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SHORT COMMUNICATION

A previously unrecognized group of Middle Jurassic triconodontan mammals from Central Asia

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Abstract *Ferganodon narynensis* gen. et sp. nov. is represented by a lower molariform tooth from the Middle Jurassic (Callovian) Balabansai Svita in Kyrgyzstan. The new genus is allied with *Klamelia zhaopengi* Chow and Rich 1984 from the Middle Jurassic Shishugou Formation in Xinjiang, northwest China to the new family Klameliidae based on parallelogram-shaped lower molariforms, imbricating rather than interlocking of cusps *e-d-f*, by a peculiar distolabial cingulid cusp, and by vertical folding of the enamel on the labial crown side. The new family Klameliidae fam. nov. is most similar to Gobiconodontidae by the structure of the molariform teeth and represents a previously unrecognized radiation of eutriconodontan mammals possibly endemic to Central Asia.

Keywords Balabansai Svita · Callovian · Eutriconodonta · *Ferganodon* · Gobiconodontidae · *Klamelia* · Kyrgyzstan

Introduction

There are three vertebrate localities within the Middle Jurassic Balabansai Svita in the northern Fergana Valley, Kyrgyzstan that have produced remains of mammals: (1) Sarykamyshsai 1 (site FTA-30), 3–4 km east of the town of Tashkumyr (lower, gray to greenish colored part of the Balabansai Svita, Callovian); (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 Svita, Callovian); and (3) Dzhiddasai (site FBX-23), 5 km west of the town of Tashkumyr (upper, red colored part of the Balabansai Svita, Callovian; see Averianov et al. 2005 for a more detailed description of localities). More than 20 mostly fragmentary mammalian teeth were recovered so far from these localities. The mammal fauna is dominated by docodonts, represented by an isolated molar of *Tashkumyrodon desideratus* Martin and Averianov 2004 from Sarykamyshsai 1 and by a lower molar and several upper molar fragments of a new docodont from the Tashkumyr 1 bonebed that is similar to *Dsungarodon zuoi* Pfretzschner and Martin, 2005 from the Late Jurassic (Oxfordian) Qigu Formation in the Junggar Basin, Xinjiang, northwestern China. This locality produced also one almost complete and several fragmentary teeth referable to one or two taxa of Eutriconodonta. The most complete eutriconodontan tooth is described here and attributed to a new taxon within the newly established family Klameliidae fam. nov.

Institute abbreviations IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; ZIN, Zoological Institute, Russian Academy of Sciences, St. Petersburg.

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Systematic Paleontology

Mammalia Linnaeus 1758
Eutriconodonta Kermack et al. 1973
Klameliidae fam. nov.
Type genus: *Klamelia* Chow and Rich 1984.

Diagnosis Triconodontan mammals with linearly arranged cusps on lower molariforms referable to the Eutriconodonta rather than to the Morganucodonta by lack of a cingular lingual cusp *g* (kühneocone). Shares with the Gobiconodontidae Chow and Rich 1984 the following derived characters on lower molariforms: crown height approximately equivalent to the crown length (reconstructed), cusps *b* (when present) and *c* diverging from rather than parallel to the central cusp *a* (in lateral view), and cusp *c* taller than cusp *b* (reconstructed), with the base of cusp *c* positioned high on the crown, well above the level of the cingulid. Differs from Gobiconodontidae by parallelogram-shaped lower molariform crowns (in occlusal view), indicating an imbrication of the molariforms rather than *e*-*d*-*f* interlocking, a peculiar distolabial cingulid cusp, and vertical folding of the enamel on the labial crown side (all derived characters).

Remarks The dental formula and dentary structure are partially known only for the type genus (see "Discussion" for the interpretation of the dental formula). *Klamelia* is similar to the majority of gobiconodontids by its steep mandibular symphysis, but differs by an enlarged and transversely expanded ultimate premolariform, distinctly larger mental foramina located below the molariforms rather than premolariforms, and possibly by the lack of a Meckelian groove (report of the Meckelian groove in *Klamelia* by Zhang (1984) is apparently a misobservation). However, with the growing diversity of known gobiconodontids, it becomes evident that at least two of these characters, the size and position of the mental foramina, are more variable than previously thought and in some gobiconodontid specimens are partially similar to the condition of *Klamelia*. For example, in a gobiconodontid dentary from the Early Cretaceous Oshish locality in Mongolia, a very large posterior mental foramen is positioned between m1 and m2 (Minjin et al. 2003, Fig. 1). In *Repenomamus giganticus* Hu et al. 2005 from the Lower Cretaceous Yixian Formation in Liaoning, China, there are three rather large mental foramina, with the largest posterior mental foramen located between the ultimate premolariform and first molariform (Hu et al. 2005, Fig. 1a,b).

Ferganodon gen. nov. and *Klamelia* show a tendency to form a functionally bicuspid lower molariform pattern, with cusp *b* reduced in the former and completely lost on the known teeth of the latter (see "Discussion" for the interpretation of the cusps in *Klamelia*). Some Early Cretaceous gobiconodontids show a similar trend, but have cusp *b* reduced only on the most anterior molariform tooth (m1; see, e.g., Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Meng et al. 2005; Minjin et al. 2003, 2004). This similar tendency and the shared derived

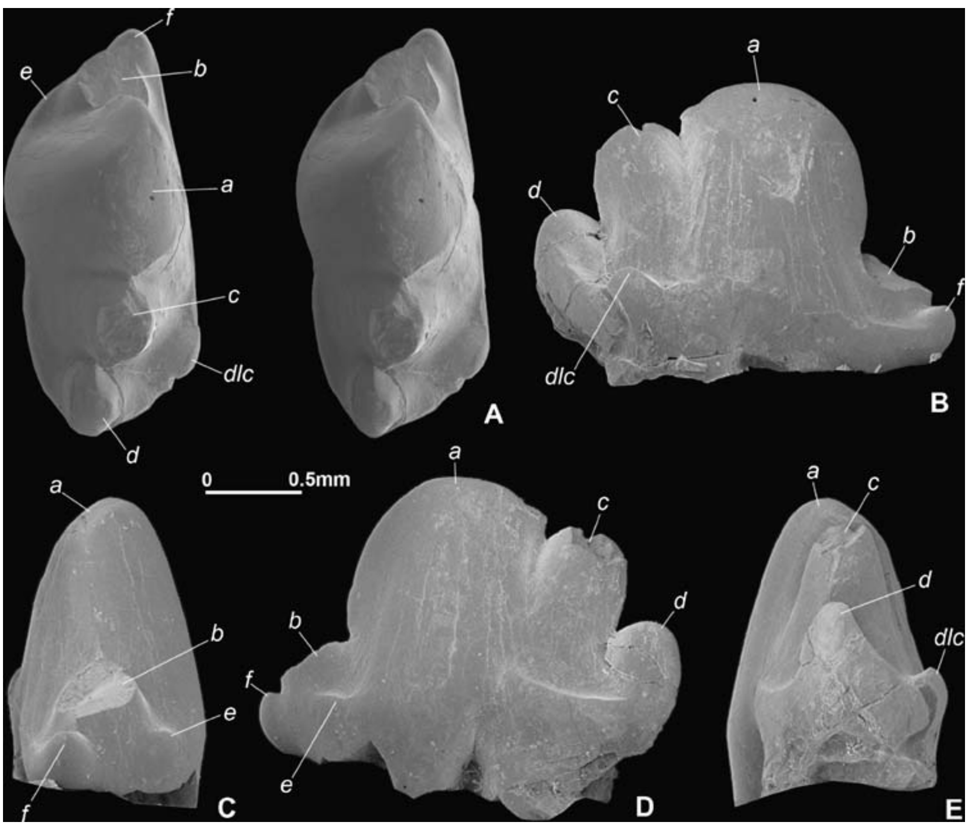

Fig. 1 *F. narynensis* gen. et sp. nov. SEM micrographs of ZIN 94214 (holotype), right lower molariform tooth, in occlusal (**a** stereopair), labial (**b**), mesial (**c**), lingual (**d**), and distal (**d**) views. *a*–*f* Corresponding cusps, *dlc* distolabial cusp. Tashkumyr 1 (site FTA-131) near the town of Tashkumyr, Fergana Valley, Kyrgyzstan; Balabansai Svita, Middle Jurassic (Callovian)

features outlined above suggest a close relationship between Gobiconodontidae and Klameliidae fam. nov.

Included genera Type genus and *Ferganodon* gen. nov., Middle Jurassic of northwest China and Kyrgyzstan.

Ferganodon gen. nov.
Type species: *Ferganodon narynensis* sp. nov.

Diagnosis Ferganodon gen. nov. differs from *Klamelia* by presence of cusp *b* (plesiomorphic character), higher cusp *d* (?derived character), better developed distolabial cingulid cusp (?plesiomorphic character), reduced mesiolingual cingulid cusp *e* and enlarged mesiolabial cingulid cusp *f* (character of uncertain polarity), and poorly developed and incomplete lingual cingulid (character of uncertain polarity).

Remarks It cannot be completely ruled out that in *Klamelia*, cusp *b* is lost only in the known anterior molariforms (m1–4) and was still present in the unknown posterior molariforms (m5–6).

Included species: Type species only
Etymology: After the Fergana Valley in Central Asia and οδον, stem of οδους (Greek), tooth
Ferganodon narynensis sp. nov.
Figure 1
Holotype: ZIN 94214, right lower molariform tooth
Type locality and horizon: Tashkumyr 1 (site FTA-131), left bank of the Naryn River near the town of Tashkumyr; 36–37 m above the base of the Balabansai Svita, Middle Jurassic (Callovian)
Diagnosis: As for the genus

Description

The crown is parallelogram-shaped in occlusal view with the corners made up by the mesiolabial cingulid cusp *f*, distolabial cingulid cusp, distal cusp *d*, and cusp *e*. There are five cusps aligned linearly along the mesiolabial–distolingual diagonal of this parallelogram: mesiolabial cingulid cusp *f*, cusp *b*, cusp *a*, cusp *c*, and distal cusp *d*. Cusp *a* is the largest cusp and its base occupies 45% of the crown length. Originally, cusp *a* was undoubtedly the highest crown cusp, but a large portion of its apical part is removed by wear, leaving a prominent wear facet along the labial slope. On this wear facet, the dentine is exposed and the pulp cavity is opened by a small hole. Cusp *b* is much smaller and placed at the mesial base of cusp *a*. Although apically incomplete, cusp *b* originally did not reach half the height of cusp *a*. Cusp *c* is positioned much higher on the crown relative to cusp *b*, with its base well above the cingulid level and approximately at the level of the midheight of cusp *a*. The distal cusp *d* is relatively higher than in the majority of other eutriconodontans and apparently was higher than cusp *b*. The mesial edge of cusp *d* and mesial and distal edges of cusps *a*, *b*, and *c* are convex, pointed and sharp, forming a series of longitudinal cutting blades. The labial side of the crown is sculptured by fine vertical irregular enamel ridges, while the lingual crown side is smooth. There is a lingual cingulid, which is interrupted at the base of cusp *a* and at the mesial embayment at the base of cusp *b*. This embayment apparently fitted against the distal cusp *d* of the preceding tooth and, thus, represents a rudimentary *e*-*d*-*f* interlocking system. In this case, a short lingual cingulid between this embayment and the cingulid-free lingual base of cusp *a* would be homologous to the mesiolingual cusp *e* of amphilestids and gobiconodontids. The labial cingulid is complete, but is very narrow at the base of cusp *a*. It is widest and shelflike distolabially of cusps *c* and *d*, where it formes a prominent distolabial cingulid cusp. The roots are broken and the base of the mesial root is somewhat longer (mesiodistally) than that of the distal root (Fig. 1).

Remarks ZIN 9214 and the molariforms of *Klamelia zhaopengi* are parallelogram-shaped, which indicates an imbricating pattern rather than a molar interlock (Fig. 2). However, in the right molariform ZIN 9214, the parallelogram is mirrored in comparison to the left molariforms of *K. zhaopengi* (Fig. 3). The interpretation of ZIN 9214 as a right molariform is based on the position of the labial wear facet and the distolabial cusp (Fig. 1).

The height of the crown in ZIN 94214 is about 70% of the crown length. However, the height of cusp *a* is significantly reduced by wear and the unworn crown possibly was as high as long.
Etymology: After the Naryn River in Kyrgyzstan

Discussion

K. zhaopengi Chow and Rich 1984 is known from a single specimen, a left dentary fragment with five teeth preserved (Fig. 2), from the basal section of the Shishugou Formation at Jianshan Wash in the Junggar Basin, Xinjiang-Uygur Autonomous Region of China (Chow and Rich 1984; Kielan-Jaworowska et al. 2004; Zhang 1984). The lower part of the Shishugou Formation was originally determined as late Middle Jurassic to Late Jurassic in age, then as Late Jurassic (Dong 1994; Kielan-Jaworowska et al. 2004), but according to more recent data is now regarded as Middle Jurassic (Clark et al. 2004; Eberth et al. 2001).

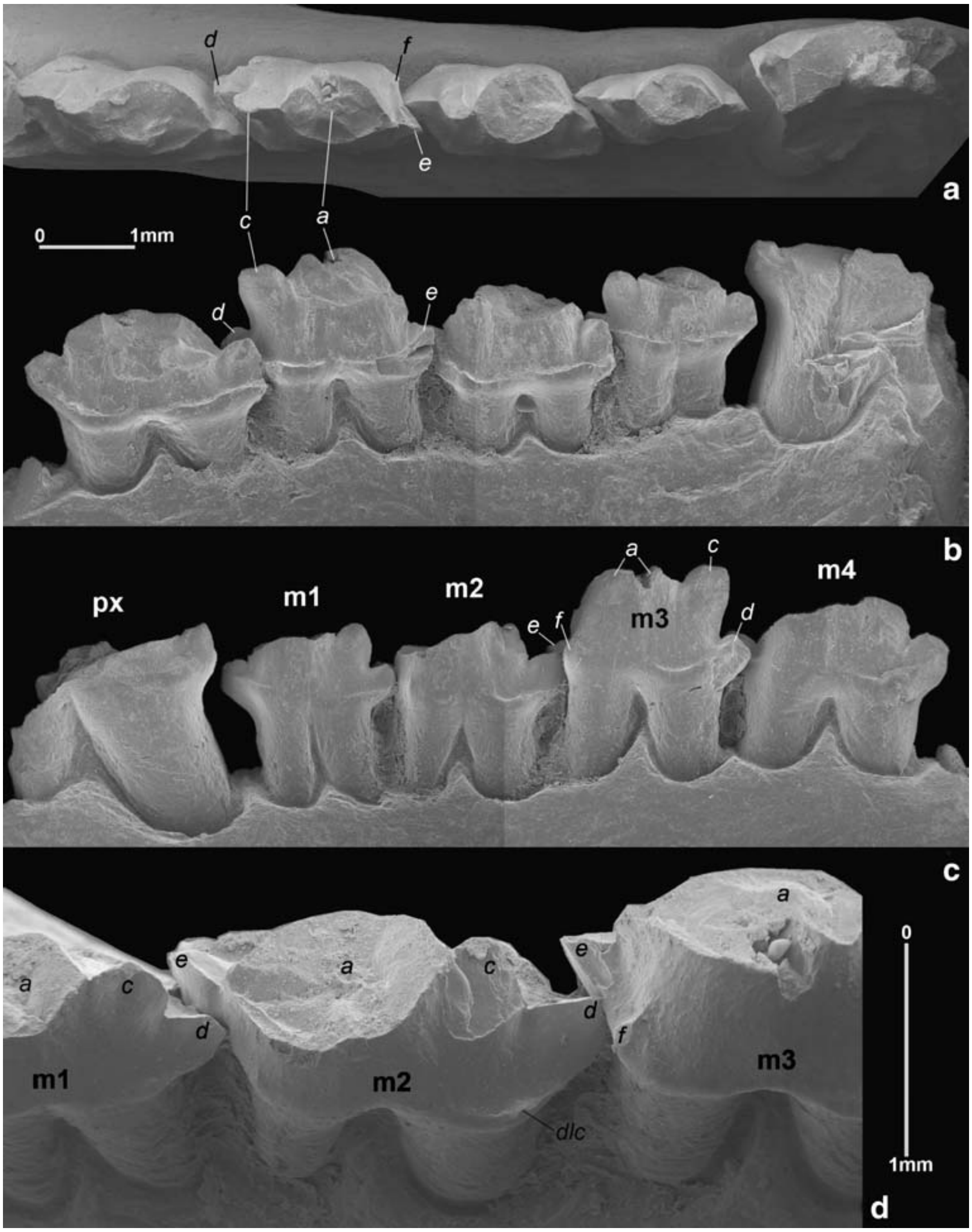

Fig. 2 *K. zhaopengi* Chow and Rich, 1984. SEM micrographs of a cast of IVPP V6447 (holotype), left dentary fragment with ultimate premolariform (*px*) and molariforms (*m1–m4*), in occlusal (**a**), lingual (**b**), labial (**c**) views, and enlarged occlusolabial view of m1–3 showing details of the imbricating of teeth (**d**). *a–f* Corresponding cusps, *dlc* distolabial cusp. Jianshan Wash, Junggar Basin, Xinjiang-Uygur Autonomous Region, China; lower Shishugou Formation, Middle Jurassic

Interpretation of the known dentition and systematic position of *Klamelia* is difficult. Chow and Rich (1984, p. 227) combined *Klamelia* with the Early Cretaceous *Gobiconodon* in the Gobiconodontinae (within Amphilestidae) based on “foreshortening of the mandible and correlative reduction of the number of antemolar teeth to six or less.” These authors considered a procumbent incompletely preserved anterior two-rooted tooth to be the last premolar and the following teeth, gradually increasing in size posteriorly, as molars. This would give, together with the preserved tooth roots, at least two premolars and six molars for *Klamelia*. That interpretation was criticized by an anonymous reviewer of Chow and Rich’s paper, who suggested that the anterior procumbent tooth is a double-rooted canine and the following preserved teeth are p1–4 (Chow and Rich 1984, p. 230). The opinion of the anonymous reviewer was upheld by Rougier et al. (2001, p. 16), who considered *Klamelia* not being closely related to *Gobiconodon* and referred it to Mammaliaformes *incertae sedis*. Kielan-Jaworowska et al. (2004, p. 239) regarded *Klamelia* as “an eutriconodont of “amphilestid” grade” noting its difference to the gobiconodontids in molariform structure and imbrication in the molariform series.

We agree with Rougier et al. (2001) that the original arguments by Chow and Rich (1984) for assessing a p1+?, m1-6+? dental formula for *Klamelia* are not sound (although their tooth count is correct). For the canine nature of the anteriormost preserved tooth in the *K. zhaopengi* holotype, with two roots and accessory distal

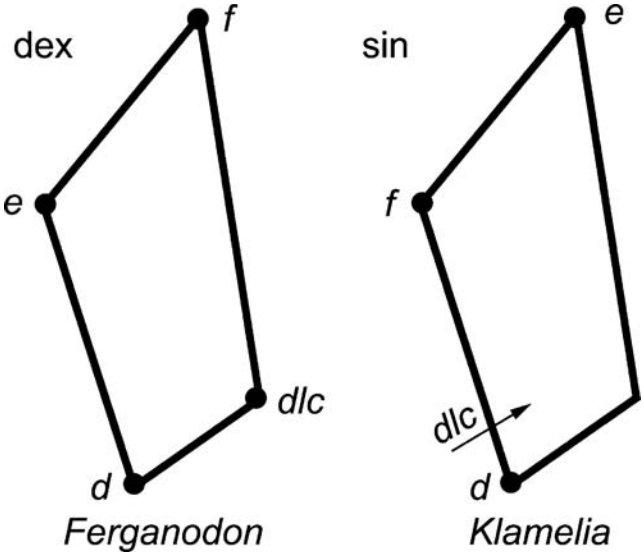

Fig. 3 Schematic line drawings of the parallelogram-shaped tooth crowns of ZIN 94214 and a lower molariform of *K. zhaopengi* in occlusal view. The letters *d*–*f* and *dlc* (distolabial cusp) designate the corresponding cups that form the corners of the parallelogram

cusp, advocates its relatively anterior position on the jaw and its projection above the level of the following teeth. A similar double-rooted canine with distal accessory cusp is present in some Mesozoic mammals, such as docodonts, symmetrodonts, and dryolestids. However, in *Klamelia* the crown base of this tooth is remarkably expanded transversely. Such a transverse expansion is not found in the canine of any Mesozoic mammal but can occur in premolariforms. In the majority of Mesozoic mammals, the premolariforms are much simpler than the cheek teeth present in *Klamelia* and are dominated by the principal cusp with small mesial and distal accessory cusps. Originally (Chow and Rich 1984; Kielan-Jaworowska et al. 2004), the cusps of the teeth of *Klamelia* were interpreted as central cusps *a* and *c* and cingulid cusps *b* and *d*. In this interpretation, the functionally bicuspid teeth of *Klamelia* with cingulid cusp *b* superficially resemble the lower molariforms of morganucodonts (which was apparently a reason for referring *Klamelia* to the Morganucodontidae by Zhang 1984). However, discovery of *Ferganodon* gen. nov., which is structurally ancestral to *Klamelia*, demonstrates that cusp *b*, already diminished in *Ferganodon* gen. nov., is completely lost in *Klamelia*. The mesial cingulid cusp of *Klamelia* is not cusp *b*, but a cingulid cusp apparently homologous with cingulid cusp *e* of amphilestids and gobiconodontids. In spite of the distinct imbrication of the molariforms in *Klamelia*, at least a pair of molariforms (m2 and m3) exhibit a rudimentary *e-d-f* interlocking pattern (Fig. 2d). A similar rudimentary interlocking can be inferred for ZIN 94214, where there is a mesial embayment at the base of cusp *b* between the mesially prominent cingular cusp (*f*) and mesiolingual cingulid (rudimentary cusp *e*; Fig. 1a,c). Thus, we consider the imbrication pattern of the molariforms in *Ferganodon* gen. nov. and *Klamelia* to be derived from a primitive *e-d-f* interlocking pattern of amphilestids and gobiconodontids. This interlocking is characteristic for the molariforms, but not for the premolariforms, which further suggests a molariform nature of the teeth in *Klamelia*. Therefore, we think that the original interpretation of dental formula of *Klamelia* as p1+?, m1-6+? by Chow and Rich (1984) is correct.

The imbrication pattern in *Klamelia* and *Ferganodon* gen. nov. may have independently evolved. In *Ferganodon* gen. nov., cusp *d* of the preceding molariform most probably was overlapped labially by mesiolabial cusp *f*; consequently, mesiolingual cusp *e* is considerably reduced. In *Klamelia* the situation is the opposite: mesiolabial cusp *f* is greatly reduced or lost, while mesiolingual cusp *e* is enlarged and overlaps cusp *d* of the preceding tooth lingually (Fig. 2d). Complementary to the peculiar parallelogram-shaped outline of the molariforms, *Ferganodon* gen. nov. and *Klamelia* can be united by the presence of a unique distolabial cusp and vertical folding of the enamel on the labial flank, which are not present in other eutriconodontans including gobiconodontids. Although the distolabial cingulid cusp is reduced in *Klamelia* compared to the condition of *Ferganodon* gen. nov., it is still clearly evident on m3–4 in the holotype of. *K. zhaopengi* (Fig. 2a).

The structure of dentary and dentition of *Klamelia* is remarkably convergently similar to those in Late Cretaceous stagodontid marsupials (Fox and Naylor 2006): the dentary is robust and high anteriorly, with large mental foramina, shortened premolars/premolariforms, with the ultimate premolar/premolariform very large, transversely expanded, and approximating the mandibular symphysis. This convergence may indicate a similar diet in both taxa, possibly associated with the crushing of shelly invertebrates.

Klamelia and *Ferganodon* gen. nov. document a previously unknown radiation of gobiconodontid-like eutriconodontan mammals. This radiation occurred much earlier than the Early Cretaceous radiation of gobicondodontids and possibly was confined to a narrow geographic area in Central Asia incorporating present-day Xinjiang and Kyrgyzstan, in contrast to the much wider, pan-Laurasian distribution of the gobiconodontids (Cuenca-Bescos and Canudo 2003; Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Li et al. 2003; Maschenko and Lopatin 1998; Meng et al. 2005; Minjin et al. 2003; Rougier et al. 2001; Trofimov 1978; Wang et al. 2001).

The Middle Jurassic mammal fauna of the Balabansai Svita in Kyrgyzstan is only at the beginning of its exploration and study, and is currently represented by three to four species of Docodonta and Eutriconodonta (Martin and Averianov 2004 and this report). Roughly coeval late

Middle Jurassic to early Late Jurassic strata in the Junggar Basin, northwest China so far produced remains of Haramiyida and Docodonta (Maisch et al. 2005; Pfretzschner et al. 2005). Ongoing investigations will show if the currently observed differences between these regional faunas reflect a temporal and/or geographic or environmental disparity or are mostly affected by a sampling bias.

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