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Early Cretaceous mammals from Bol'shoi Kemchug 3 locality in West Siberia, Russia

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ABSTRACT. A small sample of mammalian isolated teeth and edentulous dentary fragments from the Early Cretaceous locality Bol'shoi Kemchug 3 in Krasnoyarsk Territory, West Siberia, Russia, represents five taxa: amphilestid *Kemchugia magna* **gen. & sp. nov.**, Amphilestidae indet., gobiconodontids *Gobiconodon* sp. A and B, and Mammalia indet. The large sized *Kemchugia magna* **gen. & sp. nov.** is based on two isolated molariforms. Amphilestidae indet. is represented by single molariform and two edentulous dentary fragments. *Gobiconodon* sp. A is similar in size to *G. hoburensis* from the Early Cretaceous of Mongolia. *Gobiconodon* sp. B is some 20% larger than *G. borissiaki* from the Early Cretaceous of Mongolia. A minute edentulous dentary with alveoli for two posterior molariforms is referred to Mammalia indet. Dental lamina pits on the lingual side of gobiconodontid jaws, interpreted as openings for the epidermal filaments connecting the dental lamina with the growing enamel cup of a developing tooth germ, are reported here for the first time and confirm replacement of molariform teeth in Gobiconodontidae.

KEY WORDS: Amphilestidae, *Kemchugia* **gen. nov.**, Gobiconodontidae, *Gobiconodon*, Siberia, Ilek Formation, Early Cretaceous.

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Раннемеловые млекопитающие из местонахождения Большой Кемчуг 3 в Западной Сибири, Россия

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РЕЗЮМЕ. В небольшой выборке изолированных зубов и беззубых фрагментов зубных костей из раннемелового местонахождения Большой Кемчуг 3 в Красноярском Крае, Западная Сибирь, Россия, представлено пять таксонов: амфилестид *Kemchugia magna* **gen. & sp. nov.**, Amphilestidae indet., гобиконодонтиды *Gobiconodon* sp. A и B, и Mammalia indet. Крупная форма *Kemchugia magna* **gen. & sp. nov.** описана на основе двух молярифомных зубов. Таксон Amphilestidae indet. представлен единственным молярифомным зубом и двумя фрагментами зубных костей без зубов. *Gobiconodon* sp. A близок по размерам к *G. hoburensis* из раннего мела Монголии. *Gobiconodon* sp. B примерно на 20% крупнее *G. borissiaki* из раннего мела Монголии. Маленькая зубная кость без зубов с альвеолами двух последних молярифомных зубов отнесена к Mammalia indet. Отверстия на лингвальной стороне челюстей гобиконодонтид близ альвеолярного края зубов интерпретируются как отверстия для эпидермальных тяжей, соединявшие зубную пластинку с растущим эмалевым колпачком развивающегося зубного зачатка. Эти отверстия впервые описываются для гобиконодонтид и их наличие подтверждает замещение молярифомных зубов у Gobiconodontidae.

КЛЮЧЕВЫЕ СЛОВА**:** Amphilestidae, *Kemchugia* **gen. nov.**, Gobiconodontidae, *Gobiconodon*, Сибирь, илекская свита, ранний мел.

Introduction

The Early Cretaceous vertebrate locality Bol'shoi Kemchug 3 (N 56º 31′ 38″, E 91º 48′ 49″) was discovered in 2000 by the Paleontological team of Tomsk State University (Leshchinskiy & Fayngertz, 2001). Altogether about 1220 kg of matrix were screen-washed at the locality by the joint expeditions from Tomsk and Saint-Petersburg universities (470 kg in 2001 and 750 kg in 2003), that produced twelve mammal teeth or

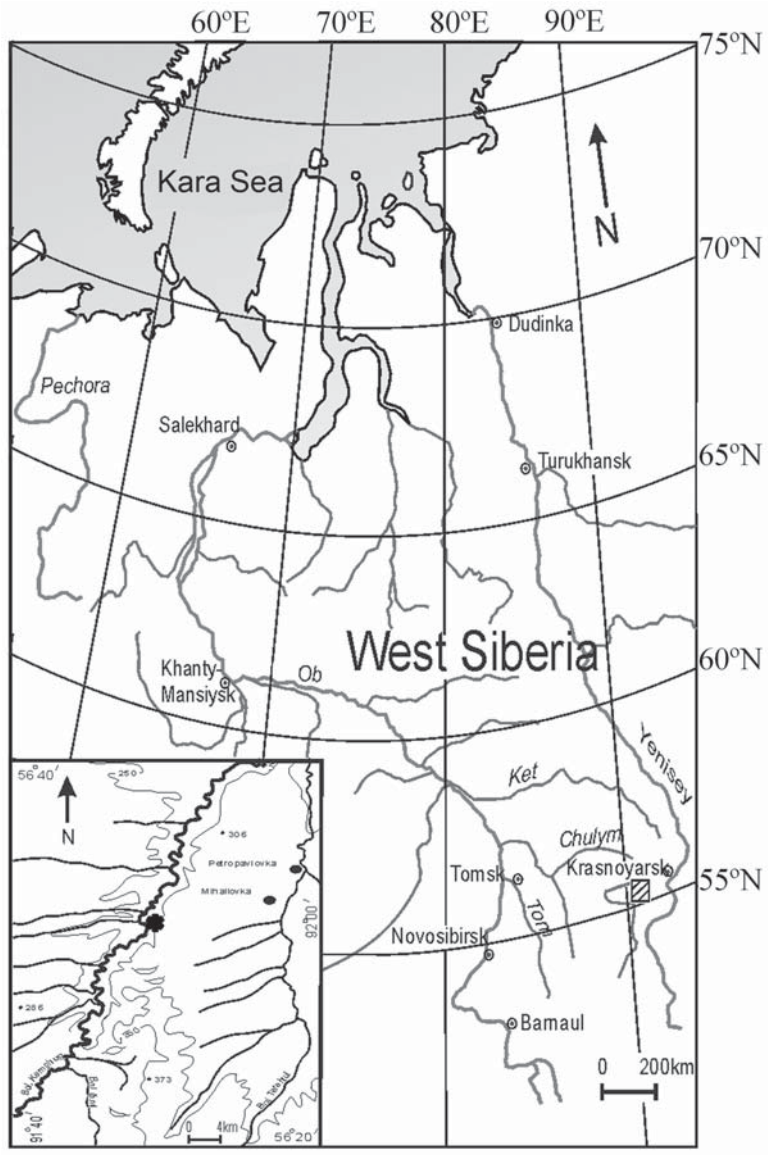

Figure 1. Geographic position of Bol'shoi Kemchug 3 locality (asterisk) on the map of West Siberia.

tooth fragments and six edentulous dentary fragments. Vertebrate remains at Bol'shoi Kemchug 3 locality are quite fragile and sometimes disintegrate in the water, which preclude from washing of a larger amount of matrix in reasonable period of time. Another obstacle impeding work at this locality is its quite remote position. It is situated on a bank of a small river deeply inside taiga forest far from the nearest settlements and roads (Fig. 1) and accessible only by canoes. A preliminary report on the Bol'shoi Kemchug 3 vertebrate fauna was published by Leshchinskiy *et al.* (2003). The purpose of this paper is to provide detailed description of the majority of mammalian remains collected during the 2001 and 2003 expeditions.

The fossiliferous bed at the Bol'shoi Kemchug 3 locality is confined to the Lower Cretaceous Ilek Formation. The vertebrate fauna from Bol'shoi Kemchug 3 locality (Tab. 1) is similar to that from Shestakovo 1 and 3 localities within the same Ilek Formation in Kemerovo Province (for a recent review of Shestakovo vertebrate fauna see Maschenko *et al.*, 2002, 2003; Leshchinskiy *et al.*, 2003; Averianov *et al.*, 2004, in press b).

In morphological terminology and classification of Mesozoic mammals we follow Kielan-Jaworowska *et al.* (2004). Generic diagnosis of a new amphilestid taxon includes a combination of what we interpret as derived characters (+), primitive characters (–), and characters of uncertain polarity (?).

Institute abbreviations. MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; PIN — Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; PM TGU — Paleontological Museum, Tomsk State University, Tomsk, Russia.

Dental measurements. H — height, L — length, W — width. All measurements are in mm.

Table 1. List of vertebrates from Bol'shoi Kemchug 3 locality, Krasnoyarsk Territory, Russia; Ilek Formation, Early Cretaceous.

Osteichthyes
- Palaeonisciformes indet.
- Sinamiidae indet.

Amphibia
- Caudata
  - *Kiyatriton leshchinskiyi*
  - Caudata indet.

Testudinata
- Testudinata indet.

Choristodera
- ?Choristodera indet.

Squamata
- Scincomorpha
  - Paramacellodidae
    - *Ilekia sibirica*
    - *Saurillodon tschebulensis*
- Anguimorpha
  - Xenosauridae
    - *Shestakovia voronkevichi*
  - Platynota
    - cf. *Parviraptor* sp.

Crocodylomorpha
- Protosuchia:
  - *Tagarosuchus* sp.
- Shartegosuchidae:
  - *Kyasuchus* sp.

Pterosauria
- ?Ctenochasmatidae indet.
- Pterodactyloidea indet.

Dinosauria
- Theropoda
  - cf. "*Prodeinodon*" sp.
- Sauropoda
  - Titanosauriformes indet.
- Stegosauria
  - Stegosauria indet.
- Ceratopsia
  - *Psittacosaurus* sp.
- Ornithopoda
  - Hypsilophodontidae indet.

Aves
- Aves indet.

Therapsida
- Tritylodontidae
  - *Xenocretosuchus* sp.

Mammalia
- Eutriconodonta
  - *Kemchugia magna* **gen. & sp. nov.**
  - Amphilestinae indet.
  - *Gobiconodon* sp. A
  - *Gobiconodon* sp. B

Mammalia indet.

Systematic paleontology

MAMMALIA Linnaeus, 1758

Eutriconodonta Kermack, Massett & Rigney, 1973

Amphilestidae Osborn, 1888

Kemchugia **gen. nov.**

Etymology. After Bol'shoi Kemchug River in West Siberia (feminine gender).

Type species. *Kemchugia magna* **sp. nov.**, Early Cretaceous of West Siberia, Russia.

Diagnosis. Primary cusps mesiodistally aligned (–). Cusp *A* high and vertical (+). Cusps *B* and *C* about half as high as cusp *A* (–). Cusps *B* and *C* close in height (+). Width of upper molariforms more than half of their length (?). Ectoflexus absent (–). Lingual crown side of upper molariforms convex (–). Cingular cusps *E* and *F* present, with a small embayment between them (–). Cusp *E* is in line with the primary cusps (+). Labial and lingual cingulum on upper molariforms complete (–). Labial and lingual cingulum on upper molariforms with cingular cuspules (–). Roots connected by a tiny bone septum at the crown (+).

Discussion. A formal comparison within the family is not possible because none of the known amphilestid (sensu stricto) taxa have upper dentition confidently attributed (Kielan-Jaworowska *et al.*, 2004). *Kemchugia* **gen. nov.** is similar with gobiconodontids in having cusps *B* and *C* distinctly lower than the primary cusp *A* and their long axes diverging mesially and distally respectively from that cusp, but differs in upper molariforms lacking the ectoflexus and a concavity at the middle of the lingual side (e.g., Jenkins & Schaff, 1988: fig.10). In *Repenomamus* Li *et al.*, 2001 from the Early Cretaceous of China upper molariforms still have a concavity both labially and lingually, but the cusps *B* and *C*, as well as the labial cingulum, are greatly reduced, while cusp *A* is strongly inflated lingually (Li *et al.*, 2001; Wang *et al.*, 2001; Hu *et al.*, 2005). All these characters distinguish *Repenomamus* from *Kemchugia* **gen. nov.**

It should be noted that *Repenomamus* may be a junior subjective synonym of *Hangjinia* Godefroit & Guo, 1999. This taxon is based on a single mostly edentulous dentary of a very juvenile animal (especially by *Repenomamus* standards) from the Early Cretaceous of China. Its dentition was originally interpreted as i1–3, c, p1, p2?, m1–2? (Godefroit & Guo, 1999), but a more conservative gobiconodontid formula i1, c, p1–2, m1–4 would be more reasonable (Rougier *et al.*, 2003; Kielan-Jaworowska *et al.*, 2004). If the latter formula is correct, *Hangjinia* would differ from *Repenomamus* only by having one instead of two lower incisors and by lacking of the fifth lower molariform. This difference can be easily explained by a young ontogenetic age of the only *Hangjinia* specimen, assuming that i2 and m5 will be added at a later ontogenetic stage.

The only specimen other than PM TGU 16/6-401 which can be considered as an amphilestid upper molariform is an isolated tooth from the Middle Jurassic Watton Cliff locality in England (Freeman, 1979: pl.16, figs.1–2). This tooth, referred to *Amphilestes broderipii* (Owen, 1845), is usually believed to be a lower molariform (e.g., Freeman, 1979: 150; Kielan-Jaworowska *et al.*, 2004: 237), but its complete cingulum around the crown suggests that it is an upper molariform. Thus its published side view (Freeman, 1979: pl.16, fig.1) is labial, not lingual. The crown has somewhat triangular primary cusps, the reason for attribution of Amphilestidae to "Symmetrodonta" by Freeman (1979). This tooth is similar with the upper anterior molariforms of *Gobiconodon* and differs from *Kemchugia* **gen. nov.** in relatively transversely narrower crown, having a distinct ectoflexus, and lack of minute cingular cusps.

By a suite of very primitive characteristics *Kemchugia* **gen. nov.** is basically similar with the upper molariforms of Morganucodontidae and therefore was provisionally referred to that family in a preliminary publication (Leshchinskiy *et al.*, 2003). The only structural differences from morganucodontid molariforms is a more vertical and higher central cusp *A* and less height differential between cusps *B* and *C* in *Kemchugia* **gen. nov.** This pattern is more suitable for the "embrasure" occlusion between upper and lower molariforms, characteristic for amphilestids, than for the "one to one" upper and lower tooth opposition, characteristic for morganucodontids (Crompton & Jenkins, 1968; Mills, 1971; Jenkins & Schaff, 1988; Kielan-Jaworowska & Dashzeveg, 1998; Kielan-Jaworowska *et al.*, 2004). Also in *Morganucodon* Kühne, 1949 the cingular cusp *E* is placed more lingually, than in *Kemchugia* **gen. nov.**

Although the lower molariform PM TGU 16/6-410, attributed here to *Kemchugia magna* **gen. & sp. nov.**, is poorly preserved, it provides some data on dental occlusion in that taxon. There is a distinct facet on the mesiolabial side of the central cusp *a*, produced by wear against the distolingual side of the cusp *C* of the preceding upper molariform, and a deeply excavated small facet on the distolabial side of the distal cusp *c*, produced by wear against the mesiolingual side of the cusp *A* of the corresponding upper molariform (Figs. 2E, 3). This wear pattern is consistent with the "embrasure" dental occlusion characteristic for amphilestids (e.g., Mills, 1971; Jenkins & Schaff, 1988; Kielan-Jaworowska & Dashzeveg, 1998; Sigogneau-Russell, 2003; Kielan-Jaworowska *et al.*, 2004).

Kemchugia magna **sp. nov.**
Figs. 2A–F, 3.

Morganucodontidae? indet. [partim]: Leshchinskiy *et al.*, 2003: 427, fig.1a–v.

Etymology. From *magnus*, Latin for great.

Holotype. PM TGU 16/6-401, right upper molariform.

Type locality and horizon. Bol'shoi Kemchug 3 locality, Krasnoyarsk Territory, West Siberia, Russia; Ilek Formation, Lower Cretaceous.

Material. PM TGU 16/6-410, fragment of a left lower molariform.

Description. The crown is relatively wide transversely (W/L ratio is 65%), with the mesial margin slightly wider than the distal margin. The crown is convex both lingually and labially. The primary cusps are almost mesiodistally aligned (trigon angle 170º). The central cusp *A* is about twice as high as cusps *B* and *C*. The mesial cusp *B* is slightly lower than the distal cusp *C*. All primary cusps are connected by a trenchant longitudinal ridge. The cingulum is robust and continuous around the whole crown. The mesial cingular cusp *E* and the distal cingular cusp *D* are aligned with the primary cusps. The mesiolabial cingular cusp *F* is offset labially from the line of primary cusps. There are minute cingular cuspules on the labial cingulum, opposite to the cusp *A*, and on the lingual cingulum, opposite to the cusp *C*. The roots are long and quite closely spaced. There is a thin bony septum between roots just below the crown.

The lower molariform is not complete. It is transversely narrower than the upper molariform, but its length was apparently similar. Cusps *a*, *c*, and *d* are mesiodistally aligned. Most of the tip of central cusp *a* is missing. However, from its great size at the breakage it is evident that it was much higher than the distal cusp *c*. The lingual cingulid on the preserved fragment is very short, extending mesially from the cusp *d* towards the base of the cusp *c*. There is a short vertical ridge extending ventrally from the cusp *d* on the labial side, forming the distalmost portion of the labial cingulid. The remaining part of the ventrolabial crown edge is missing, so it is unclear how far mesially the labial cingulid was extending. There are distinct wear facets on the mesiolabial side of cusp *a* and on the distolabial side of cusp *c* (Figs. 2E, 3).

Measurements. Upper molariform: PM TGU 16/6-401: L=3.2, W=2.1. Lower molariform: PM TGU 16/6-410: W=1.3.

Discussion. PM TGU 16/6-410 is referred to *Kemchugia magna* **gen. & sp. nov.** because it exhibits amphilestid features (primary cusps mesiodistally aligned, the central cusp *a* much higher than the distal cusp *c*) and matches the size of the holotype of this taxon. Although PM TGU 16/6-410 could be similar in size with the teeth of *Gobiconodon* sp. B described below, presence of a distolabial cingulid and *A* to *c* rather than *A* to *b* occlusion (see Jenkins & Schaff, 1988; Kielan-Jaworowska & Dashzeveg, 1998) seems to preclude attribution of this specimen to *Gobiconodon*.

Amphilestidae indet.
Figs. 2G–I, 4A–F.

Amphilestinae indet. [partim]: Leshchinskiy *et al.*, 2003: 427, fig.1g–e.

Material. PM TGU 16/6-412, left dentary fragment with alveoli of double-rooted canine, double-rooted p1 and mesial root of p2; PM TGU 16/6-415, left dentary fragment with alveoli of canine, double-rooted p1 and mesial root of p2; PM TGU 16/6-404, left lower molariform.

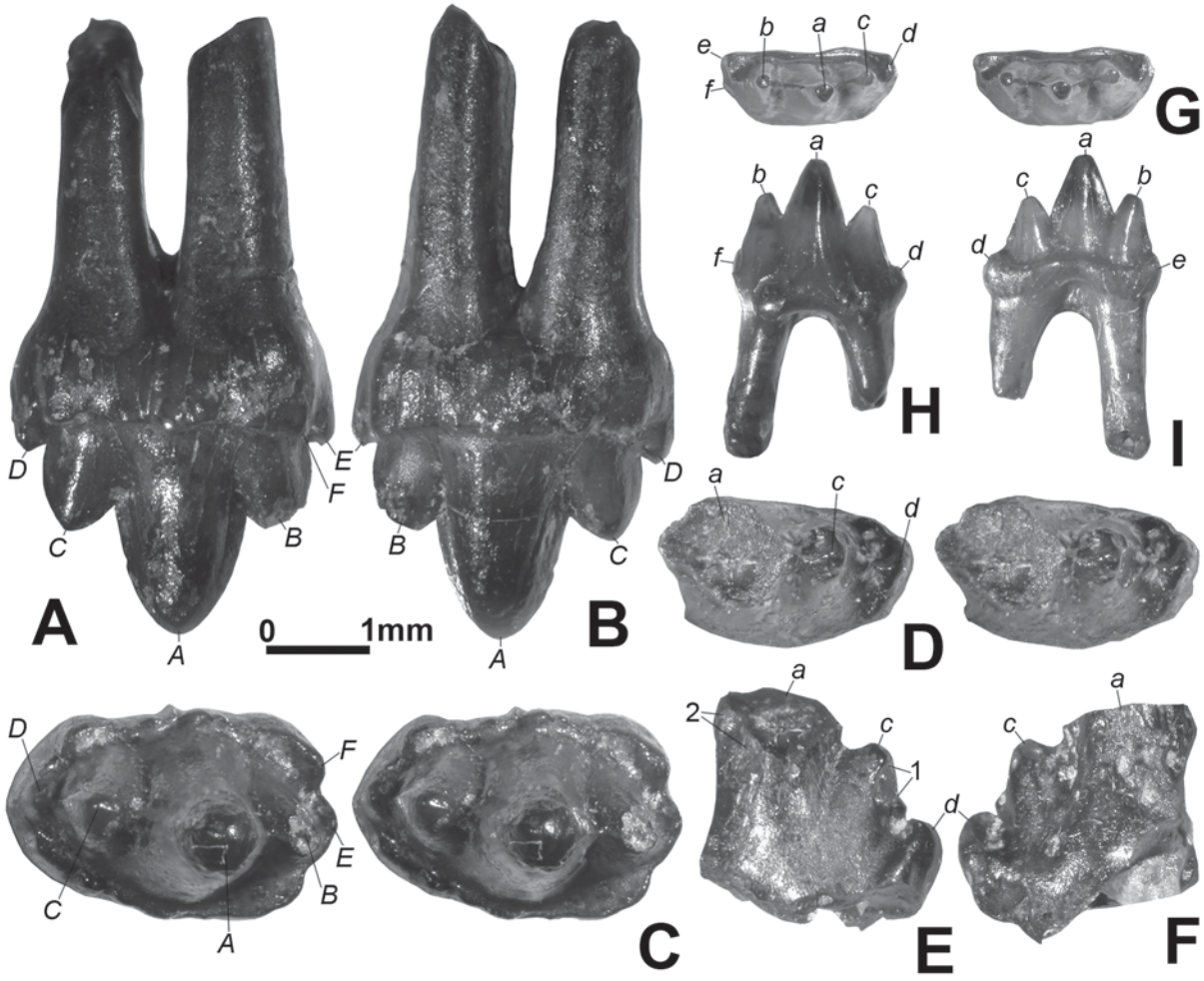

Figure 2. Isolated molariforms of *Kemchugia magna* **gen. & sp. nov.** (A–F) and Amphilestidae indet. (G–I) from Bol'shoi Kemchug 3 locality, Krasnoyarsk Territory, Russia; Ilek Formation, Lower Cretaceous.
A–C — PM TGU 16/6-401, holotype, right upper molariform in labial (A), lingual (B), and occlusal (C) views. D–F — PM TGU 16/6-410, fragment of a left lower molariform in occlusal (D), labial (E), and lingual (F) views. G–I — PM TGU 16/6-401, left lower molariform in occlusal (G), labial (H), and lingual (I) views. 1 and 2 on F — wear facets (numbering after Crompton, 1971). C, D, and G are stereo pairs. Scale bar is 1 mm.

Description. Both dentary fragments are similar in size and structure. In PM TGU 16/6-412 the canine is double-rooted (Fig. 4F). In PM TGU 16/6-415 the alveolus for the canine is somewhat larger but less complete, with a single opening preserved (for the distal root?). In both specimens alveoli for a double-rooted p1 are separated from the canine alveolus by a considerable diastema. There are two mental foramina preserved in both specimens: below diastema and distal root of p1 (PM TGU 16/6-415), or below distal root of canine and mesial root of p2 (PM TGU 16/6-412). There is no Meckel's groove on the lingual side of either specimen.

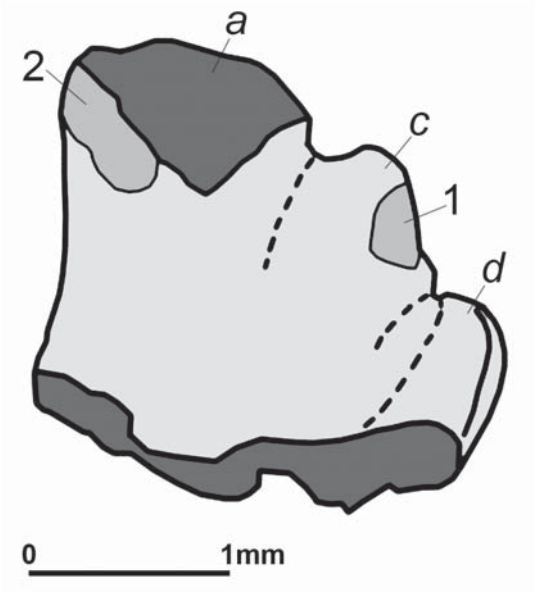

Figure 3. PM TGU 16/6-410, fragment of a left lower molariform of *Kemchugia magna* **gen. & sp. nov.**, in labial view. Bol'shoi Kemchug 3 locality, Krasnoyarsk Territory, Russia; Ilek Formation, Lower Cretaceous.
1 and 2 — wear facets (numbering after Crompton, 1971). Broken areas of the tooth are depicted by intensive gray. Scale bar is 1 mm.

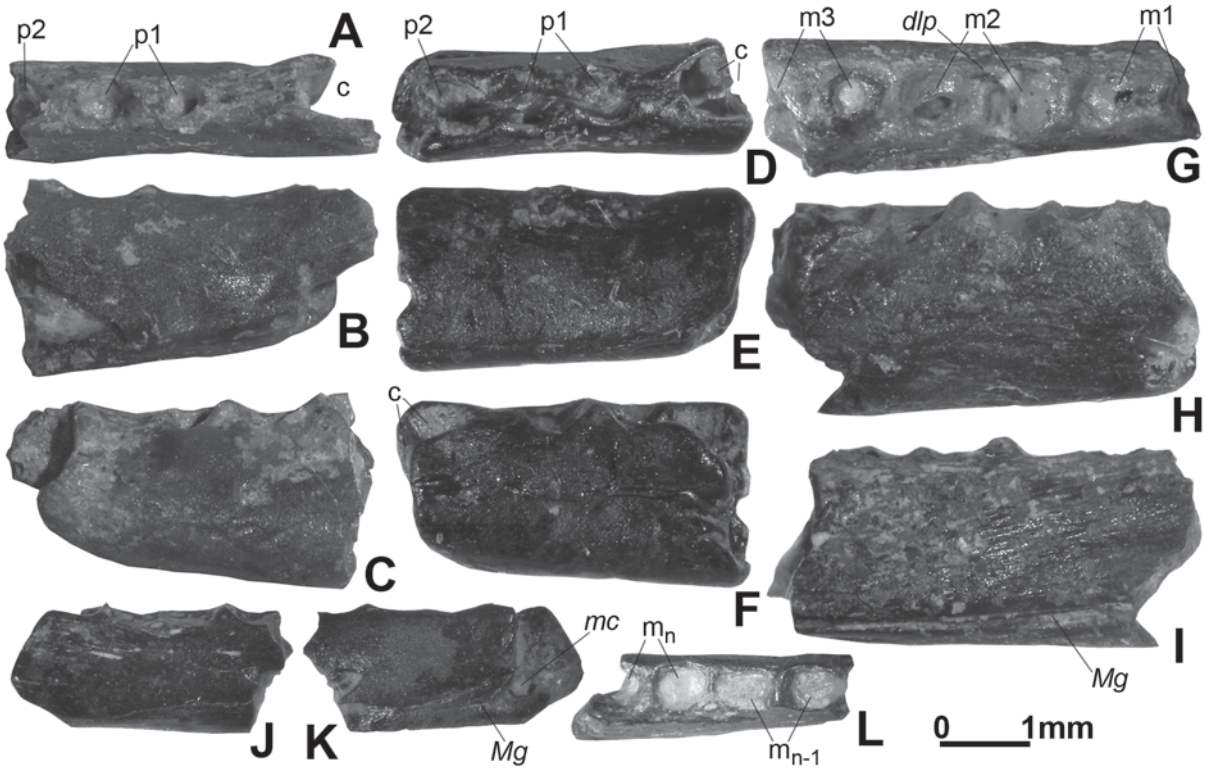

Figure 4. Edentulous dentary fragments of Amphilestidae indet. (A–F), *Gobiconodon* sp. A (G–I), and Mammalia indet. (J–L) from Bol'shoi Kemchug 3 locality, Krasnoyarsk Territory, Russia; Ilek Formation, Lower Cretaceous.
A–C — PM TGU 16/6-415, left dentary fragments with alveoli of c and p1–2 in occlusal (A), lingual (B), and labial (C) views. D–F — PM TGU 16/6-412, left dentary fragment with alveoli of c and p1–2 in occlusal (D), lingual (E), and labial (F) views. G–I — PM TGU 16/6-414, right dentary fragment with alveoli of m1–3 in occlusal (G), labial (H), and lingual (I) views. J–L — PM TGU 16/6-413, right dentary fragment with alveoli of ultimate and penultimate molariforms in labial (J), lingual (K), and occlusal (L) views. Abbreviations: dlp — dental lamina pit; mc — posterior opening of the mandibular canal; Mg — Meckel's groove. Scale bar is 1 mm.

On the lower molariform the primary cusps are slightly triangulated, with the trigonid angle 153º. The central cusp *a* is distinctly higher than cusps *b* and *c*. The mesial cusp *b* is somewhat higher than the distal cusp *c*. All primary cusps are connected by trenchant ridges. There are mesiolingual (*e*) and distolingual (*d*) cingulid cusps connected by a continuous lingual cingulid. There is a very faint mesiolabial cusp *f*, separated from the cusp *e* by a small and shallow embayment. There is no labial cingulid. The crown margin is straight or only slightly convex labially and slightly concave at the middle lingually. The crown is higher labially than lingually, with bulbous indentations above roots on labial side. Both these indentations bear wear facets. The roots are divergent ventrally. There is a thin bony septum between roots just below the crown.

Measurements. Lower molariform: PM TGU 16/6-404: L=1.7, W=0.8.

Discussion. Interpretation of PM TGU 16/6-404 poses some difficulties. In a previous preliminary publication (Leshchinskiy *et al.*, 2003) this tooth was referred to Amphilestinae indet. because of supposed lack of an embayment between the mesial cingulid cusps, which is characteristic for the amphilestid (*sensu stricto*) interlocking mechanism as exemplified by the Middle Jurassic taxa from England (Sigogneau-Russell, 2003: pl.1, figs.5, 7; personal observation by the first author). However, this tooth indeed has a very small mesial embayment between cusps *e* and vestigial *f* (Fig. 2G). This discovery shows that this tooth is left, not right as was previously thought (Leshchinskiy *et al.*, 2003: fig.1). A similar poorly differentiated interlocking involving cingulid cusps *e* and *f* is known also in the Late Jurassic amphilestid *Comodon gidleyi* (Simpson, 1925) (Sigogneau-Russell *et al.*, 1990: fig.3; Sigogneau-Russell, 2003: fig.12, pl.1, fig.6; and personal observation). In a new tinodontid from Shestakovo 1 locality in West Siberia (Lopatin *et al.*, 2005) a small cusp *f* and mesial embayment are present in only one specimen. In kuehneotheriids, other tinodontids, gobiconodontids, and therians this interlocking mechanism is usually better developed, while in morganucodontids, megazostrodontids, docodontans, and triconodontids a broad distal margin of a lower molariform fits into a shallow embayment between cusps *b* and *e* on the succeeding molariform (e.g., Kielan-

Jaworowska & Dashzeveg, 1998; Kielan-Jaworowska *et al.*, 2004).

PM TGU 16/6-404 is similar in size with m5 of *Gobiconodon* sp. A from the same locality, by its more triangulated primary cusps, cusp *b* higher than cusp *c*, poorly differentiated mesial embayment, and slightly convex or straight, but not concave at the middle, labial crown margin make attribution of this specimen to a gobiconodontid unwarranted. In gobiconodontid lower molariforms, except m5, the mesial cusp *b* is lower than the distal cusp *c*, as diagnosed by Jenkins & Schaff (1988: 2). Only in *G. hoburensis* are cusps *b* and *c* subequal in height in m2–5 (Kielan-Jaworowska & Dashzeveg, 1998).

PM TGU 16/6-404 is similar with a new tinodontid from Shestakovo 1 (Lopatin *et al.*, 2005) by approximately the same size, slightly triangulated primary cusps, poorly differentiated "therian" interlocking mechanism, and cusp *b* higher than cusp *c*, but differs from that taxon by still greater trigonid angle (153º compared with maximum 139º on m4 in that taxon), straight or slightly convex, not greatly convex, labial crown margin, and better developed lingual cingulid. However, in the more primitive tinodontid *Tinodon* Marsh, 1879 from the Late Jurassic of the USA (e.g., Sigogneau-Russell, 2003: pl.1, figs.8, 9; personal observations) primary cusps on m1 are mesiodistally aligned, approximating the condition of PM TGU 16/6-404. But in m1 of *Tinodon* cusp *b* is distinctly lower than the cusp *c* and the lingual cingulum is less pronounced, compared with PM TGU 16/6-404.

PM TGU 16/6-404 exemplifies a unique combination of the lower molariform characters, such as a slight triangulation of primary cusps, a poorly developed "therian" interlocking mechanism, mesial cusp *b* higher than distal cusp *c*, and cusps *b* and *c* lower than the central cusp *a*. Among mammals with a triconodont molar pattern (i.e. mesiodistally aligned primary cusps) such a combination is known only for some amphilestids (e.g., Jenkins & Schaff, 1988; Kielan-Jaworowska *et al.*, 2004; personal observations). Thus attribution of PM TGU 16/6-404 to the Amphilestidae indet. seems justified. Smaller size of PM TGU 16/6-404 does not allow its attribution to the amphilestid *Kemchugia magna* **gen. & sp. nov.** from the same locality (see above).

Both dentary fragments referred to Amphilestidae indet. are of suitable size for PM TGU 16/6-404. They differ from dentaries in gobiconodontids by double-rooted canine (at least in PM TGU 16/6-412) and p1, and by a marked diastema between canine and p1. A similar pattern of anterior dentary construction, with single or double-rooted canine, variably developed diastema, and double rooted p1 are characteristic for Tinodontidae and Amphilestidae (Kielan-Jaworowska *et al.*, 2004; Lopatin *et al.*, 2005). Among amphilestids a double-rooted canine alveolus was reported for the Middle Jurassic *Amphilestes broderipii* (Simpson, 1928: 72), while Kielan-Jaworowska *et al.* (2004: 226) considered this taxon as having a single-rooted canine.

Gobiconodontidae Chow & Rich, 1984

Gobiconodon Trofimov, 1978

Gobiconodon sp. A

Figs. 4G–I, 5.

Amphilestinae indet. [partim]: Leshchinskiy *et al.*, 2003: 427.

Material. PM TGU 16/6-408, left M1; PM TGU 16/6-406, right M2; PM TGU 16/6-407, mesial fragment of a left upper posterior molariform; PM TGU 16/6-414, right dentary fragment with alveoli of m1−3; PM TGU 16/6-416, right dentary fragment with alveoli of m1−3; PM TGU 16/6-409, left m5.

Description. M1 has apparently complete cingulum around the crown (the most of the labial cingulum is broken off) and relatively triangulated primary cusps (trigon angle ~150º). Cusps *B* and *C* are of similar height and well separated from the central cusp *A*. The crown is wide mesially, with an embayment between poorly differentiated cingular cusps *E* and *F*, and strongly narrowing distally. The interlocking embayment between cusps *E* and *F* continues at some extent on the root beyond the crown. The lingual crown side is broadly convex; the labial side appears to be straight. The cingular cusp *D* is small and placed at the distolabial corner of the crown. The lingual crown side is higher than the labial side, with enamel tracks extending dorsally along the roots. The only preserved mesial root is constricted mesiodistally.

M2 is more symmetrical than M1, with the primary cusps mesiodistally aligned (trigon angle 178º). The crown is concave at the middle both labially and lingually. The cingulum is complete around the crown. Only one cingular cusp (*D*) is present; it is offset labially from the line of primary cusps. The cusps *B* and *C* are low and well separated from the central cusp *A*. Tips of cusps *A*, *B*, and possibly *C*, are broken off. All space between cusps *C* and *D* is excavated by a prominent wear against the central cusp *a* of the corresponding lower molariform. The groove made by this cusp is almost perpendicular to the line of primary cusps.

An upper posterior molariform is represented by a mesial fragment only. The cusps *B* and *A* are broken off for the most part. The labial and lingual cingula are complete on the fragment preserved. A larger labial cingular cusp (*F*) is placed mesiolabially to cusp *B*. It is followed distally by a smaller cusp. On the lingual cingulum there is a smaller cusp (*E*), mesiolingual to cusp *B*, and a larger distal cusp, placed opposite to the notch between cusps *B* and *A*. The latter cingular cusp bears an extensive wear facet on its lingual side. An embayment between the cingular cusps *E* and *F* is small and shallow, almost indistinct. The crown appears to be concave in the middle both labially and lingually. The preserved mesial root is rather long and considerably constricted mesiodistally. It is convex lingually and concave labially.

The dentary is relatively straight and shallow; under m3 it is only slightly deeper than under m1. On the medial side a narrow Meckel's groove is convergent with the ventral border and approximates this border under m1. On both dentary specimens there is a dental lamina pit on lingual side of a bony septum separating the roots of the molariforms (Fig. 4J; see also General discussion).

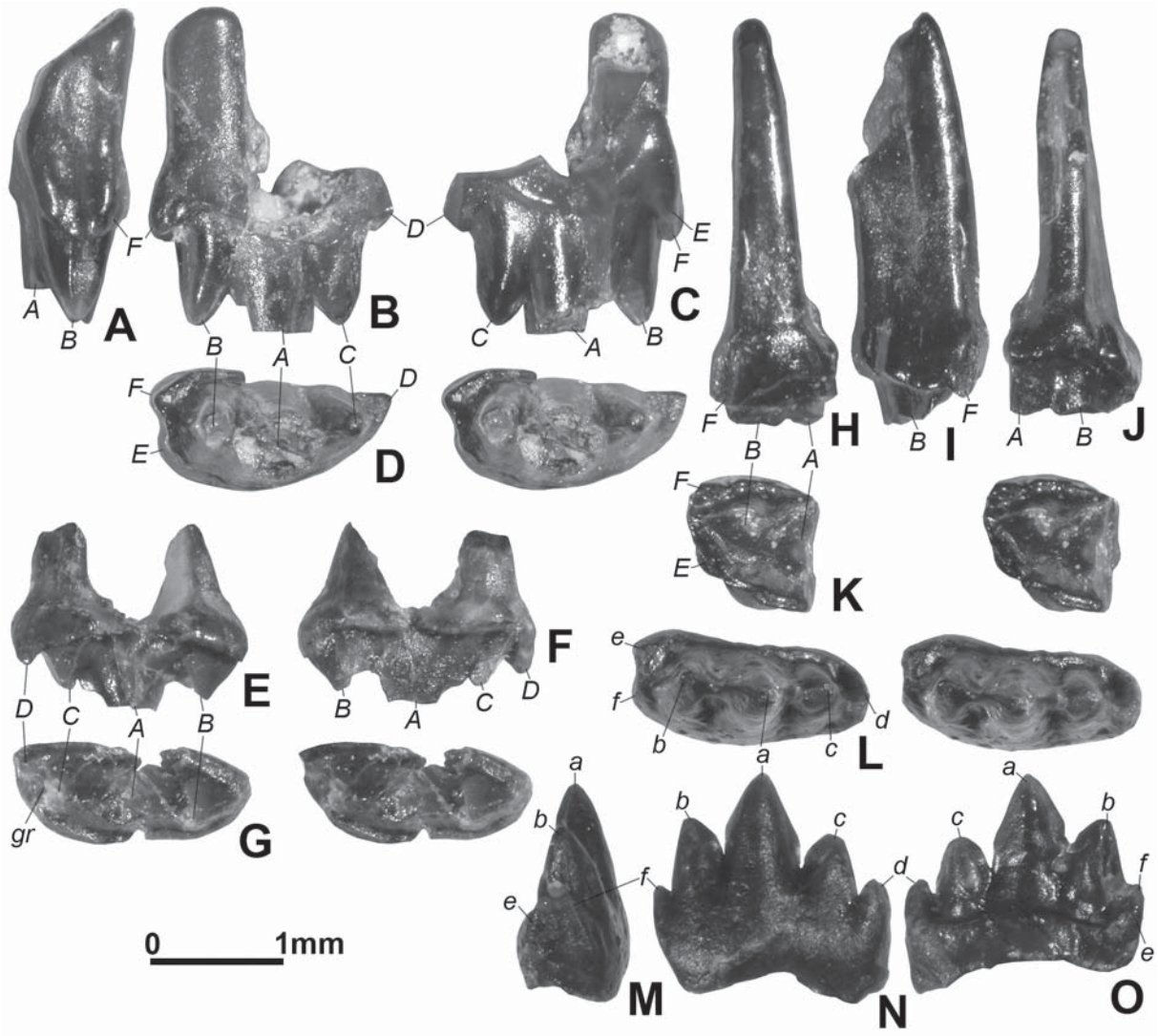

Figure 5. Isolated molariforms of *Gobiconodon* sp. A from Bol'shoi Kemchug 3 locality, Krasnoyarsk Territory, Russia; Ilek Formation, Lower Cretaceous.
A–D — PM TGU 16/6-408, left M1 in mesial (A), labial (B), lingual (C), and occlusal (D) views. E–G — PM TGU 16/6-406, right M2 in labial (E), lingual (F), and occlusal (G) views. H–K — PM TGU 16/6-407, fragment of a left upper posterior molariform in labial (H), mesial (I), lingual (J), and occlusal (K) views. L–O — PM TGU 16/6-409, left m5 in occlusal (L), mesial (M), labial (N), and lingual (O) views. D, G, K, and L are stereo pairs. Abbreviations: gr — wear groove between cusps *C* and *D* made by the central cusp *a* of the corresponding lower molariform. Scale bar is 1 mm.

In m5 cusps *b* and *c* are well individualized and separated from the central cusp *a* by deep notches; all three cusps are mesiodistally aligned and connected by trenchant ridges. Mesial cusp *b* is clearly higher than the distal cusp *c*. Mesial cingulid cusps *e* and *f* are well developed, with an embayment for reception of the cusp *d* of preceding molariform. Distal cingulid cusp *d* is distinct and relatively high. Cusps *f* and *d* are almost on the mesiodistal line of the primary cusps, while cusp *e* is offset significantly lingually. The lingual cingulid is complete between cusps *e* and *d*. There is no labial cingulid.

Measurements. M1: PM TGU 16/6-408: L=1.8, W=0.8. M2: PM TGU 16/6-406: L=1.8, W=0.8. m5: PM TGU 16/6-409: L=1.8; W=0.8.

Discussion. *Gobiconodon* sp. A is similar in size with *G. hoburensis* (Trofimov, 1978) from Höövör, Mongolia (Trofimov, 1978; Kielan-Jaworowska & Dashzeveg, 1998), but differs from that species by better separated cusps *b* and *c* on lower molariforms and by presence of a distinct cingular cusp *E* on the upper posterior molariform. PM TGU 16/6-409 is interpreted here as m5 because it has relatively low crown compared with the crown length and mesial cusp *b* distinctly higher than distal cusp *c* (Jenkins & Schaff, 1988; Kielan-Jaworowska & Dashzeveg, 1998). A mesial upper molariform PM TGU 16/6-408 is similar with M1 in *G. hoburensis* (Kielan-Jaworowska & Dashzeveg, 1998: figs.4A, B, 5) in having a broadly convex labial side (concave at the middle in M2–5) and

a crown strongly narrowing distally and thus interpreted as M1. However, the primary cusps on this tooth appear to be more triangulated than in the Mongolian species. M2 of *Gobiconodon* sp. A (PM TGU 16/6-406) is similar in outline to that tooth in *G. hoburensis* (Trofimov, 1978: fig.2g–e; the tooth is misinterpreted as P4, see Kielan-Jaworowska & Dashzeveg, 1998: 422). In Mongolian species of *Gobiconodon* the upper anterior molariforms (M1–2) have primary cusps mesiodistally aligned, while in the upper posterior molariforms (M3–5) they are triangulated. In the only known skull of Chinese *G. zofiae* there are four upper and five lower molariforms (Li *et al.*, 2003). M1–3 are described as having primary cusps mesiodistally aligned, but from the published figure (Li *et al.*, 2003: fig.1–2) it seems more likely that the primary cusps are mesiodistally aligned on M1–2 and triangulated on M3–4. Li *et al.* (2003) postulated that four upper molariforms would be characteristic for all species of *Gobiconodon*. However, in other mammals with "embrasure" occlusion and known dental formula, like therians, the number of lower and upper molariforms is equal and ultimate lower molariform occluded between penultimate and ultimate upper molariforms. Thus it cannot be ruled out that M5 simply was not yet erupted in the single specimen of *G. zofiae*.

In *Gobiconodon* sp. A, as interpreted here, M1 is more triangulated than M2. This might be caused by variation of the trigon angle between individuals or tooth generations (in *Gobiconodon* anterior molariforms undergo replacement, see Jenkins & Schaff, 1988 and General discussion). An alternative interpretation of a triangulated upper molariform PM TGU 16/6-408 would imply that this specimen does not belong to *Gobiconodon* sp. A. Indeed, this tear-shaped tooth with broad and rounded mesial end and pointed distal end is strikingly similar with the upper molariform of a tinodontid "symmetrodont" "*Eurylambda aequicrurius*" Simpson, 1925 from the Late Jurassic of the USA, usually considered congeneric with *Tinodon* (Simpson, 1925, 1929; Crompton & Jenkins, 1967; Cassiliano & Clemens, 1979; Ensom & Sigogneau-Russell, 2000; Rougier *et al.*, 2003; and personal observation by the first author). A tinodontid "symmetrodont" is abundant in a close Early Cretaceous Shestakovo mammal fauna in West Siberia (Lopatin *et al.*, 2005) and thus finding a similar taxon at Bol'shoi Kemchug 3 would not be surprising (unfortunately, a tinodontid taxon from Shestakovo is known only from the lower dentition). However, PM TGU 16/6-408 is clearly different from "*Eurylambda*" by having relatively higher "triconodont"-like cusps *B* and *C*, by having an interlocking embayment between cusps *E* and *C*, by a better developed lingual cingulum, and by a total lack of a stylar shelf between the labial cingulum and primary cusps. Thus, attribution of PM TGU 16/6-408 to *Gobiconodon* seems to be more corroborated at the moment.

Sigogneau-Russell (2003: 49) reported one unpublished lower molariform of *Gobiconodon* (of unspecified whereabouts) with interlocking sulcus between cingulid cusps *e* and *f* continuing down the root, a condition better pronounced in triconodontids (e.g., Cifelli *et al.*, 1998). A similar extension of the interlocking sulcus down the root is observed also in the upper molariform PM TGU 16/6-408.

Gobiconodon sp. B

Fig. 6.

Gobiconodon [sp.]: Leshchinskiy *et al.*, 2003: 427.

Morganucodontidae? indet. [partim]: Leshchinskiy *et al.*, 2003: 427.

Material. PM TGU 16/6-402, left I2?; PM TGU 16/6-403, left p4; PM TGU 16/6-405, left m5.

Description. A caniniform tooth is interpreted as a possible left I2 (see discussion). The tooth has a considerably convex mesial margin and a straighter distal margin (concave on the crown). The crown is about twice as short as the root. It has a bluntly pointed tip and a distinct ridge along the distal edge. On the lingual side close to the crown-root contact there is a very short and faint cingulum. The root is mesiodistally widest some distance above the crown and then tapers dorsally. The root is subdivided by a longitudinal groove both labially and lingually (the labial groove is somewhat deeper).

The p4 is one rooted with a bulbous crown dominated by the central cusp *a*. Cusps *b* and *c* are of similar size, distinctly lower and well separated from the central cusp. Cusp *b* is somewhat labially displaced from a line formed by cusps *a* and *c*. On the lingual side between cusps *b* and *c* there is a distinct cingulid. There is no labial cingulid.

The m5 has two well separated roots. The central cusp *a* is placed closer to the mesial end. All three primary cusps are mesiodistally aligned and connected by sharp ridges; their tips are considerably worn. Mesial cusp *b* more closely approximates the central cusp and apparently was somewhat higher than the distal cusp *c*. Distal cingulid cusp *d* is distinct and distally projecting. Mesial cingulid cusps *e* and *f* are not individualized, but there is an mesial embayment for reception of the cusp *d* of preceding molariform. There is a distinct continuous lingual cingulid. The labial cingulid is lacking. The labial crown side is higher than the lingual crown side, with enamel tracks extending somewhat ventrally along the roots.

Measurements. I2?: L=2.4, W=2.2, H=3.5 (crown), 10.1 (whole tooth). p4: PM TGU 16/6-403: L=2.0, W=1.4. m5: PM TGU 16/6-405: L=3.0, W=1.5.

Discussion. *Gobiconodon* sp. B is about 70% larger than *Gobiconodon* sp. A from the same locality, about 20% larger than *G. zofiae* Li *et al.*, 2003 from the Yixian Formation in Liaoning Province, China and *G. borissiaki* Trofimov, 1978 from Höövör, Mongolia (Trofimov, 1978; Kielan-Jaworowska & Dashzeveg, 1998; Li *et al.*, 2003), and distinctly smaller than *G. ostromi* Jenkins & Schaff, 1988 from the Cloverly Formation in Montana, USA (Jenkins & Schaff, 1988). By its three-cusped single-rooted p4 *Gobiconodon* sp. B is most similar with *G. borissiaki*. In *G. hoburensis*, *Gobiconodon* sp. from Oshih, Mongolia, and *G. zofiae* p4 is double-rooted (Kielan-Jaworowska & Dashzeveg, 1998;

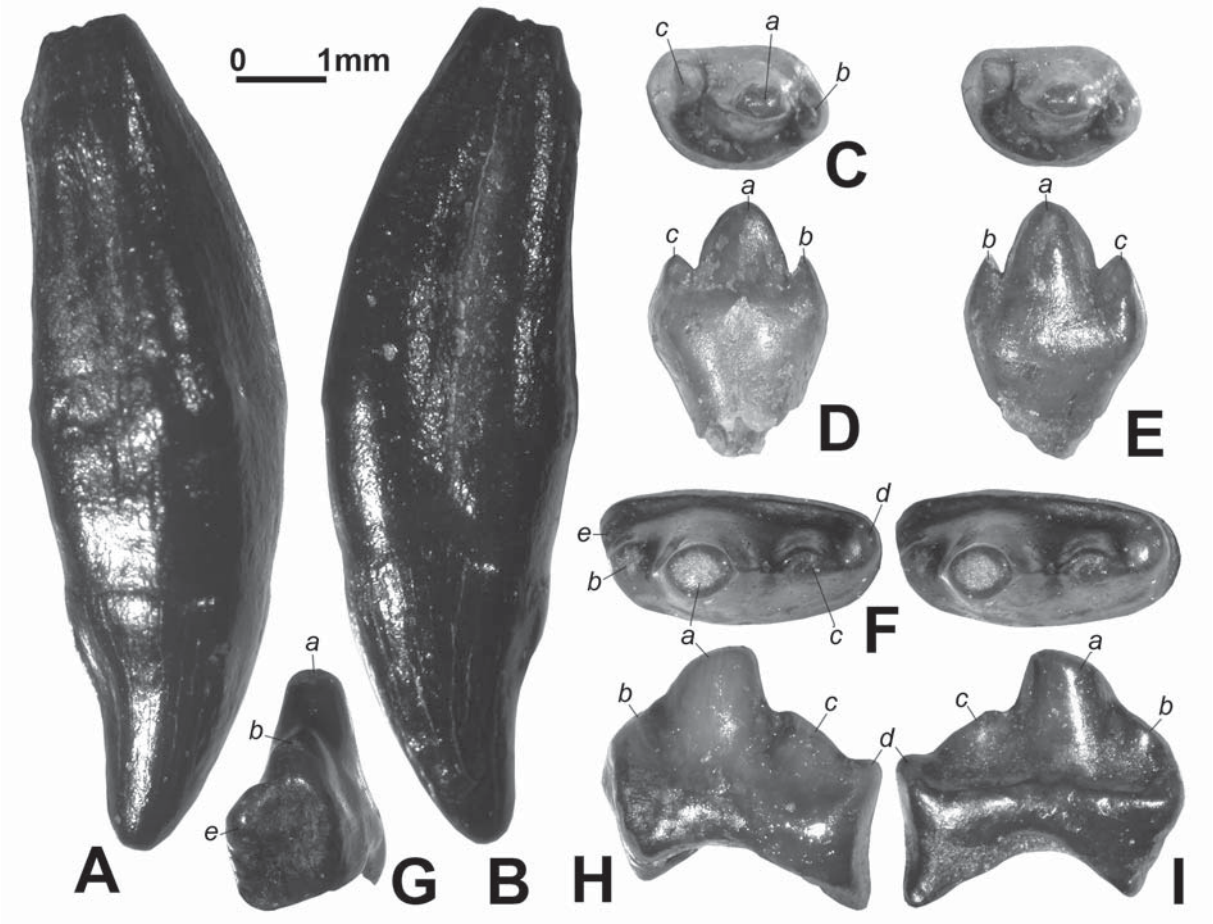

Figure 6. Isolated teeth of *Gobiconodon* sp. B from Bol'shoi Kemchug 3 locality, Krasnoyarsk Territory, Russia; Ilek Formation, Lower Cretaceous.
A–B — PM TGU 16/6-402, left I2? in lingual (A) and labial (B) views. C–E — PM TGU 16/6-403, left p4 in occlusal (C), lingual (D), and labial (E) views. F–I — PM TGU 16/6-405, left m5 in occlusal (F), mesial (G), labial (H), and lingual (I) views. C and F are stereo pairs. Scale bar is 1 mm.

Maschenko & Lopatin, 1998; Rougier *et al.*, 2001; Li *et al.*, 2003). In PIN 4463/1 from Shestakovo 1, referred to *G. borissiaki* by Maschenko & Lopatin (1998: fig.3), p4 is also double-rooted. In *G. ostromi* the root of p4 is "incipiently double" on one side, while single on the other side of the same specimen (MCZ 19860; Jenkins & Schaff, 1988: 4). In another specimen of *G. ostromi* (MCZ 19965) an alveolus between p3 and m1 is completely filled in with bone. Jenkins & Schaff (1988) interpreted this alveolus to be for a deciduous tooth. However, according to Rougier *et al.* (2001: 9) in MCZ 19965 there is no evidence for an alveolus and this specimen appears to be younger than MCZ 19860 preserving the alveoli for p4. Thus, the differential presence of a p4 in *G. ostromi* cannot be explained by resorption and plugging of its alveolus by bone in older specimens. So, the presence of p4 could be a polymorphic character in populations of *G. ostromi*, or this tooth could erupt very late in the ontogenesis of this species.

PM TGU 16/6-406 is interpreted as m5 because it has a relatively low crown compared with the crown length, and mesial cusp *b* is somewhat higher than distal cusp *c* (Jenkins & Schaff, 1988; Kielan-Jaworowska & Dashzeveg, 1998).

Interpretation of PM TGU 16/6-402 is rather difficult because in gobiconodontids incisors are procumbent and caniniform, while canines are reduced to varied extend (Jenkins & Schaff, 1988; Hu *et al.*, 2005). PM TGU 16/6-402 is generally similar with the last upper incisor (I3) in *Repenomamus giganticus* Hu *et al.*, 2005 from the Early Cretaceous of China (Hu *et al.*, 2005: fig.1b) in general shape and subdivided root. In *G. ostromi* the last upper incisor (I2) is also large and bears a low crest along its distal surface (Jenkins & Schaff, 1988). In a single procumbent lower incisor (i1) and lower canine of *Gobiconodon* there are two low crests, on labial and lingual sides, and the canine crown is somewhat spatulate (Jenkins & Schaff, 1988; Maschenko & Lopatin, 1998). Thus PM TGU 16/6-402 is more likely an upper posterior incisor, I2 if it is belonging to *Gobiconodon*. Its large size is more suitable for a larger *Gobiconodon* sp. B from Bol'shoi Kemchug 3 locality.

Mammalia indet.

Fig. 4J–L.

Material. PM TGU 16/6-413, right dentary fragment with alveoli for two last molariforms.

Description. Dentary fragment preserves alveoli for two double-rooted teeth, apparently two last molariforms. The alveoli are rounded for the ultimate molariform, while almost rectangular for the penultimate molariform. On the lingual side there is a broad Meckel's groove close to the ventral border and associated with the posterior opening of the mandibular canal (the area of the mandibular foramen is not preserved).

Discussion. PM TGU 16/6-413 is distinctly smaller than Amphilestidae indet. and *Gobiconodon* sp. A from Bol'shoi Kemchug 3 locality and thus represents additional, yet unknown taxon from this assemblage.

General discussion

A small sample of mammalian isolated teeth and edentulous dentary fragments from Bol'shoi Kemchug 3 locality produces a surprisingly diverse assemblage: amphilestid *Kemchugia magna* **gen. & sp. nov.**, Amphilestidae indet., gobiconodontids *Gobiconodon* sp. A and B, and Mammalia indet. All positively identified taxa belong to Eutriconodonta.

Although vertebrate faunas from Shestakovo 1 and 3 and Bol'shoi Kemchug 3 localities are basically similar, the mammalian component of these faunas is not easy to compare because of much difference in sampling size. Mammals from Shestakovo 1 are known from dozens of specimens, while those from Bol'shoi Kemchug 3 are represented by few very fragmentary specimens. An area of congruence is a dominance of gobiconodontid "triconodonts" in both faunas. However, in Shestakovo 1 the second dominant taxon is a tinodontid "symmetrodont" (Lopatin *et al.*, 2005), which is not yet recorded from Bol'shoi Kemchug 3. A tegotheriid docodont *Sibirotherium rossicus* Maschenko *et al.*, 2003, a rare element of the Shestakovo 1 mammal fauna, is not found in Bol'shoi Kemchug 3. Similarly, a peramuran *Kiyatherium cardiodens* Maschenko *et al.*, 2002, known from Shestakovo 1 and 3 by few specimens, is not known from Bol'shoi Kemchug 3. Amphilestidae (sensu stricto) are represented by two taxa in Bol'shoi Kemchug 3. Presence of Amphilestidae indet. in the Shestakovo fauna is based on a single questionable lower molariform. Obviously, the difference in the presence of rare taxa between both faunas might be caused largely by a sampling bias, especially by the imperfect knowledge of the Bol'shoi Kemchug 3 mammal fauna.

In Bol'shoi Kemchug 3, Shestakovo 1, Oshih, and Höövör *Gobiconodon* is represented by at least two species, a smaller one and a larger one. A larger *Gobiconodon* sp. B from Bol'shoi Kemchug 3 is closer to the Mongolian *G. borissiaki* by the presence of single-rooted p4, than to the larger *Gobiconodon* from Shestakovo 1, having a double-rooted p4. Evolutionary significance of this distinction is difficult to evaluate at the moment, because the range of variation of p4 in *Gobiconodon* is still poorly understood. A rapidly growing sample of *Gobiconodon* specimens from Shestakovo 1 and various Chinese localities may resolve this and other questions in the nearest future.

One of the peculiar characteristics of *Gobiconodon* is replacement of at least three anterior molariforms, as documented by direct evidence in *G. ostromi* and by differential wear in *G. borissiaki* (Jenkins & Schaff, 1988). The same was characteristic also for the gobiconodontid *Repenomamus*, as evident by replacement in the third molariform locus after m5 fully erupted (Wang *et al.*, 2001: fig.1C; Hu *et al.*, 2005: fig.1c). It is unclear at the moment if this is retention of a primitive feature of a cynodont level of organization or a secondary, "atavistic" modification (Jenkins & Schaff, 1988; Kielan-Jaworowska & Dashzeveg, 1998; Rougier at al., 2001; Kielan-Jaworowska *et al.*, 2004). We favor of later hypothesis. Reversal to molariform replacement in gobiconodontids might be connected with the prolonged growth and increased body size in *Gobiconodon* and in even larger and more derived *Repenomamus* (both taxa include largest Mesozoic mammals known so far: Hu *et al.*, 2005). In dentaries of *Gobiconodon* sp. A from Bol'shoi Kemchug 3 and gobiconodontids from Shestakovo 1 a slit-like pit on lingual side of a bony septum separating molariform roots (Fig. 4G) is quite common. These pits are interpreted here as openings for the epidermal filaments connecting the dental lamina with the enamel cup of a developing molariform successor. Position of these pits between the roots of a replacing molariform provides shortest access of the dental lamina tissue to the enamel cup around the central cusp of the growing germ of a molariform successor. These pits are analogous to the replacement pits in some reptiles, like lizards, and to the dental lamina groove seen in sinoconodontids, morganucodontids and some docodontans (Parrington, 1971; Luo, 1994; Averianov *et al.*, in press a) and, undoubtedly, connected with replacement of molariforms in *Gobiconodon*. Study of the distribution of dental lamina pits in isolated gobiconodontid jaws may provide and additional information about replacement pattern when direct evidence of replacement is lacking.

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