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ARTICLE

MAMMALS FROM THE MIDDLE JURASSIC BALABANSAI FORMATION OF THE FERGANA DEPRESSION, KYRGYZSTAN

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ABSTRACT—At least 10 (or more) mammal taxa have been identified from the Middle Jurassic (Callovian) Balabansai Formation in northern Fergana Depression, Kyrgyzstan, on the basis of mostly isolated and fragmentary teeth: docodontans cf. *Simpsonodon* spp., *Paritatodon* sp. [*Paritatodon*, gen. nov., is established for '*Shuotherium kermacki*' Sigogneau-Russell, 1998, from the Bathonian of England], *Tashkumyrodon desideratus*, Tegotheriidae indet.; and Docodonta indet.; eutriconodontans Amphilestidae indet.; *Ferganodon narynensis*, cf. *Ferganodon* sp., and Triconodontidae indet.; 'symmetrodontan' Tinodontidae indet.; and cladotherians Paurodontidae indet. and Amphitheriidae indet. The occurrences of Triconodontidae, Tinodontidae, and Paurodontidae in the Balabansai Formation represent the oldest-known records of these groups. The Balabansai mammal assemblage is basically similar to the Bathonian mammals of the Forest Marble in England and the Itat mammal assemblage in Siberia respectively, revealing at present knowledge a marked uniformity of the Middle Jurassic mammal fauna across Laurasia.

INTRODUCTION

Grey and red beds of the Middle Jurassic (Callovian) Balabansai Formation in the Fergana Depression, Kyrgyzstan, yielded some important fossils of terrestrial and aquatic vertebrates in this poorly studied part of Central Asia: the fossil localities are situated on the shore of the Fergana Gulf of the Tethys Ocean in the Mesozoic. Balabansai vertebrates were studied in the 1980s and 1990s by L. A. Nesov and his colleagues and from 2000 onwards by the joint expeditions of the present authors and the Institute of Geology of the National Academy of Science in Bishkek (see Averianov et al., 2005, for details). Among the many thousands of microvertebrate fossils (predominantly shark teeth, fish scales, and turtle shell fragments) recovered by screen washing during this project, some 30 teeth and tooth fragments of mammals give a picture of the most diverse Middle Jurassic mammalian assemblage that is known from Asia so far, comprising at least 10 taxa. New docodontan and eutriconodontan species have been published earlier (Martin and Averianov, 2004, 2007), and here we describe additional mammalian specimens that have been recovered since then.

In the classification of Mesozoic mammals we generally follow Kielan-Jaworowska et al. (2004), including the concept of Eutriconodonta employed in that book. According to the recent phylogenetic analysis by Rougier et al. (2007a), the Eutriconodonta are polyphyletic. The family Tegotheriidae Tatarinov, 1994, was considered a synonym of Docodontidae Simpson, 1929, by Kielan-Jaworowska et al. (2004:196). Maschenko et al. (2002) had provided an emended differential diagnosis of Tegotheriidae based on the newly discovered *Sibirotherium* from the early Cretaceous of Siberia. This taxon and the new differential diagnosis of Tegotheriidae were not considered by Kielan-Jaworowska et al. (2004), because the article by Maschenko et al. (2002) was published after the closing date for that book. Diagnoses for Klameliidae are given in Martin and Averianov (2007) and for Jeholodontidae in Luo et al. (2007b). The informal term 'amphilestid grade of eutriconodontans' is here used for Eutriconodonta retaining a plesiomorphic molariform cusp pattern with cusp A/a considerably higher than cups B/b and C/c ("Amphilestidae," Klameliidae, Gobiconodontidae, and Jeholodentidae).

Specimens were coated with gold and examined with a Cambridge CamScan MV 2300. Electronically captured images were cut out and adjusted in contrast and grey levels using Photoshop, but not otherwise retouched.

Measurements—**L**, length; **W**, width.

Institutional Abbreviation—**ZIN**, Zoological Institute, Russian Academy of Sciences, St. Petersburg. Abbreviations of names of fossil sites: FTA, FBX.

Mammal Localities within the Balabansai Formation

Three vertebrate localities within the Middle Jurassic Balabansai Formation in the northern Fergana Valley, Kyrgyzstan, have produced mammalian remains (Fig. 1). The undeterminable ?docodont upper molariform and mammalian ulnar fragment reported from Kalmakerchin in the eastern Fergana region (Nesov et al., 1994) are not considered here.

(1) Sarykamyshsai 1 (site FTA-30), about 1 km airline distance east of the town of Tashkumyr (lower, gray to greenish colored part of the Balabansai Formation, Callovian; N41°20′04.2″, E72°14′45.3″). Six and a half metric tons of matrix screenwashed here in 2000 and 2001 produced a single mammal specimen, the holotype of *Tashkumyrodon desideratus* Martin and Averianov, 2004 (ZIN 85279).

(2) Tashkumyr 1 (site FTA-131), left bank of the Naryn River close to the town of Tashkumyr (bonebed within a calcareous sandstone of the lower part of the Balabansai Formation, Callovian); N41°20′18.4″, E072°13′52.6″. In 2001 and 2003 a total of 850 kg of matrix was dissolved with acetic acid and screenwashed in the field and in the laboratory in Germany. The majority (31 specimens) of mammalian teeth known so far from the Balabansai Formation and described in this paper come from this locality.

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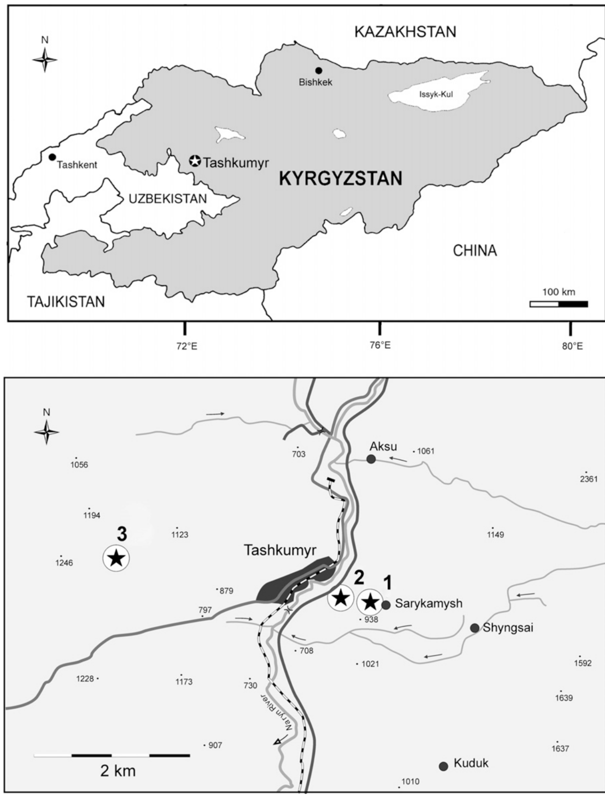


FIGURE 1. Map of Kyrgyzstan (top) and position of the mammal bearing localities of the Balabansai Formation in the surroundings of the town of Tashkumyr (bottom). Localities are denoted by asterisk: **1**, Sarykamyshsai 1 (site FTA-30); **2**, Tashkumyr 1 (site FTA-131); **3**, Dzhiddasai (site FBX-23). Numbers and dots in the map indicate elevation above sea level in meters.

(3) Dzhiddasai (site FBX-23), about 2 km airline distance west of the town of Tashkumyr (upper, red colored part of the Balabansai Formation, Callovian); N41°19′34.0″, E072°06′43.7″. A total of approximately one metric ton of matrix was screenwashed here in 2001 and 2003. A single mammalian specimen was recovered, a canine of an undetermined docodontan (ZIN 96611).

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
DOCODONTA Kretzoi, 1946
SIMPSONODON Kermack, Lee, Lees, and Mussett, 1987
cf. *SIMPSONODON* spp.
(Figs. 2 and 3)

Material—ZIN 96593 (FTA-131, 2003), right upper molariform tooth with damaged mesiolabial region (Fig. 2A–E); ZIN 96582 (FTA-131, 2003), heavily worn left upper molariform tooth (Fig. 2F, G); ZIN 96594 (FTA-131, 2003), labial fragment of a right upper molariform tooth; ZIN PH 96586 (FTA-131, 2003), lingual fragment of a right upper molariform tooth; ZIN PH 96589 (FTA-131, 2001), lingual fragment of a left upper molariform tooth; ZIN PH 96609 (FTA-131, 2001), lingual fragment of a left upper molariform tooth; ZIN 96598 (FTA-131, 2003), mesial fragment of a left lower molariform tooth (Fig. 3A, B); ZIN 96584 (FTA-131, 2003), distal fragment of a right lower molariform tooth (Fig. 3C); ZIN 97341 (FTA-131, 2003), right ultimate lower molariform tooth (Fig. 3D–F).

Description—ZIN 96593 is an almost complete upper molariform tooth, with the mesiolabial corner somewhat damaged (Fig. 2A–E). The crown is of pentagonal shape in occlusal view, with two main labial cusps (A and C) and two main lingual cusps (X and Y). The lingual cusps are opposite the labial cusps and cusp X protrudes further lingually than cusp Y. The lingual portion of the crown is distinctly shorter than the labial portion. The mesial cusps (A and X) are somewhat larger than the distal cusps (C and Y). All four main cusps are connected by variably developed crests: the most robust is the transverse crest A–X, whereas crests C–Y and X–Y are very weak. Crest A–C is moderately developed. These crests are delimiting the concave area in the center of the crown. A peculiar additional crest connects the middle of crest A–X with the cingular cusp B (the cusp itself is broken in this specimen). A small portion of the mesial cingulum is preserved at the base of cusp X. The labial cingulum is unclear because most of the labial side of the tooth is destroyed. All crests and the apices of the main cusps of ZIN 96593 are heavily worn. The tooth has three roots, two labial and one lingual.

ZIN 96582 (Fig. 2F, G) is almost one-third the size of ZIN 96593 and differs from the latter by its tetragonal shape (pentagonal in ZIN 96593) due to the reduction of the mesiolabial lobe of the former specimen. Crest A–X is straighter than in ZIN 96593, and cusp X is almost two times the size of cusp Y. Cusp B is hardly distinguishable and the mesial cingulum is weakly developed.

ZIN 96594, an upper molariform, preserves the labial portion of the crown with the labial cusps A, B, and C. Cusp B is developed as a cingular cusp situated clearly labially of cusp A. Cusp C is almost two times smaller than cusp A. An ectoflexus is lacking and there is a wide labial shelf bordered labially by a prominent ectocingulum.

There are three lingual fragments of upper molariform teeth (ZIN 96586, 96589, and 96609). The lingual cusps X and Y were connected by transverse crests with the (missing) labial cusps. Cusp Y is always smaller than cusp X; both cusps are separated by a lingual incision into the crown. There is a rather robust mesial cingulum, forming the mesial convexity of the crown.

In a mesial fragment of a left lower molariform tooth (ZIN 96598), cusps b and g and the majority of the pseudotalonid are preserved (Fig. 3A, B). Cusp b is very prominent and much higher than cusp g. Cusp b is connected to cusp g by a robust crest b–g. A well-developed mesial cingulid extends from the apex of cusp b mesiolingually around the entire preserved fragment.

ZIN 96584 is a distal portion of a right lower molariform tooth with the base of the largely missing central cusp a, distolingual cusp c, and distal cusp d (Fig. 3C). The crown is gradually sloping distally. Crest a–c is interrupted by a deep notch at the base of cusp c. Distal to this crest and lingual to a poorly defined crest a–d there is a deep transverse cleft. A flattened area distal to this cleft and lingual to the crest a–d is covered by numerous crenulations. This area is heavily worn and pitted by enamel depressions, the largest of which is adjacent to crest a–d and the distal border of the crown. Cusp d is indistinct; its apex is connected by a faint ridge with the largest enamel depression. The tooth fragment preserves part of the distal root, which is mesiodistally compressed.

ZIN 97341 is an almost complete ultimate right lower molariform tooth (Fig. 3D–F). The crown area posterior to cusp a is reduced. The crown is oval in occlusal view, with the mesial side wider than the distal side. The three remaining crown cusps (a, b, and g) and their connecting ridges are marginally positioned and enclose the central basin (pseudotalonid). The cusps are low, with cusp b being the highest and cusp g the lowest and smallest. Cusp g is situated opposite to cusp b. The floor of the pseudotalonid is finely crenulated. There are a long mesial cingulid extending labially to cusp b, and a shorter distal cingulid, connected to cusp a by two short longitudinal ridges. The latter two ridges are rudiments of crests a–c and a–d. The tooth is double rooted, with the diameter of the distal root less than half that of the mesial root.

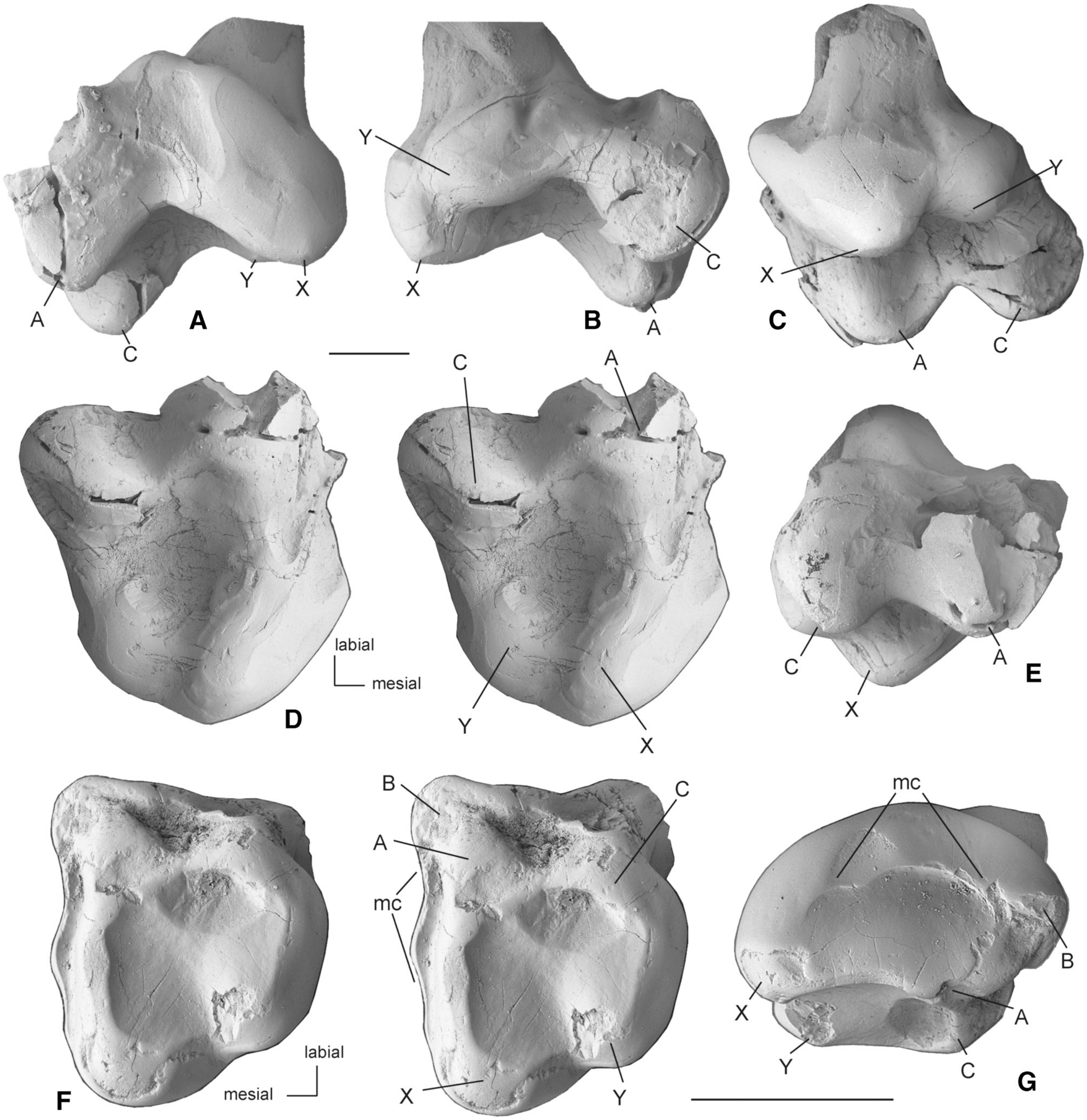


FIGURE 2. Upper molariform teeth or tooth fragments of cf. *Simpsonodon* spp. (apparently more than one species in the sample). Tashkumyr 1 (site FTA-131), Middle Jurassic (Callovian). **A**–**E**, ZIN 96593, right upper molariform tooth in (**A**) mesial, (**B**) distal, (**C**) lingual, (**D**, stereopair) occlusal, and (**E**), labial views; **F**, **G**, ZIN 96582, heavily worn left upper molariform tooth in (**F**, stereopair) occlusal and (**G**) mesio-occlusal views. Scale bars equal 0.5 mm. **Abbreviations**: **A**, **B**, **C**, **X**, and **Y**, upper molariform tooth cusps; **mc**, mesial cingulum.

Measurements—ZIN 96593: L = 1.99, W = ∼2.10; ZIN 96582: L = 0.69, W = 0.83; ZIN 96594: L = 1.15; ZIN PH 96586: length of lingual part of the crown 0.85; ZIN PH 96589: length of lingual part of the crown 1.06; ZIN PH 96609: length of lingual part of the crown 1.24; ZIN 96598: W = 0.94; ZIN 97341: L = 1.05, W = 0.74.

Discussion—Given the considerable size variation of the teeth assigned to cf. *Simpsonodon* sp. and that ZIN 96593 is exceptionally large, it cannot be ruled out that there are more than one species represented in this sample.

In general shape and proportion ZIN 96593 is very similar to the upper molariforms referred to *Simpsonodon oxfordensis* Kermack et al., 1987, from the Bathonian of England (e.g., Kermack et al., 1987:figs. 30–32). The main difference in ZIN 96593 is the presence of an additional crest connecting the (missing) cingular cusp B with the middle of the transverse crest A–X. None

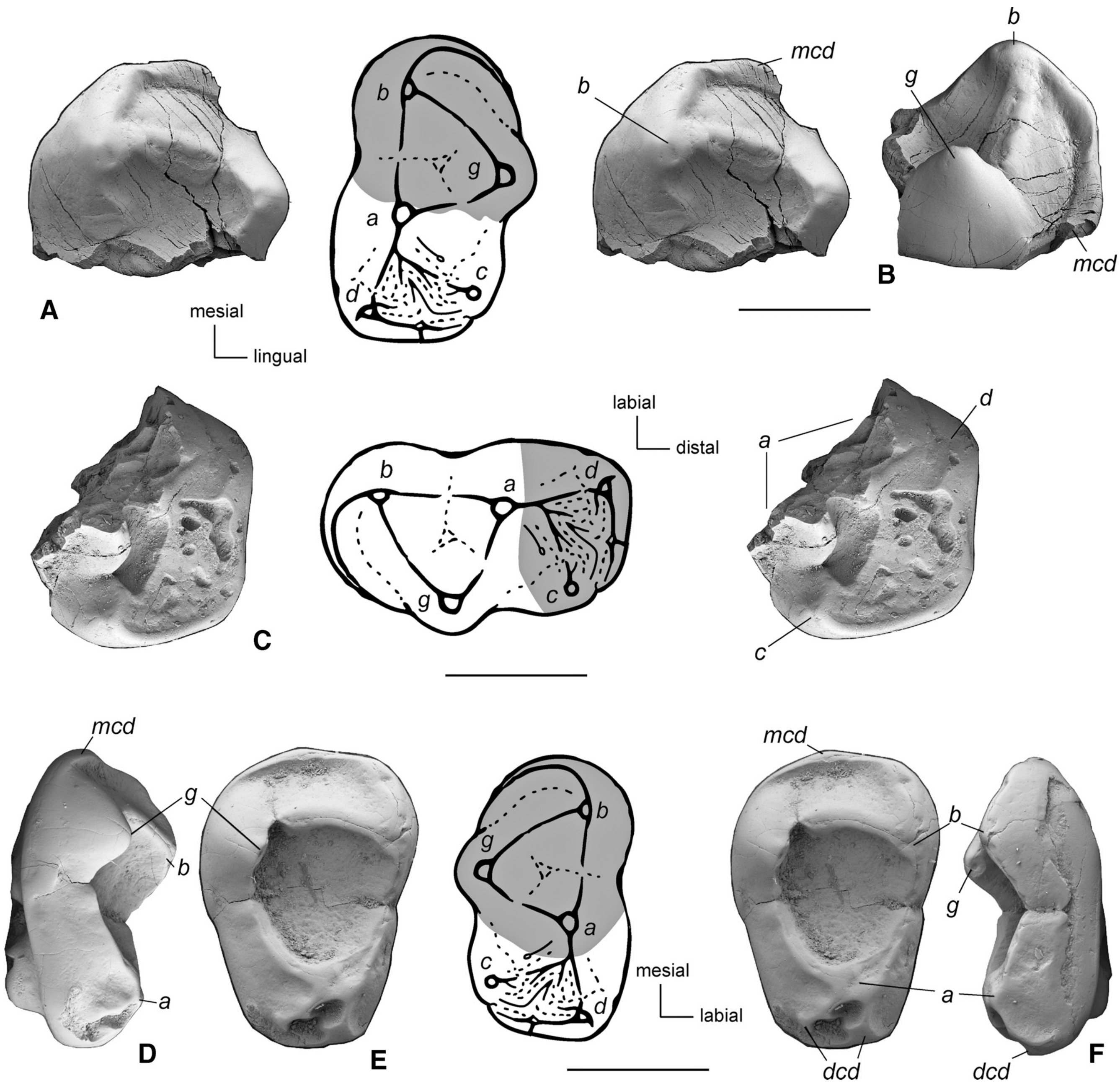


FIGURE 3. **A**–**C**, lower molariform tooth fragments of cf. *Simpsonodon* spp. with explanatory schematic drawings of *Simpsonodon* lower molariforms in occlusal view with the preserved parts shaded (redrawn after Luo and Martin (2007). Tashkumyr 1 (site FTA-131), Middle Jurassic (Callovian). **A, B**, ZIN 96598, mesial fragment of a left lower molariform tooth in (**A**, stereopair) occlusal and (**B**) lingual views; **C**, ZIN 96584, distal fragment of a right lower molariform tooth in occlusal view (stereopair); **D**–**F**, ZIN 97341, right ultimate lower molariform tooth in (**D**) lingual, (**E**, stereopair), occlusal, and (**F**), labial views. Scale bars equal 0.5 mm. **Abbreviations**: **a**, **b**, **c**, **d**, and **g**, lower molariform tooth cusps; **dcd**, distal cingulid; **mcd**, mesial cingulid.

of the upper molariform teeth attributed to *S. oxfordensis* shows this structure. The labial fragment of an upper molariform tooth (ZIN 96594) is also similar to *S. oxfordensis*, especially in the lack of the ectoflexus, the wide labial shelf, and the cingular cusp B situated well labially to cusp A.

The preserved part of ZIN 96584 (Fig. 3C) is also strikingly similar to the lower molariforms of *Simpsonodon* in having a strongly crenulated area between crests a–c and a–d and a deep cleft distal to crest a–c. Interpretation of ZIN 96598, a mesial fragment of a lower molariform tooth, is more difficult. It is similar not only to *Simpsonodon*, but also to *Dsungarodon zuoi* Pfretzschner and Martin, 2005 from the Oxfordian of Xinjiang, China (in Pfretzschner et al., 2005). However, in *Dsungarodon* the anterior cingulid is shorter and more mesially directed. In this respect ZIN 96598 is more similar to the lower molariforms of *Simpsonodon*.

ZIN 97341 is structurally similar to the ultimate lower molariforms of *Dsungarodon* (Pfretzschner et al., 2005:fig. 3B) and a new species of *Simpsonodon* from Siberia (Averianov et al., in preparation), in retention of the distal cingulid. A sculptured pseudotalonid basin suggests attribution of ZIN 97341 to cf. *Simpsonodon* sp., which is supported by a longer mesial cingulid. ZIN 97341 differs from both *Simpsonodon* and *Dsungarodon* in the more oval shape of its crown.

TEGOTHERIIDAE Tatarinov, 1994
PARITATODON, gen. nov.

Type Species—*Shuotherium kermacki* Sigogneau-Russell, 1998.

Diagnosis—Differs from *Tegotherium* Tatarinov, 1994, *Tashkumyrodon* Martin and Averianov, 2004, and *Sibirotherium* Maschenko et al., 2003, and is similar to *Itatodon* Lopatin and Averianov, 2005, in the reduction of crest a–b, a strong cingulid around the lingual side of the crown, and a comparatively small pseudotalonid. Differs from *Itatodon* in almost longitudinal labial arms and more transverse lingual arms of the crests a–c and a–g, with the angle between these arms approximating 90°, and in a less pronounced labial cingulid.

Etymology—From Greek *para*, near, and the generic name *Itatodon* Lopatin and Averianov, 2005.

Comments—*Shuotherium kermacki* Sigogneau-Russell, 1998, was established based on two isolated lower molariform teeth from the Bathonian Forest Marble Formation at Kirtlington, England, and was originally interpreted as a shuotheriid 'symmetrodontan' (Sigogneau-Russell, 1998). *Shuotherium* Chow and Rich, 1982, is a peculiar mammal with a pseudotalonid from the Middle Jurassic of England and the Middle and Late Jurassic of China (Chow and Rich, 1982; Kermack et al., 1987; Hopson, 1995; Wang et al., 1998; Kielan-Jaworowska et al., 2002, 2004; Luo et al., 2007a). Affinities of *Shuotherium* are debated, and it is considered either a theriiform (Averianov, 2002; Rougier et al., 2007b) or a basal australosphenid (Luo et al., 2007a). Sigogneau-Russell (1998) referred two lower molariforms from Kirtlington to the Chinese species *Shuotherium dongi* Chow and Rich, 1982, one tooth to *Shuotherium* sp., and two larger teeth to *Shuotherium kermacki*. However, the holotype of the latter species (Sigogneau-Russell, 1998:fig. C) shows significant differences from other shuotheriid specimens in its almost longitudinal mesial and distal crests descending from the apex of the main cusp ('protoconid' = cusp a). On the other hand, the holotype of '*Shuotherium*' *kermacki* (Fig. 4D) is extremely similar to a lower molariform of the docodontan *Itatodon tatarinovi* Lopatin and Averianov, 2005, from the Bathonian of the Itat Formation at Berezovsk Quarry, Western Siberia, Russia (Averianov and Lopatin, 2006:fig. 1a–e; pl. 8, fig. 1). Here we restrict the species '*Shuotherium*' *kermacki* Sigogneau-Russell, 1998 to the holotype (the referred specimen, Sigogneau-Russell, 1998:fig. D, might be a shuotheriid), remove it from shuotheriids, and refer it to a new genus within Tegotheriidae closely allied with *Itatodon*.

PARITATODON, sp. indet.
(Fig. 4A–C)

Material—ZIN 96590 (FTA-131, 2003), left ultimate lower molariform tooth missing cusp b.

Description—The crown is relatively narrow (W/L = 0.45) and dominated by a cone-like main cusp a, which is somewhat distally inclined. Two perfectly longitudinal ridges descend from the apex of the main cusp, separating it into an almost flat lingual side and a convex labial side. The lingual side of the main cusp has a median vertical ridge flanked by shallow side depressions. The distal ridge extends towards the distal end of the crown where it connects with the lingual cingulid. The mesial ridge terminates at the base of the mesiolingual cusp g, meeting with an almost transverse ridge descending from the apex of the latter cusp. Thus the angle between the labial and lingual rims of crest a–g is very close to a right angle (93°). Cusp g is two times lower than the main cusp. The mesiolabial side of the crown was occupied by the mesiolabial cusp b, which unfortunately was broken off and lost before photographing the specimen. It was lower than cusp b and had a flattened lingual side. The whole lingual side of the crown is flanked by a prominent cingulid. There is no labial cingulid on the preserved crown and no cingulid was present labial to the missing cusp b. The tooth has two roots of approximately similar size.

Measurements—ZIN 96590: L = 0.81, W = 0.39.

Discussion—ZIN 96590 is very similar to the holotype of *Paritatodon ('Shuotherium') kermacki* (Fig. 4D) from England in an almost right angle between the labial and lingual arms of crests a–c and a–g, a strong and complete lingual cingulid, a small and simple pseudotalonid basin, and the shape of (now missing) cusp b with a flattened lingual side. It has no distolingual cusp c because it was the ultimate tooth in the jaw, whereas the holotype of *P. kermacki* comes from a more anterior position (compare with ultimate and more anterior teeth of *Itatodon tatarinovi*: Averianov and Lopatin, 2005:pl. 8, fig. 1). ZIN 96590 is only 41% of the length of the holotype of *P. kermacki*. This size discrepancy can be attributed either to the positional variation in the tooth row (the ultimate molariform tooth is, for example, considerably reduced in *Haldanodon* [Martin and Nowotny, 2000; Luo and Martin 2007]), or to interspecific variation within the genus *Paraitotodon*, gen. nov. Similar variation in molariforms occurs in *Itatodon tatarinovi*, in which the length of the ultimate molariform is 81% of the length of the penultimate molariform (Averianov and Lopatin, 2006).

TASHKUMYRODON Martin and Averianov, 2004
TASHKUMYRODON DESIDERATUS Martin and Averianov, 2004

Material—ZIN 85279, left lower molariform.

Description—See Martin and Averianov, 2004:196.

Comments—*Tashkumyrodon desideratus* was based on a single lower molariform tooth from the Balabansai Formation at Sarykamyshsai (site FTA-30), Kyrgyzstan. In the original description and interpretation of this specimen we erroneously described the pseudotalonid as being bordered by crests b–e and e–g. Actually the very narrow pseudotalonid of this specimen is bordered by crests a–b, b–g, and a–g, suggesting that this tooth should be formally referred to the Docodontidae. However, the peculiar narrow pseudotalonid at the holotype of *T. desideratus* implies that this tooth is a m1 and that the reduction of the pseudotalonid is related to its occlusal relationships with the upper ultimate premolar, which has only a slightly expanded lingual portion of the crown. In the structure of the pseudotalonid, the holotype of *T. desideratus* is very similar to the holotype of *Krusatodon kirtlingtonensis* Sigogneau-Russell, 2003b, from the Bathonian Forest Marble Formation at Kirtlington, England, which is also likely a m1 (Sigogneau-Russell, 2003b:fig. 3B). But in a more posterior lower molariform of *K. kirtlingtonensis* (Sigogneau-Russell, 2003b:fig. 3A), the pseudotalonid is more expanded and has a distinct cusp e on its border. Averianov et al. (in preparation) will argue that *Krusatodon* is a tegotheriid docodontan very close to *Tegotherium* based on new materials of the latter genus from the Middle Jurassic of Siberia. *Tashkumyrodon* appears to be very close to *Krusatodon* in most respects (m1 is not known for *Tegotherium*) and should be retained in Tegotheriidae. Actually we see no diagnostic differences between these two genera. The distal portion of the crown in the holotype of *K. kirtlingtonensis* has a more complicated pattern than in the holotype of *T. desideratus.* In an additional specimen of *Krusatodon* this region is designed exactly as in *Tashkumyrodon*. However, currently we refrain from synonymizing the genera *Tashkumyrodon* and *Krusatodon* because of the lack of full information on the positional variation of the lower molariform teeth in tegotheriid docodontans.

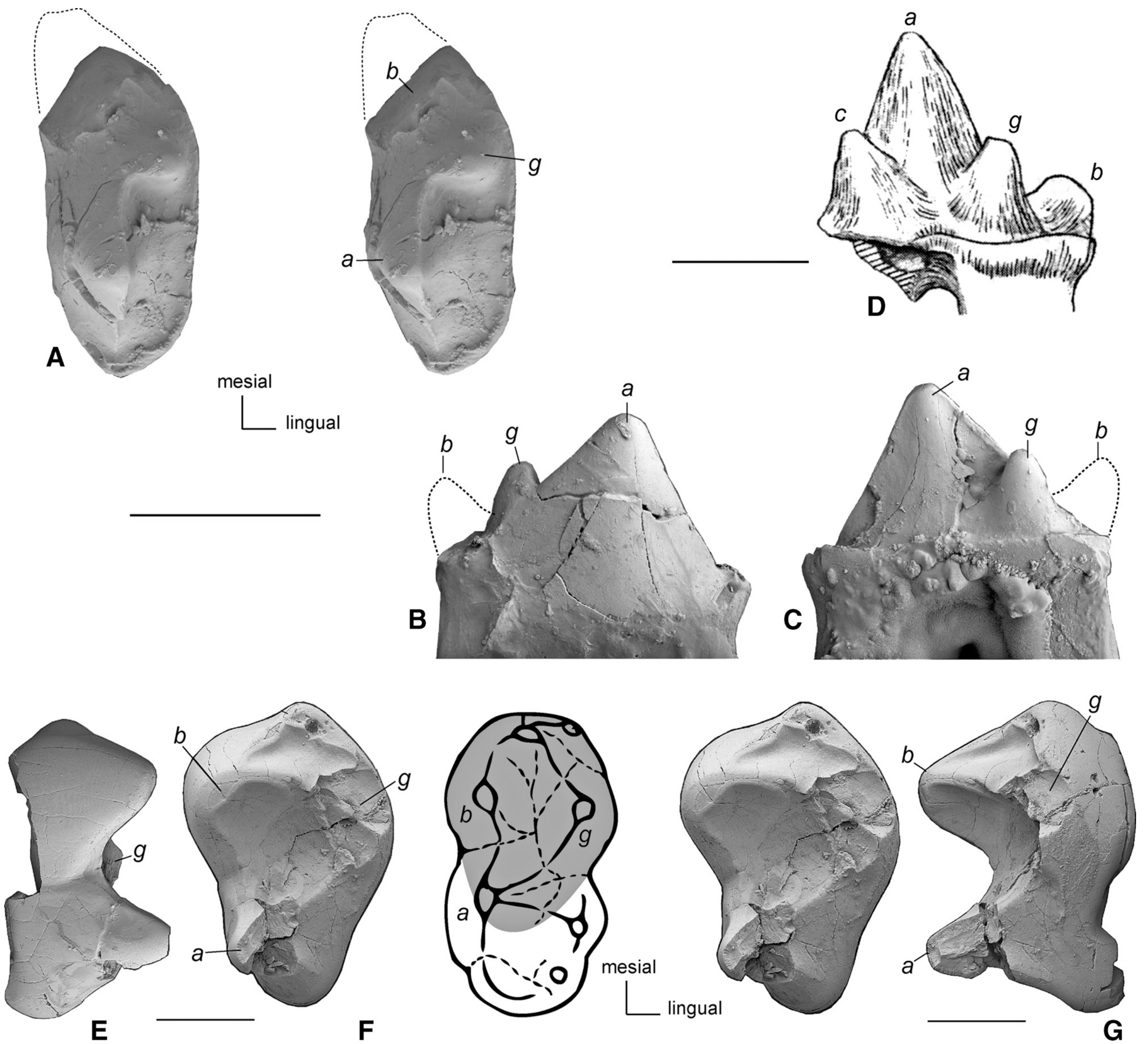


FIGURE 4. Lower molariform teeth of *Paritatodon* sp. (**A**–**C**) and Tegotheriidae indet. (**E**–**G**) with explanatory schematic drawing of a *Tegotherium* lower molar in occlusal view with the preserved part shaded (redrawn after Luo and Martin (2007). Tashkumyr 1 (site FTA-131), Middle Jurassic (Callovian). **D**, left lower molar of *Paritatodon ('Shuotherium') kermacki* (holotype) in lingual view from the upper Bathonian of Kirtlington, England (from Sigogneau-Russell, 1998:fig C). **A**–**C**, ZIN 96590, left ultimate lower molariform tooth missing the pseudotalonid in (**A**, stereopair) occlusal, (**B**) labial, and (**C**) lingual views (the pseudotalonid is reconstructed by a dotted line in **A**). **E**–**G**, ZIN 97340, left ultimate lower molariform tooth in (**E**) labial, (**F**, stereopair), occlusal, and (**G**), lingual views. Scale bars equal 0.5 mm. **Abbreviations**: **a**, **b**, and **g**, lower molariform tooth cusps.

TEGOTHERIIDAE, gen. et sp. indet.
(Figs. 4E–G, 5)

Material—ZIN 96610 (FTA-131, 2001), lingual fragment of a left upper molariform tooth (Fig. 5A–C); ZIN PH 96608 (FTA-131, 2001), labial fragment of a left upper molariform tooth (Fig. 5D, E); ZIN PH 96596 (FTA-131, 2003), labial fragment of a right upper molariform tooth (Fig. 5F–G); ZIN 97340 (FTA-131, 2003), left ultimate lower molariform tooth (Fig. 4E–G).

Description—In ZIN 96610 the labial sides of the labial cusps A and C and the mesiolabial projection of the crown are broken off (Fig. 5A–C). The preserved lingual portion of the tooth is rather wide and short, with a very deep central talon basin bordered lingually by the large mesiolingual cusp X and distally by distolingual cusp Y, which is about two times smaller. There is a robust, heavily worn crest ascending mesiolabially from the apex of cusp X. Further mesially it continues as a finer, but still worn crest that apparently represents the mesial cingulum. Cusp Y is connected with cusp X by a heavily worn crest X–Y and there are two more strongly worn crests ascending from the apex of cusp Y towards the floor of the talon basin. The latter exhibits wear on its entire surface from contact with cusp b of the lower molariform. This wear facet is connected with a similarly heavily worn distal cingulum. On the damaged labial cusps a heavily worn crest A–C can be recognized. On

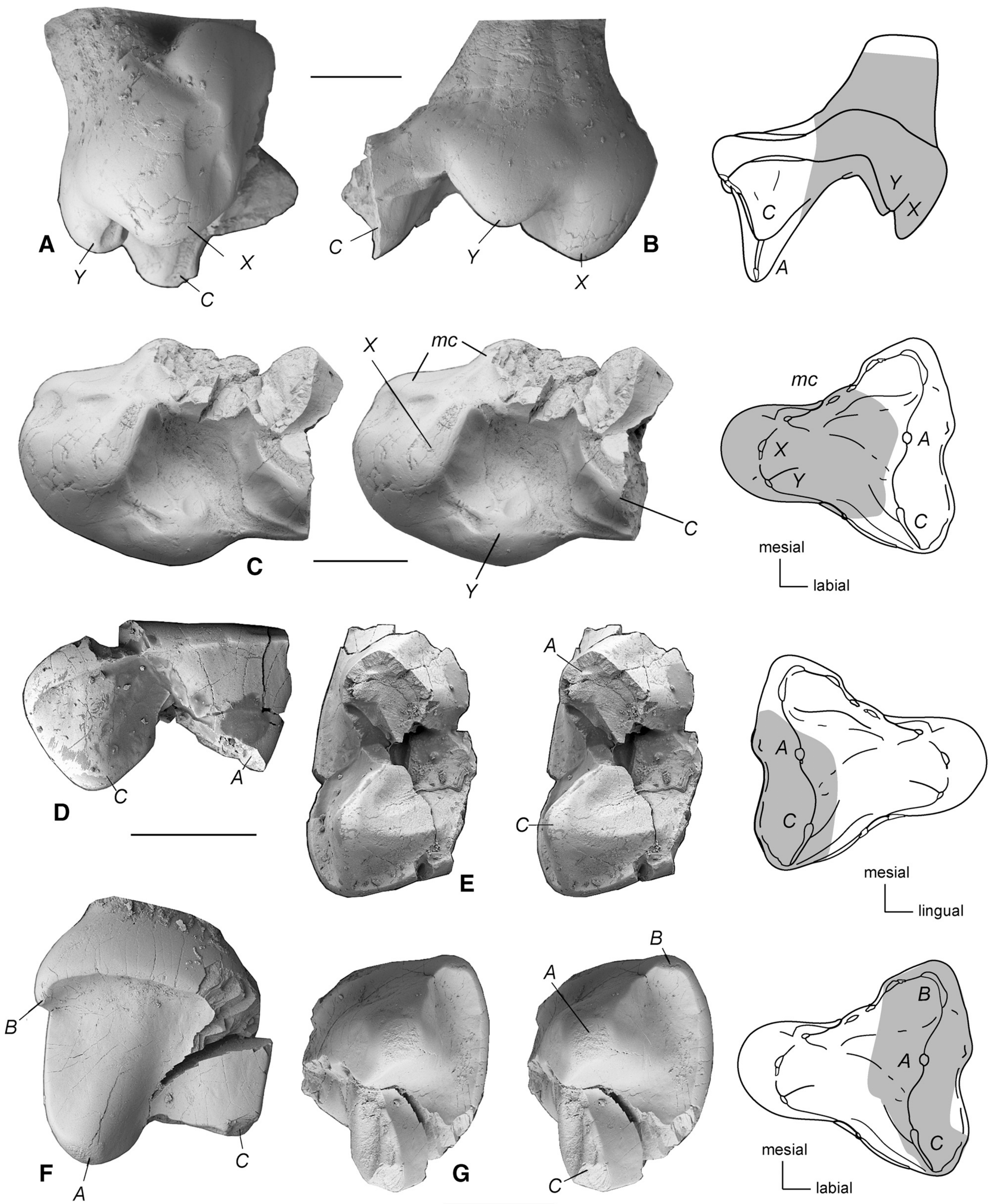


FIGURE 5. Upper molariform tooth fragments of Tegotheriidae indet. with explanatory schematic drawings of *Sibirotherium* upper molariforms in corresponding views with the preserved parts shaded (redrawn after Lopatin et al. 2009). Tashkumyr 1 (site FTA-131), Middle Jurassic (Callovian). **A**–**C**, ZIN 96610, lingual fragment of a left upper molariform tooth in (**A**) lingual, (**B**) distal, and (**C**, stereopair) occlusal views; **D**, **E**, ZIN 96608, labial fragment of a left upper molariform tooth in (**D**) labial and (**E**, stereopair) occlusal views; **F**, **G**, ZIN 96596, labial fragment of a right upper molariform tooth in (**F**) labial and (**G**, stereopair) occlusal views. Scale bars equal 0.5 mm. **Abbreviations**: **A**, **B**, **C**, **X**, and **Y**, cusps of the upper molariform tooth; **mc**, mesial cingulum.

the mesiolingual slope of cusp X there are two peculiar shallow cavities.

The labial portion of the crown ZIN 96608 (Fig. 5D, E) corresponds very closely in size and morphology with the preserved portion of the labial side of ZIN 96610. Mesiolabial cusp A is the highest cusp. Distolabial cusp C is linguolabially compressed and its apex is oriented distoventrally. Crest A–C is heavily worn along cusp C, but not along cusp A, whereas the apex of cusp A is somewhat worn. The ectoflexus was apparently lacking and there is a robust ectocingulum along the entire preserved labial side of the tooth. The most mesial point of this cingulum can be identified as the mesial stylar cusp B.

The labial fragment ZIN 95596 (Fig. 5F, G) is similar to the previously described fragment by the lack of an ectoflexus, but differs in a distinctly narrower labial shelf. There is a marked crest on the lingual slope of the cusp C. The ectocingulum is connected with the similarly developed distal cingulum.

ZIN 97340 is an almost complete left ultimate lower molariform tooth (Fig. 4E–G). The crown consists of three cusps (a, b, and g). The part of the crown distal to cusp a is completely reduced. In occlusal view the crown is considerably narrowed at cusp a. Cusps a and b are equal in height. The pseudotalonid basin is of triangular shape and relatively shallow. The mesial cingulid forms a mesiolingual projection; its labial branch is connected with cusp b and its lingual branch with cusp g. There is no distal cingulid. The tooth is double rooted with the distal root considerably thinner than the labial root.

Measurements—ZIN 96608: L = 1.13; ZIN 96596: L = 1.24; ZIN 96610: length of the lingual part of the crown 1.2; ZIN 97340: L = 1.59, W = 1.10.

Discussion—Three fragments of upper molariform teeth that are referred to Tegotheriidae indet. are similar in size and likely represent a single species (the differences between two labial fragments probably are due to the positional variation). These upper molariforms are more similar in size to the lower molariforms of *Tashkumyrodon desideratus* than to those of *Paritatodon* sp., although the small size of the single known lower molariform of *Paritatodon* sp. might be related to its posteriormost position in the jaw. We refrain from attribution of these teeth to *Tashkumyrodon* because they were found in a different locality and because the taxonomic diversity of docodontans in the Balabansai assemblage and occlusal relationships between upper and lower molars are currently insufficiently known.

The ultimate lower molariform tooth (ZIN 97340) is quite similar to the ultimate molariform of *Dsungarodon* (Pfretzschner et al., 2005:fig. 3B) in structure and proportions, especially in the shape of the labial part of the mesial cingulid, but differs in the presence of a lingual branch of the mesial cingulid and lack of a distal cingulid.

DOCODONTA indet.

Material—ZIN 96611 (FBX-23, 2001), canine; ZIN 96605 (FTA-131, 2003), lingual fragment of a left upper premolar; ZIN 96601 (FTA-131, 2001), fragmentary (?) right lower premolar.

Description—ZIN 96611 is a double-rooted canine with a robust, sharply pointed, and distally curved crown. There is a prominent hook-like distal accessory cusp, connected with the main cusp by a sharp distal ridge, whereas the anterior margin of the crown is rounded. There is a very short labial cingulum (or cingulid) at the base of accessory cusp. An anterior accessory cusp is not present, nor a cingulum (cingulid) at other regions of the crown. Only the distal root is preserved, which is undoubtedly narrower (mesiolingually) than the mesial root. The distal root is remarkably short (dorsoventrally), shorter than the crown height.

The large lingual projection suggests that ZIN 96605 is the lingual portion of an ultimate, upper premolar. The lingual cusp is placed closely to the lingual margin of the crown. It is connected with the main labial cusp by a distinct, distolabially directed ridge. The distal side of the fragment is convex and the mesial side is somewhat concave. The fragment is surrounded by a weak cingulum. The lingual cusp is connected with the cingulum by two ridges, a stronger distal and a weaker mesial. The lingual side of the crown between these two ridges and the cingulum is flattened. There is one big lingual root preserved at the fragment.

ZIN 96601 is most probably a lower, possibly right premolar. It lacks the ?distal portion of the crown with the ?distal root. The crown is narrow, in side view dominated by a triangular main cusp. The apex of the main cusp is somewhat distally bent. The ?labial side of the crown is more convex than the ?lingual side. Both sides are separated by mesial and distal sharp crests that descend from the apex of the main cusp. At the base of the crown the mesial crest connects to the weak ?lingual cingulid. There is no distinct accessory mesial cusp. The roots were connected dorsally by a thin longitudinal dentine plate.

Measurements—ZIN 96611: L = 0.79, W = 0.40; ZIN 96605: length of the lingual portion of the crown: 0.82; ZIN 96601: W = 0.49.

Discussion—The canine ZIN 96611 resembles that of *Docodon* rather than *Haldanodon* in shape and reduction of the cingulum, but has a better developed distal accessory cusp. The upper premolar ZIN 96605 also resembles those of *Docodon* rather than those of *Haldanodon* in the state of development of the lingual lobe, but differs from the former in weaker mesial and distal cingula. The lower premolar ZIN 96601 differs from those of *Haldanodon*, *Docodon*, *Simpsonodon*, and *Sibirotherium* in the restriction of the cingulid to one side of the crown. The canines and premolars of tegotheriid docodontans are currently poorly known. Thus an identification of the teeth described in this section beyond Docodonta indet. is not possible.

EUTRICONODONTA Kermack, Mussett and Rigney, 1973
"AMPHILESTIDAE" Osborn, 1888
"AMPHILESTIDAE," gen. et sp. indet.
(Fig. 6A–D)

Material—ZIN 96606 (FTA-131, 2001), distal fragment of a left lower molariform tooth.

Description—The crown fragment preserves two distal cusps (c and d) and half of the base of a more mesial main cusp (cusp a). The crown is almost symmetrical in occlusal view, with a triangular pointed distal end and cusps a and c aligned along the crown midline, and cusp d shifted lingually of this midline. The midline is marked by a sharp crest connecting the cusp apices (worn on cusp c). The base of cusp a is about two times wider than the base of cusp c. The apex of cusp c is heavily worn and a prominent strap-like wear facet exposing the dentine extends basally and somewhat medially along the labial side of cusp c. Cusp d is small, approximately one-third of the height of cusp c. Cusp d is placed relatively high on the crown, with the space between the crown-root boundary and the apex of this cusp comparable to the preserved height of cusp c. There is a prominent lingual cingulid extending from the apex of cusp d towards a point somewhat mesial to the notch between cusps a and b.

Discussion—Although cusp a is not complete in ZIN 96606, it must have been considerably higher than cusp c. Thus ZIN 96606 is referable to the eutriconodontans with an 'amphilestid-like' cusp pattern. Below we describe and refer to the Triconodontidae ZIN 96595 from the same locality. The latter tooth combines an 'amphilestid-like' cusp pattern with a derived tongue-in-groove interlock of the molariform teeth. This raises the question if ZIN 96606 could belong to a triconodontid with a plesiomorphic cusp pattern. First, ZIN 96606 is not referable to the same genus as ZIN 96595 because it is at least two times larger than the latter. Second, the symmetrical triangular distal end of ZIN 96606 is suitable for both tongue-in-groove and e–d–f interlock mechanisms. Thus we cannot reject the possibility that ZIN 96606 actually represents a member of the Triconodontidae. But in absence of information on the structure of the mesial end of ZIN 96606, it is more parsimonious to refer this specimen to eutriconodontans of the 'amphilestid' grade.

In the Balabansai assemblage eutriconodontans of the 'amphilestid' grade were previously represented by *Ferganodon* Martin and Averianov, 2007 (Klameliidae). ZIN 96606 is clearly different from the only known specimen of *Ferganodon* (ZIN 94214; Martin and Averianov, 2007:fig. 1) in its smooth enamel, smaller cusp d, better-developed lingual cingulid, and complete lack of the labial cingulid and the distolabial cusp. In some molariform teeth of *Klamelia* (Martin and Averianov, 2007:fig. 2), cusp d is significantly smaller than in *Ferganodon*, approximating the height difference between cusps c and d of ZIN 96606. The distolabial cingulid, though less developed than in *Ferganodon*, is always present and distinctive. Therefore ZIN 96606 cannot be assigned to the Klameliidae. In the remaining taxa of the 'amphilestid'-grade eutriconodontans ("Amphilestidae," Gobiconodontidae, and Jeholodentidae), the structure of the lower molariform teeth is rather similar. This makes the attribution of the incompletely preserved specimen ZIN 96606 to one of these taxa difficult. ZIN 96606 is referred here to the "Amphilestidae" simply because this group is known in the fossil record at least since the Middle Jurassic (Kielan-Jaworowska et al., 2004), whereas jeholodontids (Luo et al., 2007b) and gobiconodontids (Sigogneau-Russell, 2003a; Cuenca-Bescos and Canudo, 2003) are confined to the Cretaceous.

In the original description of *Ferganodon* (Martin and Averianov, 2007) we did not compare this taxon with *Kryptotherium* from the Early Cretaceous of Morocco (Sigogneau-Russell, 2003a). *Kryptotherium* is similar to *Ferganodon* in the parallelogram shape of at least some lower molariform teeth, indicating an imbrication rather than interlock of the molariforms, a strong reduction of cusp b, and functionally bicuspid crowns. *Kryptotherium* differs from *Ferganodon* and *Klamelia* Chow and Rich, 1984, in smooth enamel, absence of any cingulid, angulation of the main crown cusps in at least some of the lower molariform teeth, and by presence of an additional minute cupsule mesial to the cupsule f. *Kryptotherium* was originally referred to the ?"Amphilestidae," but its referral to the Klameliidae is equally possible.

cf. *FERGANODON*
(Fig. 6E–G)

Material—ZIN 96583 (FTA-131, 2003), distal fragment of a right lower molariform tooth.

Description—ZIN 96583 is a poorly preserved distal half of a molariform tooth with the distal root and part of the crown bearing cusp d, broken cusp c, and piece of the base of cusp a. The cusps of the crown are longitudinally aligned. There is a well-developed labial cingulid bearing a large distolabial cusp opposite to cusp c and a much smaller and less distinct cuspule just distal to the former.

Discussion—The most conspicuous feature of ZIN 96583 is the well-developed labial cingulid with a large distolabial cusp. In this feature ZIN 96583 closely resembles the holotype of *F. narynensis*; the teeth are similar in size. ZIN 96583 differs from *F. narynensis* in having smooth enamel and a smaller hook-like (not bulbous) cusp d. This and the incompleteness of ZIN 96583 makes an attribution of this specimen to *Ferganodon* provisional.

TRICONODONTIDAE Marsh, 1887
TRICONODONTIDAE, gen. et sp. indet.
(Fig. 7A–C)

Material—ZIN 96595 (FTA-131, 2003), mesial fragment of a right lower molariform tooth.

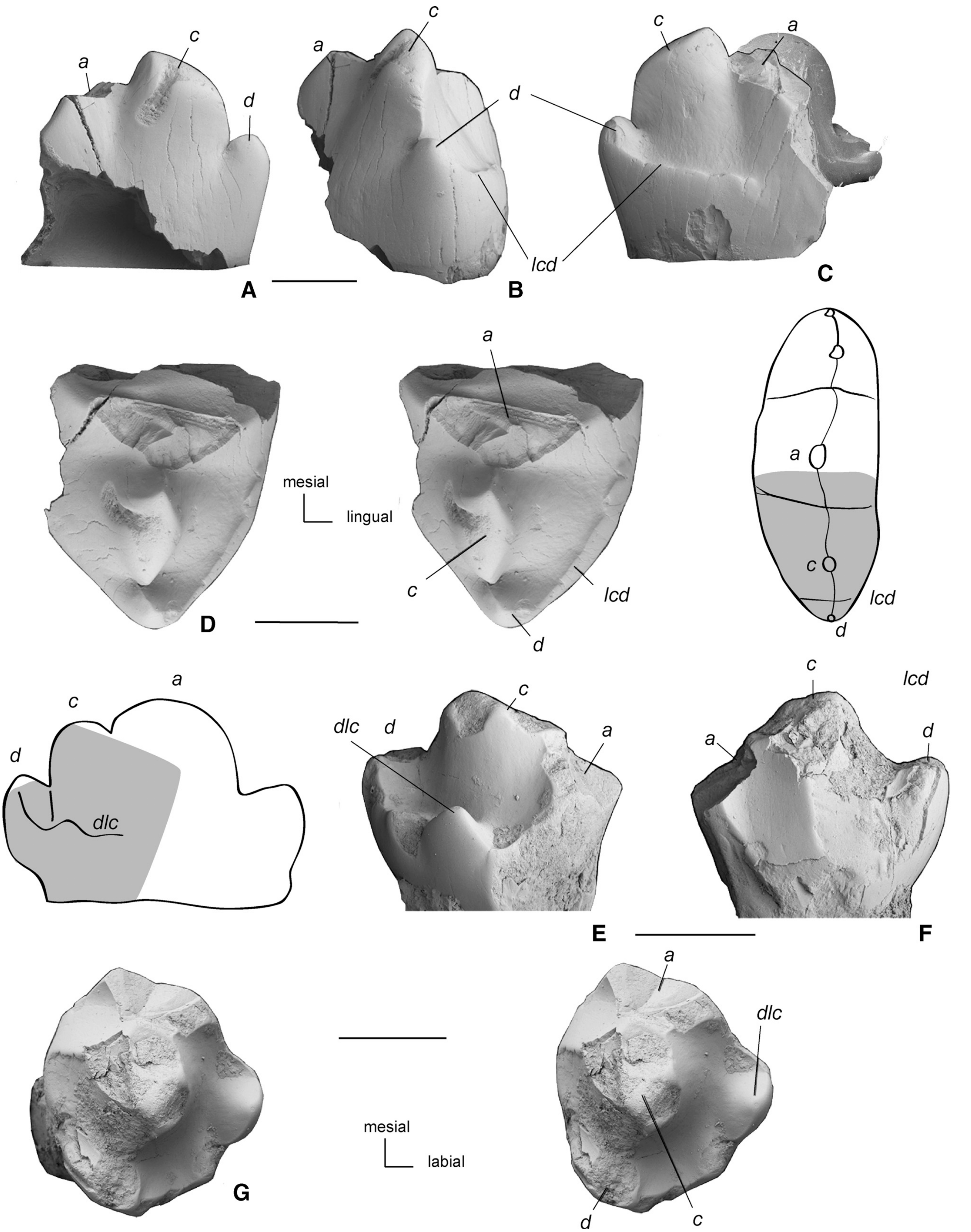
Description—The crown fragment preserves two mesial cusps and the base of a third, more distal cusp. The cusps are labiolingually compressed. A sharp longitudinal crest extends along the entire fragment, connecting the cusps apices, and dividing the crown into two unequal parts in occlusal view. The lingual side of the crown is narrower in occlusal aspect and seems to be more vertical than the labial side, with a shallow depression between the bases of the first and second cusps. The labial side of the crown appears wider in occlusal view and less steep. Both sides of the crown are covered by very faint and irregular enamel ridges. The two preserved mesial cusps are almost vertical. The second preserved cusp is distinctly higher and well separated from the most mesial cusp (cusp b), but it is barely separated from the next distal cusp. Although the apex of the latter cusp is missing, it was apparently higher than the adjacent mesial cusp. On the mesial side of the crown at the base of cusp b there is a relatively deep and wide arch-shaped embayment that is flanked laterally by distinct ridges. The lingual ridge is more pronounced and apparently represents the vertical portion of a lingual cingulid.

Discussion—Interpretation of ZIN 96595 is difficult because of its fragmentary condition and combination of plesiomorphic, derived, and autapomorphic characters. A plesiomorphic character is that cusp b is distinctly lower than the more distal cusp, which exemplifies the 'amphilestid' level of molariform construction ("Amphilestidae," Klameliidae, Gobiconodontidae, and Jeholodontidae,). A derived character is the well-developed vertical tongue-in-groove interlock characteristic for the molariforms of advanced Eutriconodonta (Triconodontidae and Austrotriconodontidae). Although an embayment for cusp d of the more mesial molariform can be variably present on the mesial side of cusp b in some amphilestids and gobiconodontids, it is flanked by lateral ridges only in the triconodontids (Sigogneau-Russell, 2003a:fig. 12; pers. observ.). A unique character of ZIN 96595 is the presence of an additional cusp between cusps b and a (if cusp a was the highest crown cusp). An alternative but less likely interpretation of ZIN 96595 is that cusp c was the highest crown cusp and cusp a was reduced and confined to the base of cusp c. Neither of these two cusp patterns are currently known among the Eutriconodonta. ZIN 96595 is referred here to the Triconodontidae because of the derived tongue-in-groove interlock of the molariform teeth and because the height difference between cusp b and the next distal cusp is variably present in some triconodontids (e.g., Sigogneau-Russell, 2003a:fig. 13). If corroborated by additional fossils, ZIN 96595 would represent the oldest fossil record for the Triconodontidae; the currently oldest record for this family was from the Upper Jurassic (Kimmeridgian) Morrison Formation of USA (Kielan-Jaworowska et al., 2004).

"SYMMETRODONTA" Simpson, 1925
TINODONTIDAE Marsh, 1887
TINODONTIDAE, gen. et sp. indet.
(Fig. 7D–G)

Material—ZIN 96607 (FTA-131, 2001), mesial fragment of a left lower molariform tooth.

Description—ZIN 96607 preserves approximately half of the crown with the incomplete main cusp a and mesial accessory cusp b. The base of cusp a is larger than that of cusp b and the former cusp was apparently higher. Although most of cusp a is missing, it appears that the apex of this cusp was more or less longitudinally aligned with cusps b and c. The deeply concave mesial side of cusp a faces the distal side of cusp b, whereas in the tinodontid molariform teeth with angulated main cusps there is a rather large trigonid basin between cusp b, cusp c, and the longitudinally oriented lingual side of cusp a. The crown is heavily worn, with a prominent flat vertical wear facet occupying all the apex of the preserved labial side of cusp a and the distal half of the labial side of cusp b. This facet extends mesiodorsally towards the apex of cusp b. This strap-like facet lies in a plane different from that of the wear facet of cusp a, and exposes the dentine on cusp b. Cusp b is cone-like, not labiolingually compressed, and slightly


a
c
d
lcd
A
B
C
mesial
lingual
D
dlc
E
F
labial
G

inclined mesially. There is a prominent mesial shelf at the base of cusp b that is flanked labially, mesially, and lingually by a distinct, continuous cingulid. This cingulid extends lingually towards the broken end of the fragment between cusps a and b; labially its distal portion has been eliminated by wear. On the mesial cingulid there is a slight undulation that is possibly a remnant of an embayment between the cingular cuspules e and f, but neither of these cuspules is distinct.

Discussion—In spite of the supposed almost longitudinal alignment of the main crown cusps, ZIN 96607 is referred here to the "Symmetrodonta" rather than to the Eutriconodonta because of the shape of the individual cusps, specifically cusp b. It is cone-like and rounded, not compressed labiolingually, as in eutriconodontans, and on the crown there is no medial sharp crest connecting the apices of the crown cusps. Also the shelf-like structure of the cingulid differs from that observed in the eutriconodontans. In tinodontids the first and last lower molariforms are usually less angulated compared to the teeth from the middle of the toothrow. Among the comparable sample, ZIN 96607 most closely matches the last molariform (m4) of *Gobiotheriodon* Trofimov, 1997, from the Early Cretaceous of Mongolia (Averianov, 2002:fig. 2B). On both specimens there is a characteristic strap-like wear facet on cusp b set off from the plane of the main wear facet along cusp a, a similarly shaped notch between cusps a and b, and a similar mesial shelf at the base of cusp b. However, in ZIN 96607 the lingual cingulid is much better developed than in *Gobiotheriodon*. ZIN 96607 represents the oldest fossil record for the Tinodontidae; this group was known previously from the Late Jurassic and Early Cretaceous of Laurasia (Kielan-Jaworowska et al., 2004; Lopatin et al., 2005).

CLADOTHERIA McKenna, 1975
DRYOLESTOIDEA Butler, 1939
PAURODONTIDAE Marsh, 1887
PAURODONTIDAE, gen. et sp. indet.
(Fig. 8)

Material—ZIN 96604 (FTA-131, 2001; Fig. 8A–D), left anterior-most upper molar, preserving only the lingual portion of the crown. ZIN 96592 (FTA-131, 2003; Fig. 8E–G), fragment of a left lower molar.

Description—ZIN 96604 is an equilaterally triangular shaped tooth with the preserved crown length exceeding the preserved crown width (Fig. 8A–D). The paracone is a prominent cusp at the center of the lingual side of the crown. The 'trigon' basin is shallow, almost flat. It has a swelling median ridge that does not contact the paracone. The tip of the paracone and the preparacrista and postparacrista are considerably worn. The skewed distolabial side of the crown is intact suggesting that the crown width was not much greater than the crown length.

ZIN 96592 is a major part of the crown with the labial side of the trigonid and most of the talonid missing (Fig. 8E–G). The trigonid length is 1.24 mm. The trigonid cusps form an isosceles triangle. The bases of the paraconid and the metaconid are approximately of the same size; the paraconid is somewhat lower than the metaconid. The paraconid and the metaconid are separated, with the trigonid basin open lingually. All the space of the trigonid basin is filled by the bases of the trigonid cusps. The protoconid is about two times higher than the metaconid. There is a vertical ridge-like swelling on the lingual side of the protoconid. All trigonid cusps and the ridges connecting them (the paracristid and the metacristid) are heavily worn. Moreover, there are prominent wear facets along the mesial and distal sides of the trigonid. The paracristid is shorter and straighter than the metacristid and is directed mesiolingually. The metacristid is not transverse. The protoconid arm of the metacristid is directed distolingually, whereas its metaconid arm is directed lingually or mesiolingually (both arms are separated by the metacristid notch). Very little is preserved of the talonid; from what is preserved it can be concluded that the talonid was in a lingual rather than in a medial position. On the lingual side a portion of the hypoconulid crest is preserved.

Discussion—Both tooth fragments correspond in size and may be referred to a single species based on comparison with *Henkelotherium guimarotae* Krebs, 1991, from the Late Jurassic of Portugal (Krebs, 1991). They are referred to the Paurodontidae because the upper molar is not much wider than long and has only a swelling-like median ridge; and because on the lower molar there is not a great height difference between the paraconid and the metaconid. The paraconid in ZIN 96592 is not shelf-like, in contrast to the majority of paurodontid genera; however, in this feature and in general crown morphology ZIN 96592 is similar to the lower molars of *Henkelotherium* (Krebs, 1991:fig. 3). The upper molar is also similar to the anterior-most molar (M1) of *Henkelotherium* (Krebs, 1991:fig. 3), although the presence of a prominent parastylar lobe characteristic for *Henkelotherium* cannot be verified due to the fragmentary nature of the tooth.

Paurodontidae indet. from the Balabansai Formation represent the first record of Paurodontidae in Asia and the oldest record of this group in general. The Paurodontidae were known previously from the Late Jurassic to Early Cretaceous in Europe and North America (Kielan-Jaworowska et al., 2004); the African Late Jurassic *Brancatherulum tendagurense* Dietrich, 1927, known from a single edentulous dentary most likely does not belong to this group.

Stem lineage of ZATHERIA McKenna, 1975
AMPHITHERIA Kermack, Kermack and Mussett, 1968
AMPHITHERIIDAE Owen, 1846
AMPHITHERIIDAE, gen. et sp. indet.
(Fig. 9)

Material—ZIN 96600 (FTA-131, 2001), fragment of the trigonid of a left lower molar. The specimen was unfortunately destroyed after taking the SEM images.

Description—The fragment preserves most of the protoconid and metaconid. Both cusps are conical, with flattened lingual and mesial sides. These flattened areas are clearly delimited by marked crests, the paracristid and protocristid. The protocristid is oblique relative to the mesiodistal axis of the crown. The protoconid is more than two times higher than the metaconid. The protoconid is almost vertical whereas the metaconid is slightly deflecting lingually. The distal side of the trigonid is almost vertical, with a distinct distal metacristid running towards the notch on the protocristid between the protoconid and the metaconid, somewhat closer to the metaconid. The distolabial side of the metaconid is convex, without a 'paraconal sulcus' (Sigogneau-Russell,

← FIGURE 6. Fragments of lower molariform teeth of (**A–D**) "Amphilestidae" indet. and (**D–G**) cf. *Ferganodon* sp. with explanatory schematic drawings of an *Amphilestes* left lower molar in occlusal view (redrawn from Sigogneau-Russell 2003) and a *Ferganodon* lower molar in labial view (redrawn from Martin and Averianov, 2007). Tashkumyr 1 (site FTA-131), Middle Jurassic (Callovian). **A–D**, ZIN 96606, distal fragment of a left lower molariform tooth in (**A**) labial, (**B**) distal, (**C**) lingual, and (**D**, stereopair) occlusal views. **E–G**, ZIN 96583, distal fragment of a right lower molariform tooth in (**E**) labial, (**F**) lingual, and (**G**, stereopair) occlusal views. Scale bars equal 0.5 mm. **Abbreviations**: **a**, **c**, **d**, lower molariform tooth cusps; **dlc**, distolabial cusp; **ig**, interlock groove; **lcd**, lingual cingulid.

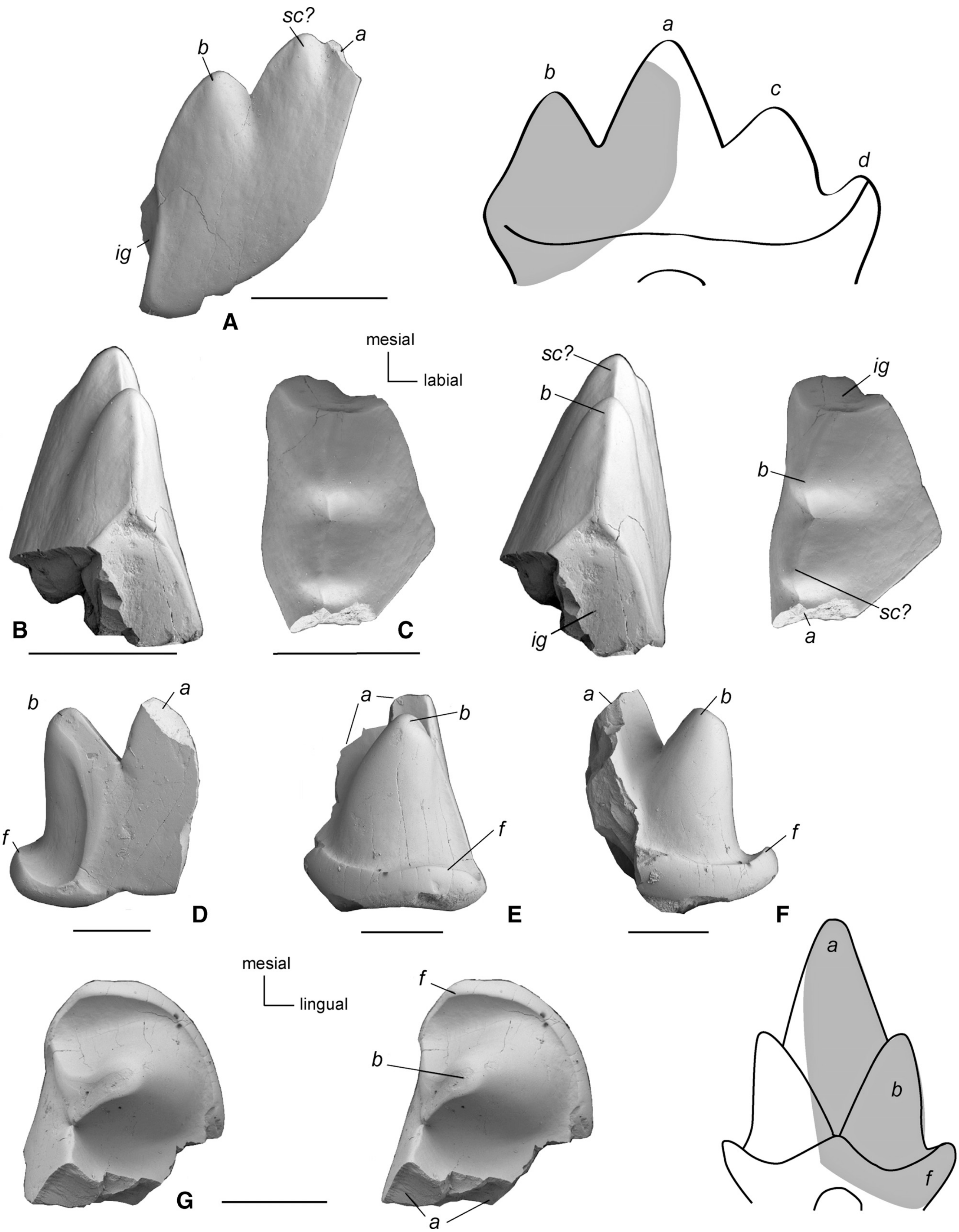

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TABLE 1. Distribution of four characters of the trigonid of lower molariform teeth of stem lineage zatherians and of *Tinodon*.

Taxa	Characters 1	2	3	4
Tinodon Marsh, 1879	0	0	NA	0
Kennetheredium Sigogneau-Russell, 2003c	0	0	NA	0
Palaeoxonodon Freeman, 1976	0	1	0	1
Amphitherium de Blainville, 1838	1	1	0	1
Amphibetulimus Lopatin and Averianov, 2007	0	1	0	1
Amphitheriidae indet. (ZIN 96600)	0	1	1	0
Nanolestes Martin, 2002	1	0	NA	1
Arguimus Dashzeveg, 1979	0	1	0	1

Characters: 1, protocristid oblique (0), transverse (1); 2, distal metacristid absent (0), present (1); 3, distal metacristid terminates at the metaconid apex (0), at the protocristid notch (1), not applicable (NA); 4, lingual cingulid present (0), absent (1).

2003c:fig. 1A). At the base of the metaconid there is a well developed lingual cingulid.

Discussion—The considerable difference in height between the protoconid and the metaconid and the presence of the distal metacristid advocate for attribution of ZIN 96600 to the stem lineage of Zatheria rather than to 'symmetrodontans' or dryolestoidans. Even in its partial preservation, ZIN 96600 bears at least four diagnostic characters that have a complex distribution among the known stem lineage zatherians (Table 1). ZIN 96600 is unique among the compared taxa in termination of the distal metacristid at the protocristid notch (derived state), and is plesiomorphic in retention of the lingual cingulid. A heuristic PAUP search of the data matrix presented in Table 1 with *Tinodon* as outgroup produced a single most parsimonious tree (TL = 5, CI = 0.80, HI = 0.20, RI = 0.80, RC = 0.64) with ZIN 96600 nested between *Kennetheredium* Sigogneau-Russel, 2003c, and the remaining stem lineage zatherians. Comparison of ZIN 96600 with primitive zatherians (peramurans and 'tribotheres') is limited because they differ from the stem lineage zatherians mostly in the structure of the talonid, which is missing in ZIN 96600. ZIN 96600 is also similar to *Tribactonodon* Sigogneau-Russell, Hooker and Ensom, 2001, from the Early Cretaceous of England, in a well-developed lingual cingulid, which is unique for a zatherian. The metaconid is much larger and has a prominent 'paraconal sulcus' on its distolabial side in *Tribactonodon*. Moreover, in *Tribactonodon* the distal metacristid apparently shows a primitive course towards the metaconid apex (missing on the single known specimen), unlike the condition in ZIN 96600. With the limited data at hand, ZIN 96600 is best classified within the Amphitheriidae. ZIN 96600 represents only the second record of an amphitheriid outside Great Britain (after a new genus, *Amphibetulimus*, described by Lopatin and Averianov, 2007).

GENERAL DISCUSSION

The present and previous papers (Martin and Averianov, 2004, 2007) document the presence of 10 to 12 taxa representing eight mammalian families in the Middle Jurassic Balabansai Formation of the Fergana Depression, Kyrgyzstan (Table 2). In spite of the fragmentary nature of most specimens, the Balabansai mammal fauna is currently among the most diverse mammalian assemblages in the Jurassic of Asia (Kielan-Jaworowska et al., 2004). Worldwide, this fauna is of lesser taxonomic diversity only to three other Jurassic assemblages: The Middle Jurassic Forest Marble assemblage in Great Britain and the Late Jurassic Guimarota fauna and Morrison assemblage in Portugal and USA, respectively (Kielan-Jaworowska et al., 2004).

TABLE 2. List of mammals from the Middle Jurassic (Callovian) Balabansai Svita in northern Fergana Valley, Kyrgyzstan.

Docodonta		
		cf. *Simpsonodon* spp.*
	Tegotheriidae	
		Tashkumyrodon desideratus
		Paritatodon sp.
		Tegotheriidae indet.**
Eutriconodonta		
	Amphilestidae	
		Amphilestidae indet.
	Klameliidae	
		Ferganodon narynensis
		cf. *Ferganodon* sp.***
	Triconodontidae	
		Triconodontidae indet.
"Symmetrodonta"		
	Tinodontidae	
		Tinodontidae indet.
Dryolestida		
	Paurodontidae	
		Paurodontidae indet.
Stem Zatheria		
	Amphitheriidae	
		Amphitheriidae indet.

*Apparently more than one species. **Possibly referable to *Tashkumyrodon* or/and *Paritatodon*. ***Possibly referable to *Ferganodon*.

The Balabansai assemblage is only slightly younger (Callovian) than the better-known Bathonian mammal assemblage from the Forest Marble Formation at Kirtlington and other sites in England (Freeman, 1976, 1979; Kermack et al., 1987, 1998; Sigogneau-Russell, 1998, 2003b, 2003c; Kielan-Jaworowska et al., 2004; Butler and Hooker, 2005). In spite of the immense geographic distance between these two areas, the composition of the assemblages is quite similar. Both are dominated by docodontans. The most conspicuous docodontan is *Simpsonodon*, represented by the same or closely related species in England and Kyrgyzstan. Docodontidae are represented in the Forest Marble by *Borealestes*, known also from the Bathonian of Scotland (Waldman and Savage, 1972). *Borealestes* is quite close to the Late Jurassic docodontids *Haldanodon* from Portugal and *Docodon* from the USA (Simpson, 1929; Krusat, 1980; Luo and Martin, 2007) and the Docodontidae might be geographically restricted to the North American–European Jurassic realm. This group so far has not been reported from Asia.

Tegotheriid docodontans are represented by very similar taxa in both assemblages: *Krusatodon–Tashkumyrodon* and *Paritatodon kermacki–Paritatodon* sp. The British tegotheriids (as

← FIGURE 7. Fragments of lower molariform teeth of (**A–C**) Triconodontidae indet. and (**D–G**) Tinodontidae indet. with explanatory schematic drawings of a *Priacodon* lower molariform and a *Tinodon* lower molariform in lingual views with the preserved parts shaded (redrawn from Simpson 1929). Tashkumyr 1 (site FTA-131), Middle Jurassic (Callovian). **A**–**C**, ZIN 96595, mesial fragment of a right molariform tooth in (**A**) lingual, (**B**, stereopair) mesial, and (**C**, stereopair) occlusal views. **D–G**, ZIN 96607, mesial fragment of a left lower molariform tooth in (**A**) labial, (**B**) mesial, (**C**) lingual, and (**D**, stereopair) occlusal views. Scale bars equal 0.5 mm. **Abbreviations**: **a**, **b**, **f**, lower molariform tooth cusps; **ig**, interlock groove; **sc?**, supplementary cusp (?).

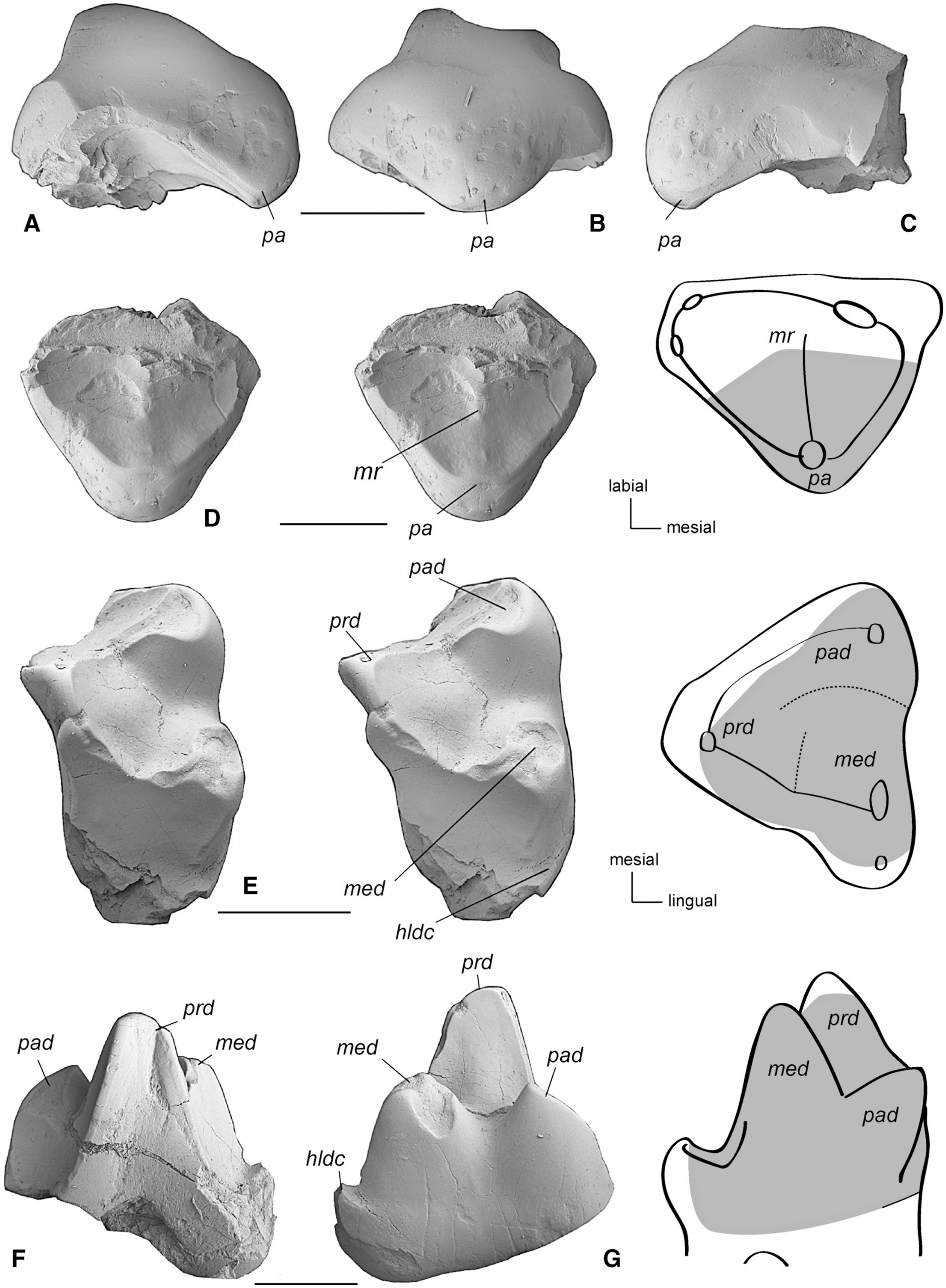

FIGURE 8. Fragmentary molars of Paurodontidae indet. with explanatory schematic drawings of an upper first molar of *Henkelotherium* (redrawn from Krebs, 1991) and a lower molar of *Laolestes* (redrawn from Martin, 1999) in corresponding views. Tashkumyr 1 (site FTA-131), Middle Jurassic (Callovian). **A**–**D**, ZIN 96604, lingual fragment of a left upper first molar in (**A**) distal, (**B**) lingual, (**C**) mesial, and (**D**, stereopair) occlusal views; **E**–**G**, ZIN 96592, left lower molar missing the talonid in (**E**, stereopair) occlusal, (**F**) labial, and (**G**) lingual views. Scale bars equal 0.5 mm. **Abbreviations**: **hldc**, hypoconulid crest; **med**, metaconid; **mr**, median ridge; **pad**, paraconid; **pa**, paracone; **prd**, protoconid.

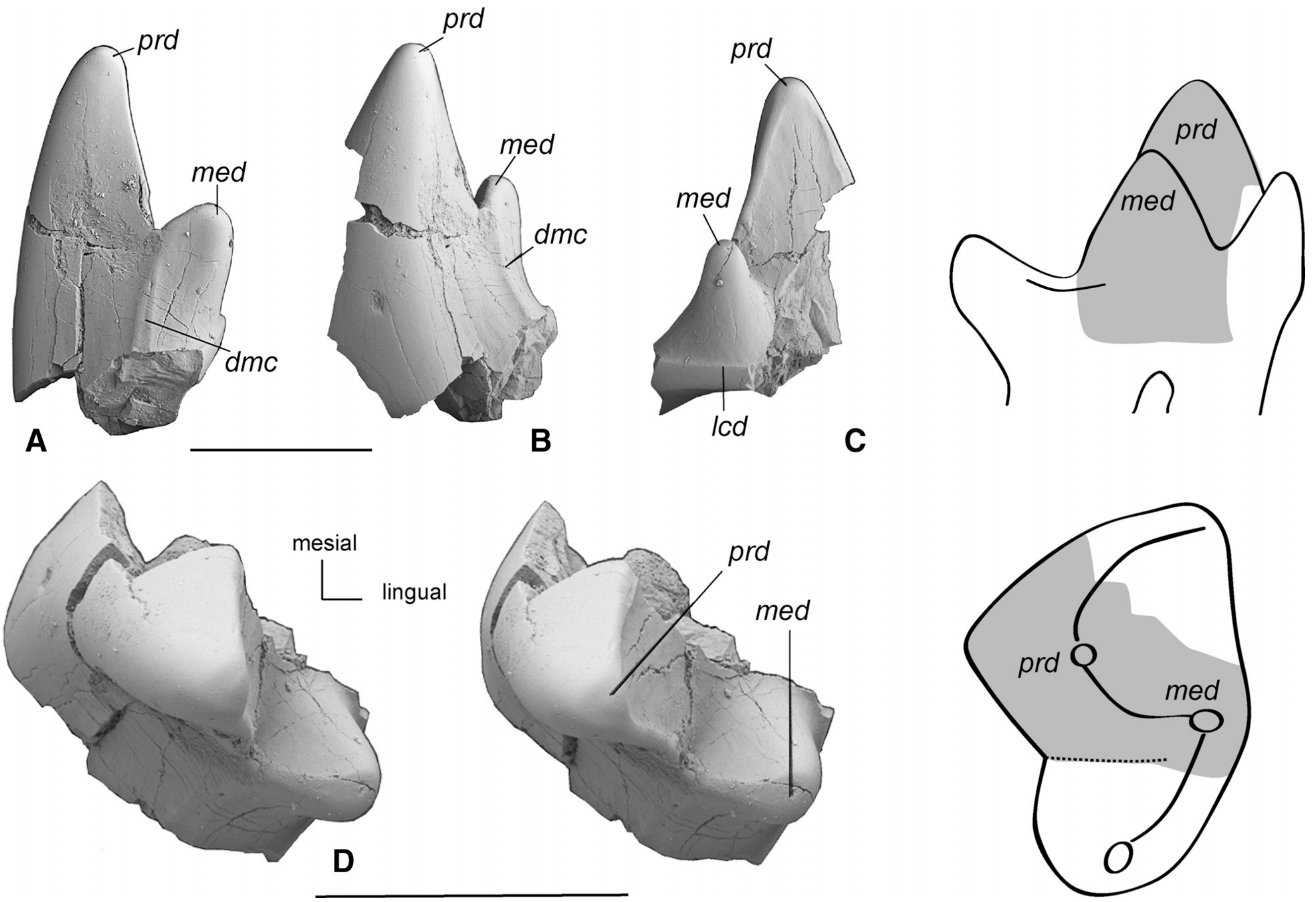

FIGURE 9. Lower molar of Amphitheriidae indet. with explanatory schematic drawings of *Amphitherium* lower molars in lingual and occlusal views (redrawn after Simpson 1928) with the preserved parts shaded. Tashkumyr 1 (site FTA-131), Middle Jurassic (Callovian). **A–D**, ZIN 96600, trigonid fragment of a left lower molar in (**A**) distal, (**B**) labial, (**C**) lingual, and (**D**, stereopair) occlusal views. Scale bars equal 0.5 mm. **Abbreviations**: **dmc**, distal metacristid; **lcd**, lingual cingulid; **med**, metaconid; **prd**, protoconid.

well as the *Shuotherium*) are probably Asian immigrants and diversification of this group occurred mostly in Asia (Averianov and Lopatin, 2006).

A rare but diverse component of the Forest Marble assemblage are the allotherians, represented by eleutherodontids and the first multituberculates (Kermack et al., 1998; Butler and Hooker, 2005). Allotherians have not yet been found in the Balabansai Formation, but they are present in the Middle Jurassic of Siberia (Averianov et al., in preparation) and the earliest Late Jurassic (Oxfordian) of the Junggar Basin in northwest China (Maisch et al., 2005). Current absence of allotherians in the Balabansai assemblage is most probably due to the sampling bias.

Eutriconodontans are rare in the Forest Marble assemblage being represented there by a single tooth identified as "Amphilestidae" indet. (Freeman, 1979). In the Balabansai assemblage they are more diverse, but also quite rare, known by one almost complete tooth and three fragments referable to "Amphilestidae" (based on stratigraphical age), Klameliidae, and Triconodontidae. "Amphilestids" are a Laurasian group known in Europe, Asia, and North America (Kielan-Jaworowska et al., 2004). Klameliids were possibly endemics of Central Asia (Martin and Averianov, 2007). Phylogenetically they are close to the Gobiconodontids, a group that underwent a marked diversification in the Early Cretaceous of Asia and spread to North America, Europe, and northern Africa (see reviews in Kielan-Jaworowska and Dashzeveg, 1998; Cuenca-Bescos and Canudo, 2003; Sigogneau-Russell, 2003a; Martin and Averianov, 2007). The triconodontid from the Balabansai assemblage is the oldest representative of this group worldwide.

'Symmetrodontans' are very rare in both the Forest Marble and Balabansai assemblages and are represented by different taxa: *Shuotherium* in the former and an unidentified tinodontid in the latter. Shuotheriids link the Forest Marble fauna with the Middle and Late Jurassic of China (Chow and Rich, 1982; Wang et al., 1998; Luo et al., 2007a), whereas tinodontids appear in the Late Jurassic of North America (Simpson, 1929). Tinodontids underwent a modest radiation in the Early Cretaceous of Asia and Europe (see review in Lopatin et al., 2005) and undoubtedly were also present in Asia in the Late Jurassic.

Dryolestidans, a very common and diverse component of the Late Jurassic faunas in Europe and North America, are quite rare in both the Forest Marble and Balabansai assemblages. In the former they are known from a few teeth identified as Dryolestidae indet. (Freeman, 1979), in the latter by two teeth identified as Paurodontidae indet. (this report). Possibly the origin and early diversification of the Dryolestida took place in Asia, but there is currently not enough information available to do more than speculate.

The most derived Middle Jurassic mammals are stem lineage zatherians belonging to the amphitheriids. In the Forest Marble they are represented by two taxa (*Palaeoxonodon* and *Kennetheredium*: Freeman, 1976, 1979; Sigogneau-Russell, 2003c), and the closely related *Amphitherium* is known also from the Bathonian Stonsfield Slate assemblage in England (see review in Butler and Clemens, 2001). In the Balabansai assemblage this group is known from a tooth fragment of an unidentified amphitheriid.

In conclusion, the Balabansai and Forest Marble localities show a relatively uniform distribution of Middle Jurassic mammalian assemblages over a wide geographic range. Both assemblages also indicate the advent of a more derived, Late Jurassic mammalian community, with first dryolestids in the Forest Marble and first triconodontids, tinodontids, and paurodontids in the Balabansai Formation. A peculiar group of the Middle Jurassic, unknown in later times, were the amphitheriids. In the Late Jurassic they were replaced by more derived stem lineage zatherians: *Nanolestes* in the Kimmeridgian of Portugal and in the Oxfordian of Xinjiang, China (Martin, 2002; Martin et al., 2010).

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