial wall of hypoflexus. Mesoflexus is slightly inclined posteriorly. There is a small enamel prominence near posterior end of the lingual part of mesoflexus. Apparently, this is a remnant of a mark. Because posterolabial corner of the occlusal surface is broken

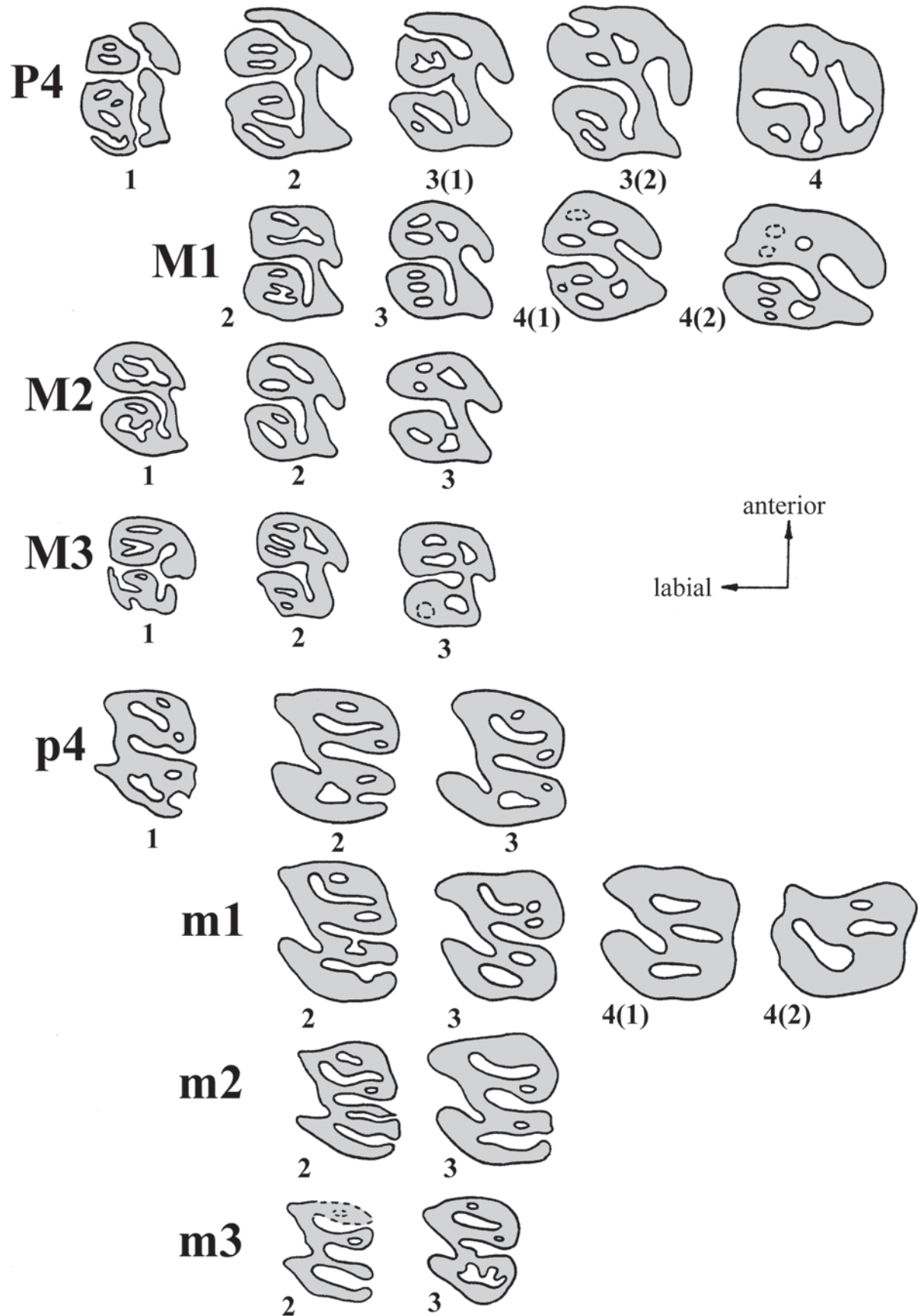
off, the precise quantity and position of the fossettes on the posterior lobe are unknown. The heavily worn P4 has closed hypoflexus (hypofossette). Mesoflexus is divided on two parts. The labial part is a short and straight flexus, and lingual one is a large fossette at the center of the occlusal surface. Anterofossette is small, rounded, approached to the anterolabial corner of the tooth. Parafofsette is large, having the posteriorly turned lingual end. Posterior to mesoflexus, there are two small rounded fossettes in one transverse row.

The p4 has two stout roots. The crown is rounded-rectangular in outline. Anterior lobe is narrower than posterior one. Hypostriid descends across two thirds of the labial height. An additional column is located inside bifurcated hypostriid (Fig. 6C, D). Mesostriid extends across one fifth of the lingual height. Hypoflexid is deepening into occlusal surface. The exit is very narrow, and the enamel walls are almost adjoined in this region. Lingual part of hypoflexid is wide. It is directed posteriorly and slightly lingually. The large metafofsettid is located in the middle of the anterior lobe of occlusal surface. It is inclined anteriorly, but the lingual end turns posteriorly. More lingually, there is a small rounded mark, a possible remnant of premesofossettid. Mesoflexid is long, having the wide and anteriorly curved labial part. Posteriorly, there is a small oval postmesofossettid mark. Entofossettid is divided in two fossettid. The lingual entofossettid is the rounded mark, which is smaller than postmesofossettid. The labial entofossettid is relatively large, rounded-triangle in shape, closely approached the lingual part of hypoflexid. The anterior wall of the latter fossettid is weakly crimped. Preserved fragment of the little worn p4 (PIUZ) has a distinct long hypostriid with the additional column in the base, relatively short hypoflexid, as well as metafofsettid, mesoflexid with crimped walls and labial entofossettid. They are generally similar to above described elements of the worn tooth, respectively. There are two small rounded marks between mesoflexid and entofossettid.

The m2 in advanced wear stage has the subquadrate occlusal surface. Hypostriid is expressed by a small notch. Hypoflexid is very deepening and reaches the middle of occlusal surface. Mesofossettid is long, almost straight, and slightly posteriorly inclined. A small rounded metafofsettid is located anterior to the labial end of mesofossettid. More lingually, there is very small enamel hollow. Entofossettid is equal to metafofsettid in size and approached to the lingual end of hypoflexid. Lingually to entofossettid, there are two small enamel hollows.

Measurements (all in mm). Length × width: P4 (PIN 4516/306) 4.5 × 5.2 (base); p4 (PIN 4516/321) 4.7 × 4.0 (occlusal surface), 5.6 × 4.8 (base).

Comparison. *S. schokensis* differs from *S. kazakhstanicus*, *S. kumbulakensis*, and the majority of other species in having larger size and absence of metaflexid and entoflexid. Additionally, it differs from *S. minimus* and *S. wenzensis* in having anteroflexus in P4, and from *S. shevyrevae* and *S. zaissanensis* in having weakly crimped walls of mesoflexus.



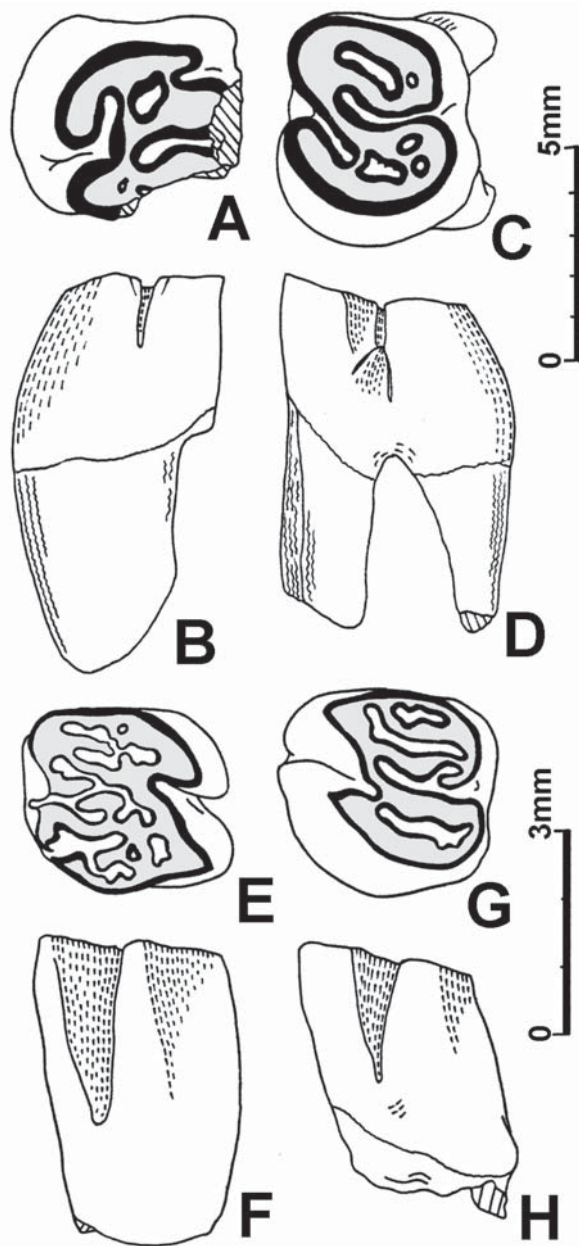


Figure 6. *Steneofiber schokensis* (Bendukidze, 1993) (A–D) and *Asiastor* sp. (E–H). Kazakhstan, North Aral Region, Altynshokysu; Aral Svita, Lower Miocene.

A, B — PIN 4516/306, fragmented left P4 (A — occlusal view, B — lingual view); C, D — PIN 4516/321, left p4 (C — occlusal view, D — labial view); E, F — PIN 4516/13, right M2 (E — occlusal view, F — lingual view); G, H — PIN 4516/302, left m3 (G — occlusal view, H — labial view).

Remarks. Bendukidze (1993) referred this species to the North American genus *Capatanka* Macdonald, 1963. On my opinion, the presence of anterostria on the middle worn P4, mesoflexus in the advanced wear stages (when hypofossette is formed), as well as number of additional fossettes and fossettids suggest that this species can not be referred to the genus *Capatanka* (Macdonald, 1963). On the other hand, the lower jaw and teeth of discussed form show considerable similarity with different Oligocene and Early Miocene species of the genus *Steneofiber*, especially with the Early Oligocene *S. shevyreva* from Zaissan depression (in having short mesoflexus on P4, presence of anteroflexus, and absence of metaflexid and entoflexid; Lytshev & Shevyreva, 1994: figs.3–4) and Early Miocene European *S. eseri* Meyer, 1846 (in having two mental foramina and p4 structure; Hugueney, 1975: pl.1, fig.12; pl.2, fig.4). On this base, I refer the species described above to the genus *Steneofiber*. Bendukidze (1993) compared this species with “*Capatanka*” *kazakhstanicus* (Borisoglebskaya, 1967), originally described by Borisoglebskaya (1967) as *Propalaeocastor kazakhstanicus*, but Lytshev & Shevyreva (1994) argued that this species should be referred to the genus *Steneofiber*.

Distribution. Kazakhstan; Early Miocene.

Discussion

The quality and quantity of the material described on *S. kumbulakensis* permits to establish the succession of the changes of the occlusal surface structure in wear process. The unworn teeth have uneven occlusal surface with number folds. Hypostria extends across more than two thirds of the lingual height. Mesostria runs across approximately two thirds of the labial height. Anterostria extends across one third of the anterolabial height. Occasionally, there is a weak metastrid. Hypostriid descends across two thirds to three fourths of the labial height. Mesostriid extends across one third to half of the lingual height. In next stages, the structure of occlusal surface became gradually simplified. Four main wear stages may be established for the isolated teeth.

1. Initial wear stage. This stage is characterized by retention of the primary pattern and total flatness of the occlusal surface. Commonly, the tooth has three (or more) flexi (hypoflexus, anteroflexus, mesoflexus, and, occasionally, metaflexus) or flexids (hypoflexid, mesoflexid, entoflexid, and, occasionally, premesoflexid) with the crimped enamel walls. The striae and striids lengths are subequal to those of the unworn teeth.

2. Little wear stage. Commonly, there are three flexi (hypoflexus, anteroflexus, and mesoflexus) or flexids (hypoflexid, mesoflexid, and entoflexid). Hypostria

Figure 5. The *Steneofiber kumbulakensis* cheek teeth occlusal surface transformation in wear process.

1–4 — wear stages: 1 — initial wear stage (the presence of three or four flexi/flexids and crimped enamel walls); 2 — little wear stage (usual presence of three flexi/flexids); 3 — middle wear stage (usual presence of two flexi/flexids); 4 — heavy wear stage (only hypoflexus/hypoflexid is present as a rule or all folds are closed); (1)–(2) — successive wear substage within one wear stage.

runs across one third to half of the lingual height. Mesostria extends across one third of the labial height. Anterostria is expressed as a small notch or absent. Hypostriid descends across approximately half labial height. Mesostriid extends across one fifth to one fourth of the lingual height.

3. Middle wear stage. Commonly, there are two flexi (hypoflexus and mesoflexus, but P4 has these two and anteroflexus) or flexids (hypoflexid and mesoflexid). Hypostria extends across one fourth to half of the lingual height. Hypostriid descends across approximately half the labial height. Mesostriid extends across one fifth to one fourth of the lingual height.

4. Heavy wear stage. As a rule, there is one flexus/flexid only — hypoflexus/hypoflexid. In this stage, hypostria extends across one fifth of the remaining lingual height, and hypostriid descends across one third of the labial height. Progressively, all striae/striids extinct and all folds are closed.

The different time of the cheek teeth eruption (M1→M2→M3→P4) determinates the presence of the teeth of the different wear stages in the tooth row. For example, the fragment of the left dentary (PIN 210/767; Figs. 2G, H, 3) from Akеспе has a middle worn p4 (with open hypoflexid and mesoflexid) and heavy worn m1 (only hypoflexid is open, other folds are closed). The right dentary fragment (PIN 4516/320; Fig. 2I) from Altynshokysu has a middle worn m1 (with hypoflexid and mesoflexid) and little worn m2 (these two folds and entoflexid).

In addition to the described fossils of *Steneofiber kumbulakensis* and *S. schokensis*, two isolated high crowned (semihypsodont) beaver molars were collected. They are M2 (PIN 4516/13; Figs. 4O, 6E, F) and m3 (PIN 4516/302; Fig. 6G, H), referring to small beaver of the genus *Asiacastor* Lytshev, 1971 (Castoroidinae, Trogontheriini: Korth, 2002). They differ from teeth of the Middle-Late Miocene *A. baschanovi* Lytshev, 1971 and *A. major* Lytshev, 1971 (Lytshev & Aubekerova, 1971) by the absence of cement in flexi and flexids. The Aral form differs from the Early Miocene (~MN3) *A. antecessens* Lytshev, 1982 from Ayaguz locality (south-eastern Kazakhstan) by having postmesofossette and premesofossettid (Lytshev, 1982). These valleys are observed in *A. orientalis* Lytshev, 1987. The latter was described by Lytshev (1987) on the isolated P4, M3 and p4 from the upper Lower Miocene Akzhar (=Dzhamangora) Svita of Eastern Kazakhstan (according to Lytshev & Shevyreva, 1994 the precise stratigraphic position of these finds is unknown). There are not corresponding teeth in the available material from the North Aral Region. The structure pattern and size of the teeth discussed are similar to those in *A. orientalis*. Bendukidze (1993) referred to *Asiacastor* aff. *orientalis* isolated P4, M2, p4, and m3 from the North Aral Region. Later, Bendukidze (1997) cited this form as *Anchitheriomys* aff. *orientalis* (Lytshev, 1987). Moreover, I suggest that the isolated teeth, determined by Bendukidze (1993) as *Capacikala* cf. *sciuroides* (Matthew, 1907) and cited later (Bendukidze, 1997) as *C.*

antecessens (Lytshev, 1982), should be referred to this small beaver too. However, the structure of these teeth is not so similar to that of *A. orientalis*. Therefore, there are no grounds for suggestion that the discussed Aral form is conspecific or closely related to Akzhar *A. orientalis*. Apparently, its determination as *Asiacastor* sp. appears to be most reasonable.

The so-called *Asiacastor* dental pattern is shared by four genera: *Asiacastor*, *Youngofiber*, *Trogontherium*, and *Anchitheriomys* (Xu, 1994). Xu (1994) considers that they comprise a monophyletic group, and large-sized *Youngofiber* could be derived from an early *Asiacastor* species with low crowned teeth. Recently, Korth (2002) unites the former three genera in the tribe Trogontheriini of the subfamily Castoroidinae, and he refers *Anchitheriomys* to the tribe Anchitheriomyini of the subfamily Agnotocastorinae. Korth (2002) believes that the later Miocene *Asiacastor* is directly derived from *Youngofiber*. I share the Xu's phylogenetic hypothesis and consider the Aral form as the most ancient member of the genus *Asiacastor*, that escorted by the precise stratigraphic data.

Thus, three beaver species are presented in the Aral Faunal assemblage. They are *Steneofiber kumbulakensis* (Lytshev, 1970), *S. schokensis* (Bendukidze, 1993), and *Asiacastor* sp. The disappearing of the former *Capatanka* and *Capacikala* determinations eliminates the zoogeographical controversies, determined by presumable local presence of these Miocene North American genera in Western Kazakhstan.

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