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Mammals from the Late Jurassic Qigu Formation in the Southern Junggar Basin, Xinjiang, Northwest China

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Abstract Five mammalian taxa based on teeth and jaw fragments are reported from a bonebed of the Late Jurassic (Oxfordian) Qigu Formation at the Liuhuanggou site in the southern Junggar Basin. The mammals recovered to date comprise a new eleutherodontid haramivid, the docodonts Dsungarodon and Tegotherium, an undetermined amphilestid triconodont, and a new species of the stem zatherian Nanolestes and represent the most diverse Late Jurassic mammal assemblage of Asia. The Liuhuanggou mammal assemblage is dominated by docodonts. Acuodulodon Hu et al., 2007 from the upper part of the Shishugou Formation (Oxfordian) of the Wucaiwan area in the central Junggar Basin is a junior synonym of Dsungarodon Pfretzschner and Martin, 2005. Tegotherium has been reported from the Late Jurassic Shar Teeg locality in Mongolia. With the exception of the common occurrence of Nanolestes, the mammalian assemblage from the Late Jurassic of the Guimarota coal mine (Portugal) is quite different from that of the Late

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H.-U. Pfretzschner Institut für Geowissenschaften, Universität Tübingen, Sigwartstraße 10, 72076 Tübingen, Germany Jurassic Qigu Formation. The Guimarota assemblage is dominated by five genera of dryolestidans and several genera of multituberculates, which have not been reported from the Qigu assemblage. The known Late Jurassic mammalian assemblages of Asia are similar to the Middle Jurassic assemblages known from Asia and elsewhere in the world.

Keywords Junggar basin · Jurassic · Liuhuanggou · Mammals · Qigu Formation

Introduction

The Junggar Basin in northwestern China (Xinjiang Autonomous Region; Fig. 1) is one of the largest continental basins in Central Asia and represents a landlocked sedimentary environment that has been cut off from marine influence since the late Paleozoic by the uplift of the ancestral Tian Shan and Bogda Shan orogenic systems (Allen et al. 1993, 1995; Windley et al. 1990). It contains a sedimentary succession from the Permian to the Late Cretaceous. Of the 16,000 m of sedimentary infill at the center of the basin, about 6,000 m represent fluviolacustrine Mesozoic deposits (Dong 1992). The Early Jurassic to Early Cretaceous strata have been grouped into four megasequences, representing a climatic change from warm and humid to hot and seasonally arid conditions (Eberth et al. 2001). Relatively rich fossil vertebrates are mainly concentrated on the central and northern parts of the basin where the Middle Jurassic Wucaiwan and Late Jurassic Shishugou Formations have produced spectacular finds of well-preserved dinosaurs and associated fauna at the classic sites of Pingfenchan and Jianjunmiao, among others (e.g., Currie and Zhao 1993; Peng and Brinkman 1993; Wu et al. 1996; Xu et al. 2006). The Mesozoic strata on the southern rim of the Junggar basin received very little

Fig. 1 Map of Xinjiang Autonomous Region in northwestern China. *Asterisk* indicates the Liuhuanggou locality 40 km southwest of Urumqi. *AFG* Afghanistan, *TADZ* Tadzhikistan



attention until 1999, when the Sino-German Project began to search for fossils in this area (Maisch et al. 2001). At the Liuhuanggou locality 40 km southwest of the city of Urumqi, at the southern margin of the Junggar Basin, a highly fossiliferous bonebed within the lower Qigu Formation has been intensively screen-washed since 2004. Discovered in 2000 (Maisch et al. 2001), the bonebed initially was considered to be a lower member of the Toutunhe Formation (Maisch et al. 2003), but detailed geological mapping of the area demonstrated that it actually belongs to the upper part of the Qigu Formation. The Qigu Formation has been dated to the Oxfordian Age, based on palynomorph data (Ashraf et al. 2001, 2004, 2010, this issue), and is 731 m thick at the Liuhuanggou locality. The bonebed is 20 to 40 cm thick and consists of unstratified greenish clay- to siltstone with numerous small (diameter mostly <10 mm) intraclastic clay pebbles. The bones and teeth are generally concentrated in lenses but can also be dispersed in the bonebed. The base of the bonebed is irregular, and the contact with the underlying fossil-free red claystone is erosional. Near the upper surface, the bonebed changes into a greenish to reddish fine sandstone, with numerous turtle plates at the base. The fine sandstone is characterized by a trough-like cross-bedding and is about 50 cm thick. Towards the top it continues into a greenish to reddish silt- to claystone. The bonebed has yielded a large amount of bones and teeth of aquatic and terrestrial vertebrates, such as hybodontid sharks, actinopterygians, temnospondyles, xinjiangchelyid turtles, crocodiles, dinosaurs, pterosaurs, and mammals (Klug et al. 2010, this issue; Maisch et al. 2001, 2003, 2004; Martin et al. 2008; Pfretzschner et al. 2005; Richter et al. 2010, this issue; Skutchas et al. 2009; Wings et al. 2010, this issue).

The mammals are of particular interest for two reasons: (1) little is currently known about Jurassic mammals in Central Asia; (2) mammals provide important information on faunal interrelationships with Western Europe as well as with Mongolia. Three major groups of mammals have been reported from the Liuhuanggou site to date: haramiyids, docodonts, and stem zatherians. In terms of number of specimens and taxa, at Liuhuanggou, the mammalian fauna is dominated by docodonts. The docodont *Dsungarodon zuoi* has been described previously (Pfretzschner et al. 2005). In this report, we describe the other docodonts and the new stem zatherian as well as additional material of the haramiyid.

Materials and methods

The clay and siltstones from the bonebed were quarried and transported by horse and car to the nearby Totounhe river. The sediment was dissolved overnight with 5% peroxide

solution in plastic tubs and subsequently screen washed (applying the Henkel process (Henkel 1966; Kühne 1971)). A screen of 10-mm mesh size was used to remove larger components, and the screen window in the barrel had a mesh size of 0.5 mm. The coarse fraction (>10 mm) was dried and picked in the field. The fine fraction was dried, separated into two fractions (2-10 mm, and 0.5-2 mm) and picked under a stereomicroscope in the laboratory. In 2004, a total of 3,380 kg of matrix was screen-washed (780 kg directly from the bonebed and 2600 kg from the weathered surface), which produced 270 kg of concentrate (8% of the original amount). In 2005, a total of 1380 kg of matrix taken directly from the bonebed was screen-washed. For further reduction, the concentrate was treated with the tensid Rewoquat W 3690 (Goldschmidt-Rewo, Steinau an der Straße, Germany) and subsequently screen washed in the laboratory.

For scanning electron microscopic (SEM) examination, specimens were coated with gold and photographed with a CamScan MV 2300 (CamScan, Cambridge, UK). Electronic images were cut and adjusted (contrast and brightness) using Photoshop, but not otherwise retouched. Measurements were taken on specimens studied in the SEM and are given in millimeters (mm).

In the classification of Mesozoic mammals, we generally follow Kielan-Jaworowska et al. (2004).

Institutional abbreviations: **BDUC**, Biology Department, University College, London; **BMNH**, Natural History Museum, London; **Gui Mam**, a collection of mammals from Guimarota coal mine in Portugal; **SGP**, Sino-German Project, a collection currently housed at the Steinmann-Institut at the Universität Bonn, Germany. After completion of the investigation, the material will be permanently deposited under the SGP collection numbers in the Research Center of Paleontology and Stratigraphy at the Jilin University in Changchun, China.

Measurements: L, length, W, width. An asterisk (*) denotes preserved length or width of a damaged specimen.

Systematic paleontology

Mammalia Linnaeus, 1758 Allotheria Marsh, 1880 Eleutherodontidae K.A. Kermack, D.M. Kermack, Lees, and Mills, 1998 *Sineleutherus* gen. nov.

Etymology: After Sina (Latin) for China and the generic name *Eleutherodon* Kermack et al., 1998.

Type species: Sineleutherus uyguricus sp. nov.

Diagnosis: Referred to the Eleutherodontidae. Differs from other allotherians by exhibiting ovoid lower molariform

teeth, with two rows of cusps that are continuous around the distal end and placement of the largest cusp on the lower molariforms at the mesial end of the labial row. Differs from Multituberculata by retaining an extensive orthal component of occlusion. Differs from *Eleutherodon* Kermack et al., 1998, the only other genus of the family, by having larger and fewer marginal cusps on the lower molariform teeth and the absence of numerous transverse ridges (crenulations, or "fluting") in the central basin.

Included species: Type species only.

Distribution: Late Jurassic of Asia (northwest China).

Comments: The holotype of *Eleutherodon oxfordensis* Kermack et al., 1998 from the British Middle Jurassic Forest Marble Formation is an upper molariform tooth (Kermack et al. 1998, figs. 1–4). Kermack et al. (1998) referred to this species as having three types of lower molariform teeth (β , γ , and ζ), of which only type β is now attributed to *Eleutherodon* (Butler and Hooker 2005). This tooth (Kermack et al. 1998, figs. 15, 16) clearly differs from the Chinese lower molariform teeth by being much smaller and having numerous marginal cusps and numerous irregular enamel crenulations (cusps and short ridges) which completely fill the central basin, contra Maisch et al. (2005, p. 42) who state that "the Chinese specimen is indistinguishable from [...] *Eleutherodon oxfordensis.*"

The current diagnosis of Eleutherodontidae (Butler 2000, p. 335; Kermack et al. 1998, p. 586; Kielan-Jaworowska et al. 2004, p. 258) mentions numerous marginal cusps and enamel "fluting". These characters should be restricted to *Eleutherodon* only, as *Sineleutherus* gen. nov. has fewer marginal cusps and no enamel "fluting". Maisch et al. (2005, p. 42) described the holotype of *S. uyguricus* sp. nov. as "transverse fluted ridges caused by wear" which "extend from the margins of the lingual and buccal cusps towards the center of the basin." These ridges (more precisely, grooves) do not correspond to the enamel fluting of *Eleutherodon* that is formed by enamel crenulations.

Sineleutherus uyguricus sp. nov., Figs. 2, 3, 4

2005 including *Eleutherodon* sp. of Maisch et al., p. 41, figs. 1, 2

Etymology: After the Uygur people living in the Xinjiang-Uygur Autonomous Region of China.

Holotype: SGP 2001/33, a left lower molariform tooth.

Referred specimens: SGP 2001/34, right upper incisor; SGP 2005/5, right upper incisor fragment; SGP 2005/3, right upper premolariform; SGP 2004/15, left lower premolariform; SGP 2004/16, left lower premolariform; Fig. 2 Upper teeth of Sineleutherus uyguricus gen. et sp. nov. Liuhuanggou locality, 40 km southwest of Urumqi, Xinjiang. Upper part of the Late Jurassic Qigu Formation (Oxfordian). a-c SGP 2001/34, right upper incisor in occlusal (a, stereopair), lingual (b), and labial (c) views, d-g SGP 2005/5, right upper incisor in occlusal (d. stereopair), lingual (e), labial (f), and labio-distal (g) views, h-j SGP 2005/3, right upper premolar in occlusal (h, stereopair), lingual (I), and labial (j) views



SGP 2004/17, right lower premolariform; SGP 2004/6, left ultimate lower premolariform; SGP 2004/12, right lower ultimate molariform tooth.

Description: There are two upper incisor-like teeth attributable to *S. uyguricus* sp. nov. SGP 2001/34 has a complete crown with three cusps (Fig. 2a–c). The mesial half of the crown is formed by a large and slightly curved mesial cusp with a prominent apical wear facet. This wear facet is connected to a band-like wear facet along the ridge connecting the apex of the mesial cusp with an extensive, flat wear area on the distolingual side of the crown. There is a strong lingual cingulum on the mesial cusp. The

distolingual cusp is shorter than the mesial cusp but has a longer base. Both cusps are connected by a strong, straight labial ridge that is inflated in the center. Three longitudinal enamel ridges that increase in length and robustness lingually run along the mesiolingual side of the distolingual cusp, between the labial ridge and lingual flat wear area. Distal to the lingual flat wear area is a deep pocket housing the distolingual side of the distolingual cusp and the base of the distolabial cusp. There is a prominent longitudinal ridge on the distolingual cusp that extends from the apex of the cusp. The distolabial cusp is much smaller than the two other cusps and is confined to the base of the crown. Its lingual side is completely covered by an extensive flat wear area. Two faint vertical ridges are on the labial side. The single root is labiolingually compressed.

SGP 2005/5 lacks most of the crown, including the largest mesial cusp (Fig. 2d–g). The distolingual cusp is prominent, with a small apical wear facet. Three enamel ridges are on its mesiolingual side, as in SGP 2001/34, but the arrangement of these ridges is somewhat different. The smallest distolabial cusp is broken off. SGP 2005/5 is distinctly larger than SGP 2001/34 and could be an I2, while SGP 2001/34 is possibly an I1 or I3.

There are five premolariform single-rooted teeth which we think belong to *S. uyguricus* sp. nov. The crown of all teeth is dominated by a large cusp at the end of the crown (mesial on lower teeth and distal on upper teeth). Wear facets are situated on the labial side in the lower teeth and on the lingual side in the upper teeth. The teeth show an interlocking system, with a projection of the base of the crown on the distal side which abuts the following tooth in the series. The combination of these characters allows us to recognize upper and lower, and left and right teeth.

SGP 2005/3 (Fig. 2h-j) is the only known upper premolariform. The base of the largest distal cusp B3 occupies the distal half of the crown. The apex of the cusp is turned mesially and bears a prominent apical wear facet. The base of the central cusp (B2) is about twice the size of the base of the mesial cusp (B1); both cusps are heavily worn. The lingual crown side is remarkably flat and almost completely covered by an extensive wear facet which unites the apical wear facets of cusps B1 and B2, but does not reach the apex of cusp B3. The lingual cingulum is confined to the mesial half of the crown, opposite to cusps B1 and B2. It bears four cuspules with apical wear. The mesial cingular cuspule (A1) is set off the row of the other cuspules and is situated mesially close to the cingular shelf. The other cuspules (A2-A4) are mesiodistally aligned and poorly differentiated. On the distal end of the crown, at the base of cusp B3, there is a prominent distal projection of the crown that apparently interlocked with the subsequent tooth.

SGP 2004/15 is a left lower premolariform (Fig. 3a–c). It is simpler than the other lower premolariforms described below by possessing only a single row of three cusps and by the lack of a lingual cingulid; it may derive from a more anterior position in the tooth row. The apex of the largest mesial cusp (b2) is curved distally. The central cusp (b3) is about 2.5-fold lower than the main cusp, and the distal cusp (b4) is much smaller than the central cusp. The labial crown side is flat and longitudinally concave, with a prominent wear facet extending to the mesial and distal ends towards the apices of the mesial and distal cusps. The lingual crown side is convex, and the mesial crown side is straight. On the distal side there is a distal projection of the base of the crown that interlocks with the next tooth.

SGP 2004/16 and 2004/17 are left and right lower premolariforms (Fig. 3d-g and h-j, respectively). They have a similar shape and are described together. Both teeth have a row of three cusps aligned along the flattened labial crown side which bears a prominent wear facet, and a cuspidate cingulid confined to the distal half of the lingual crown side. The mesial cusp (b2) is the largest in the row and is distinctly curved distally. The central cusp (b3) is also large-more than half of the height of the mesial cusp (preserved only in SGP 2004/16; in SGP 2004/17 it is worn down or broken). It is not curved, but directed somewhat distally. The distal cusp (b4) is the smallest. On the lingual cingulid, there are two (SGP 2004/16) or four (SGP 2004/17) cuspules (a1-a4). The mesial side of the crown is convex. On the distal side, there is a prominent projection at the base of the crown for the interlock with the following tooth.

A lower premolariform SGP 2004/6 has two rows of cusps: a row of larger cusps along the flattened labial side and a row of smaller cingular cusps along the lingual side (Fig. 4a-d). These two cusp rows surround the central basin, which is larger than that observed in any previously described premolariform teeth. Thus, SGP 2004/6, being the most molariform of these teeth, is considered here as an ultimate lower premolariform. The mesial cusp of the labial row (b2) is the largest and is distally curved. The central cusp (b3) has less than half the height of the mesial cusp, and the distal cusp (b4) is much lower than the latter. The row of cingular lingual cusps consists of two cusps (a1 and a2), both of which are similar in size to the distal cusp (b4) but are positioned lower on the crown than the latter. The two rows of cusps converge slightly distally. The central basin is closed distally by a small additional cusp. On the labial side of the crown there is a wear facet along the bases of cusps b2 and b3.

Two lower molariform teeth are attributed to this species. The holotype, which is an anterior molariform-possibly a m1—has been described by Maisch et al. (2005, pp. 41-42). SGP 2004/12 (Fig. 4e-j) is approximately 60% of the length of the holotype tooth (it is incomplete mesially because of the broken main mesiolabial cusp, b2) and has fewer labial cusps. It is considered here as the ultimate lower molariform (m?3). In the African Late Jurassic haramiyid Staffia aenigmatica Heinrich, 1999 the size difference between the supposed last and first lower molariform teeth is even larger: the ultimate tooth is only 44% of the length of the first molariform tooth (Heinrich 1999, 2001). The crown of SGP 2004/14 is oval-shaped, with the mesial side as wide as the distal side and with a deep central basin surrounded by three labial cusps and four lingual cusps. Although the larger portion of the mesiolabial cusp b2 is missing, it undoubtedly was the largest cusp of the crown judging from its preserved base. Cusp b3 is Fig. 3 Lower premolarifoms of S. uyguricus gen. et sp. nov. Liuhuanggou locality, 40 km southwest of Urumqi, Xinjiang. Upper part of the Late Jurassic Oigu Formation (Oxfordian). a-c SGP 2004/15, left lower premolariform in occlusal (a, stereopair), lingual (b), and labial (c) views, d-g SGP 2004/ 16, left lower premolariform in occlusal (d, stereopair), lingual (e), labial (f), and distal (g) views, h-j SGP 2004/17, right lower premolariform in occlusal (h, stereopair), lingual (I), and labial (j) views



the second largest of the crown, and cusp b4 is distinctly smaller than b3. In the lingual row, the height gradient of the cusps is: $a^2 > a^3 > a^4 > a^2$, but a1 has a longer base than a4. Cusps $a^2 - a^3$ are mesiodistally aligned, while cusp a4 is offset labially and is aligned in an oblique row with cusps b3 and b4. The central basin is closed distally by a ridge between cusps a4 and b4. There is a peculiar small cusp in the center of the central basin opposite to cusp a2. All preserved cusps show apical wear, with the dentine exposed and surrounded by fluted ridges. These ridges variably extend downwards towards the central basin but do not reach the bottom of the basin. There are also fluted wear ridges between the cusps; the longest ridge is between b2 and b3. The tooth has a single root, is slightly subdivided on the labial side, and has a strong lingual curvature.

Measurements: SGP 2001/34: L=1.67, W=0.74; SGP 2005/ 5: width of lateral cusp:1.23; SGP 2005/3: L=0.75; W=0.41; SGP 2004/15: L=0.92, W=0.44; SGP 2004/16: L=1.03, W= 0.57; SGP 2004/17: L=1.06, W=0.54; SGP 2004/6: L=0.73, W=0.44: SGP 2004/12: L=1.48; W=1.09.

Comments: Maisch et al. (2005) assigned the Liuhuanggou locality, i.e., and the locality of SGP 2001/33 and the other teeth described here, to the Toutunhe Formation. This locality

Fig. 4 Lower premolariforms and molariforms of *S. uyguricus* gen. et sp. nov. Liuhuanggou locality, 40 km southwest of Urumqi, Xinjiang. Upper part of the Late Jurassic Qigu Formation (Oxfordian). **a**–**d** SGP 2004/6, left ultimate lower premolariform in occlusal (**a**, stereopair), lingual (**b**), labial (**c**), and distal (**d**) views, **e–I** SGP 2004/12, left lower molariform in occlusal (**e**, stereopair), lingual (**f**), labial (**g**), mesial (**h**), and distal (**I**) views



is now attributed to the Qigu Formation based on geological mapping (A.R. Ashraf, personal communication).

The upper incisor SGP 2001/34 is quite similar to BMNH M46234 from the Forest Marble Formation of England (Butler and Hooker 2005, figs. 6D, 13). Both teeth have three-cusped crowns with similarly arranged cusps, with the larger mesial and distolabial cusps aligned along the labial side of the crown and the distolingual cusp being the smallest. Both have an extensive flat wear facet along the lingual side, a lingual cingulum and a central longitudinal ridge on the mesial cusp, and longitudinal ridges on the distolabial cusp. Butler and Hooker (2005) formally referred BMNH M46234 to Allo-

theria *incertae sedis*, but noted that it possibly belongs to *Eleutherodon*, a conclusion with which we concur.

No premolariforms were identified for *Eleutherodon* by Kermack et al. (1998) or Butler and Hooker (2005), but in the BMNH collection from Kirtlington, Forest Marble Formation, there are at least five teeth that are very similar to the Chinese premolariform teeth described above. These specimens are housed in a box labeled "ornithopod teeth" and possess BDUC numbers (BDUC J287, J473, J608, J658, and J776; personal observation by Averianov). The British teeth differ from the Chinese teeth mainly by a more elaborated interlocking system, with a vertical groove on the mesial side (and mesial cingular cusps in BDUC J473).

SGP 2004/6 is similar to the haramiyid dental type from the Late Triassic of France and England designated as *Thomasia*, group II (Butler and MacIntyre 1994; Sigogneau-Russell 1989) which are most likely lower premolariforms of *Thomasia* Poche, 1908. The Chinese tooth has a similar two-cusped, distally confined labial cingulum, but differs by its distinctly higher and wider mesial cusp. As a result, the mesial crown side is wider than the distal side, while the situation is just the opposite in *Thomasia*. By its large mesial cusp it is more similar to the p4 of *Haramiyavia* Jenkins et al., 1997 from the Late Triassic of Greenland (Jenkins et al. 1997,fig. 1c). SGP 2004/6 is probably an ultimate lower molariform of *S. uyguricus* sp. nov.

Docodonta Kretzoi, 1946

Docodontidae Simpson, 1929

Dsungarodon Pfretzschner and Martin in Pfretzschner et al. 2005

2005 *Dsungarodon* Pfretzschner et al., p. 800 2007 *Acuodulodon* Hu et al., p.176

Type species: *Dsungarodon zuoi* Pfretzschner and Martin in Pfretzschner et al., 2005.

Revised diagnosis: Differs from all other docodontans by a large pseudotalonid basin bordered by crests a-b, a-g, and b-g, crenulations on the distal side of the lower molar crowns, and an additional groove above the Meckelian groove separated from the more posterior trough for the postdentary bones (see description for details). Differs from Simpsonodon Kermack et al., 1987 by the structure of the mesial cingulid on the lower molars: in Dsungarodon it consists of two parts, a robust labial rim pointing mesiolingually and a weaker lingual rim extending to the base of cusp g; the two rims meet mesially at an acute angle. In Simpsonodon there is a continuous mesial cingulid wrapping around the mesial end of the crown between cusps b and g, with a rounded mesial end. Additionally, Dsungarodon has a somewhat more developed cusp dd compared to Simpsonodon.

Included species: Type species only.

Distribution: Late Jurassic of Asia (northwestern China).

Comments: In the original diagnosis by Pfretzschner et al. (2005, p. 800), *Dsungarodon* was differentiated from *Simpsonodon* by upper molar characters only. However, one of the then known upper molars (SGP 2001/23) is referred here to *Tegotherium*, and the lingual fragments of upper molars that are here attributed to *Dsungarodon* closely resemble those of *Simpsonodon*. We amend the

diagnosis of *Dsungarodon* by the structure of the mesial cingulid in the lower molars, which is different from that in *Simpsonodon*. At least one additional lower molar character possibly distinguishes *Dsungarodon* from *Simpsonodon*: in *Dsungarodon*, a weakly developed cusp c is present on the ultimate lower molar, while it is completely absent in *Simpsonodon*. However, this character is known only for the Siberian species of *Simpsonodon* because the ultimate lower molar of the British *Simpsonodon* is not known.

Acuodulodon Hu et al., 2007 from the Oxfordian Shishugou Formation in northern Junggar Depression (Hu et al. 2007) is extremely similar to *Dsungarodon* and is here synonymized with the latter. The only known specimen of *Acuodulodon* is a poorly preserved dentary with partial dentition coming from the same stratigraphic level and region as *Dsungarodon*. Hu et al. (2007, p. 185) distinguish *Acuodulodon* from *Dsungarodon* by the structure of the premolars with larger a posterior cusp [actually this cusp is large only in p3], the lack of a labial cingulid, and the structure of the distal crown side of the lower molars.

The premolar characters are no longer useful to distinguish between Acuodulodon and Dsungarodon because the isolated premolar SGP 2001/26 that originally was referred to Dsungarodon (Pfretzschner et al. 2005, fig. 3C) is reassigned to Docodonta indet. here (see below for details). The newly collected sample of Dsungarodon contains a premolar (SGP 2005/6) with a large posterior cusp and with restricted labial cingulid that closely resembles the p3 of Acuodulodon. We doubt the reconstruction of the dental formula of Acuodulodon with only eight postcanine teeth (including three or four premolars). This interpretation was apparently influenced by comparison with Haldanodon and Docodon, which have three or three to four premolars. However, Asian docodontans may have as many as five premolars (Castorocauda: Ji et al. 2006) or even six (Sibirotherium: Lopatin et al. 2009). It is not clear how much the anterior and posterior portions of the holotype of Acuodulodon sunae have been displaced. If they are still in their original position, there is certainly space for more than eight postcanine teeth.

The most important similarity between the two taxa is evident from the newly collected dentary fragment SGP 2004/ 18, with the partial canine and p1 preserved in situ (see description below). The structure of p1 is identical to that of *Acuodulodon*, with a long, sharp, almost horizontal mesial crest and a short and vertical distal crest. This peculiar sectorial specialization of the anterior premolars may be a synapomorphy of Simpsodontidae. A sectorial m1 (or p?6) is known for *Castorocauda* (Ji et al. 2006), but the anterior premolars are not known for that taxon.

The comparison of the lower molars of *Acuodulodon* and *Dsungarodon* by Hu et al. (2007, p. 185) is partly invalid because of the misinterpretation of this region in the

holotype and the only known lower molar (apart from one vestigial ultimate molar) of Dsungarodon. The cusp identified and described as cusp d by Pfretzschner et al. (2005, fig. 1A) is actually the central eminence of the distal crenulation system (see description below); the actual cusp d is missing on this specimen. Among newly collected lower molar fragments of Dsungarodon, only SGP 2004/24 has the distal portion completely preserved. Here, the structure of the distal cingulid and cusps d and dd is not distinct from that in Acuodulodon (see description below). Hu et al. (2007, p. 185) noted that Dsungarodon is unique among docodontans in having "the second crest from cusp a toward but not reaching the base of cusp c." However, this crest is actually a part of the crenulation system, and exactly the same crest is present in Simpsonodon (Kermack et al. 1987; personal observation by Averianov). Hu et al. (2007) also noted some differences in the construction of the mesial portion of the crown between the two taxa, but we cannot confirm these observations. We see no difference in this region between the holotypes of Dsungarodon zuoi and Acuodulodon sunae, except that the only preserved molariform of the latter is poorly preserved, with part of the enamel possibly eroded.

Acuodulodon and *Dsungarodon* have very similar lower molars in terms of the structure of the distal cingulid and a rudimentary and variable cusp c (see description below). All docodonts have the last molar reduced to some extent, and the state of this reduction is potentially diagnostic for docodontan genera.

In conclusion, we can confirm only one difference between *Dsungarodon* and *Acuodulodon*: the lack of the crenulation system on the distal crown side of the lower molars in the latter. We consider this character to be diagnostic for the family Simpsodontidae. However, since there is only a single and poorly preserved lower molar known for *Acuodulodon*, the lack of the distal crenulation might be an artifact of preservation (enamel erosion could easily destroy the superficial crests). According to Hu et al. (2007), *Acuodulodon* differs from *Dsungarodon* by the lack of the crests a–g and b–e. This is apparently due to heavy wear of the mesial area in the single known lower molar of *Acuodulodon*; a remnant of the crest a–g is visible in fig. 4 of Hu et al. (2007).

Our interpretation of *Acuodulodon* as a junior synonym of *Dsungarodon* is in contrast with the phylogenetic analysis of docodontan genera by Hu et al. (2007) where these taxa are remotely related. This cladogram also shows a distant relationship for *Haldanodon* and *Docodon*, two taxa that are almost universally considered to be close relatives (Ji et al. 2006; Krusat 1980; Luo and Martin 2007; Martin and Averianov 2004; Pfretzschner et al. 2005). This contradiction is most likely due to the exclusion of upper tooth characters from the data matrix of Hu et al. (2007). *Dsungarodon zuoi* Pfretzschner and Martin in Pfretzschner et al., 2005, Figs. 5, 6, 7

2005 *Dsungarodon zuoi* [partim] Pfretzschner et al., p. 800, figs. 2B, 3A, B [non figs. 2A, C, 3C]

Holotype: SGP 2001/21, a right lower molar.

Referred specimens: SGP 2004/39 and SGP 2005/15, left upper molar fragments; SGP 2004/9, a left lower deciduous premolar; SGP 2001/24, a fragmentary left lower deciduous premolar; SGP 2004/19, a fragmentary right lower deciduous premolar; SGP 2004/18, a right dentary fragment with broken canine and complete p1; SGP 2005/6, a left lower premolar; SGP 2004/21, a fragmented right lower molar; SGP 2004/24, a right lower molar distal fragment; SGP 2004/22, a right lower molar fragment; SGP 2004/31, a left lower molar pseudotalonid fragment; SGP 2004/31, a left lower molar in dentary fragment; SGP 2004/7, a left ultimate lower molar.

Description: Of the six specimens originally referred to *D. zuoi* by Pfretzschner et al. (2005) we consider now only three to belong to this taxon. An upper molar (SGP 2001/23) and a fragment of a lower molar (SGP 2001/25), originally described as a milk premolar of *D. zuoi*, are here attributed to *Tegotherium* sp. The isolated premolar SGP 2001/26 referred previously to *D. zuoi* is now identified as Docodonta indet. Here we focus on the description of the newly collected specimens of *D. zuoi*.

The upper molars of D. zuoi are known by two lingual fragments of similar morphology, SGP 2004/39 and 2005/ 15 (Fig. 5a-c and d-f, respectively). Cusp X is about twofold larger and higher than cusp Y and projects more lingually than the latter. The lingual side of the crown is concave between cusps X and Y, as in Simpsonodon (Kermack et al. 1987), while in Tegotherium, it is convex (see Pfretzschner et al. 2005, fig. 2A1 and description below). The crest A-X is stronger than the crest C-Y and straight, extending directly labially from cusp X, as in Simpsonodon. In Tegotherium, this crest is not stronger than crest C-Y and extends somewhat mesiolabially and then labially, delimiting a relatively wider talon basin compared to that of Simpsonodon and Dsungarodon. The mesial cingulum is well developed, forming a bulge at the base of cusp X; it extends up onto the crown and almost reaches the apex of cusp X. In another specimen, SGP 2004/39, the mesial cingulum is considerably worn (Fig. 5c). The lingual side of the crown is supported by a single root and is straight in SGP 2004/39 and posteriorly deflected in SGP 2005/15.

SGP 2004/9 and SGP 2004/19 are lower deciduous premolars (Fig. 6a–c and d–f); the last one is lacking the distal portion. They are almost identical with SGP 2001/24 (Pfretzschner et al. 2005, fig. 2B) in size and structure. The teeth have three cusps (a, b, and c), a pointed mesial end, a labial and lingual cingulid around cusp b, and a deep

Fig. 5 Upper molar fragments of Dsungarodon zuoi with explanatory schematic drawing of Sibirotherium upper molar in occlusal view with the preserved part shaded (redrawn after Lopatin et al. 2009). Liuhuanggou locality, 40 km southwest of Urumqi, Xinjiang. Upper part of the Late Jurassic Qigu Formation (Oxfordian). a-c SGP 2004/ 39, left upper molar lingual fragment in occlusal (a, stereopair), lingual (b), and mesial (c) views, d-f SGP 2005/15, left upper molar lingual fragment in occlusal (d, stereopair), lingual (e), and mesio-occlusal (f) views



vertical groove on the distal crown side between a and c. The only difference between these specimens is the structure of the labial cingulum: it is very short in SGP 2001/24 and long in SGP 2004/9 and SGP 2004/19. This difference may reflect positional or individual variation. The distal crown side is known only in SGP 2004/9. The posterior basin is a flat platform confined to the lingual side and surrounded by prominent crests descending from the apexes of cusps a and c. At the base of the crest that descends from cusp c, immediately posterior to that cusp, there is a small additional cusp. The distal cingulid is a rather long oblique crest along the labial slope of the "talonid",

resembling the postcingulum of metatherians. The crest descending from cusp a is heavily worn, and the wear facet continues into a deep groove mesial to the distal cingulid and extends downwards almost to the ventral margin of the crown. This wear facet was apparently produced by the main labial cusp A of the upper deciduous premolar.

SGP 2004/18 is a dentary fragment with broken canine and complete p1 (Fig. 6g–h). The only preserved portions of the canine are the distal root and the base of the distal crown side. The root has a groove along the mesial side as in other docodontans. The broken dorsal part of the root and the crown base were posteriorly displaced and have

Fig. 6 Lower deciduous premolars and mandible fragment of Dsungarodon zuoi. Liuhuanggou locality, 40 km southwest of Urumqi, Xinjiang. Upper part of the Late Jurassic Qigu Formation (Oxfordian). a-c SGP 2004/ 9, left lower deciduous premolar in occlusal (a, stereopair), lingual (b), and labial views (c), df SGP 2004/19, right lower deciduous premolar in occlusal (d, stereopair), lingual (e), and labial (f) views. g-h SGP 2004/ 18, right dentary fragment with damaged c and complete p1 in occlusal (g, stereopair), lingual (**h**), and labial (**I**) views. *lacd* Labial cingulid, *licd* lingual cingulid, dcd distal cingulid



pushed the p1 out of its alveoli. The crown of p1 is relatively long and narrow, with a main central cusp and a small distal cusp. The mesial and distal crests of the main cusp are quite prominent and sharp. The mesial crest is long. The mesial end of the crown is turned dorsally, possibly due to postmortem distortion. The horizontal position of the mesial crest is exaggerated by a postmortem tooth rotation. The distal crest has only half the length of the mesial crest, but it is confluent with the crest-like distal cusp. The lingual cingulid is distinct and complete, and a labial cingulid is missing. The p1 is double-rooted. On the labial side of the dentary there is a large mental foramen; on the lingual side there is no detectable Meckelian groove.

The complete premolar SGP 2005/6 (Fig. 7a–c) is attributable to *Dsungarodon*. We consider it provisionally as a lower premolar but cannot exclude that it is actually an upper premolar (we think that the upper premolars should have a better developed labial cingulum). The tooth has a mesial cusp (b), a large central cusp (a), a distal cusp (c), and a distal cingular cusp (d). Cusp c is about double the length of cusp a. Cusps a and c are somewhat distally curved. Cusp b is smaller than cusp c but is larger than cusp d. Lingually to cusp a is a basin-like structure bordered by the

Fig. 7 Lower premolar and molars of Dsungarodon zuoi. Liuhuanggou locality, 40 km southwest of Urumqi, Xinjiang. Upper part of the Late Jurassic Oigu Formation (Oxfordian). a-c SGP 2005/6, left lower premolar in occlusal (a, stereopair), lingual (b), and labial (c) views, d-f SGP 2004/7, left lower ultimate premolar in occlusal (d, stereopair), lingual (e), and labial (f) views. g SGP 2004/24, right lower molar distal fragment in distal view. mcd Mesial cingulid; other abbreviations as in Fig. 6



lingual cingulid that resembles the pseudotalonid basin of the lower molars. The lingual cingulid is quite distinct and complete. It is very narrow at the base of cusp a and expands in the mesial and distal direction. The labial cingulid is restricted to the distal part of the crown and does not extend mesially beyond cusp c. The tooth is double-rooted, and the roots are remarkably well separated. The space between the roots is equal to the mesiodistal length of the root. The mesial root is somewhat shorter (mesiodistally) than the distal root.

A lower molar, SGP 2004/21, is missing most of the pseudotalonid and is somewhat smaller than the holotype but structurally quite similar. It has the same crenulation

pattern on the distal side of the crown as the holotype, with a curved crest extending from cusp a towards the base of cusp c without reaching it. This crest is connected by a vertical ridge to the distal cingulid. SGP 2004/21 is probably an anterior—possibly the first lower—molar of *D. zuoi.*

SGP 2004/22 is a fragment of a lower molar with cusps a and c preserved and a distal crenulation pattern similar to the holotype and SGP 2004/21.

The lower molar fragment SGP 2004/24 (Fig. 7g) is the only specimen that shows a complete distal cingulid with cusps d and dd (this cusp designation is after Hu et al.

2007; this cusp is f in Martin and Averianov 2004 and df in Luo and Martin 2007). The crenulation is formed by four crests that meet at the central eminence and connect the apexes of cusps g, d, dd, and the crest extending between the apex of cusp a and the base of cusp c. This central eminence was incorrectly identified as cusp d in the original description of *D. zuoi* (Pfretzschner et al. 2005, p. 804, fig. 1A). Actually, the distal cingulid and cusp d are missing in the holotype. The distal cingulum is short and extends between the bases of cusps d and dd (the latter cuspule is merely the termination of the distal cingulid). As far as it can be compared, this crenulation pattern corresponds to that of the holotype.

The left ultimate lower molar SGP 2004/7 (Fig. 7d-f) is somewhat smaller but structurally very similar to the tooth of SGP 2001/22 (Pfretzschner et al. 2005, fig. 3B). Both teeth have three cusps (a, b, and g) with their connecting ridges forming a triangle that surrounds the pseudotalonid basin. There is a long and prominent mesial cingulid extending along the mesial side of the crown from the apex of cusp b in the labial direction towards the base of cusp g. The mesial cingulid is labially broken in SGP 2001/22. The distal cingulid is a relatively long transverse ridge connected to the apex of cusp a by a longitudinal crest. At the base of this crest sits a rudimentary cusp c. In SGP 2001/22, cusp c is somewhat better developed, with two short distal crests, of which the labial one connects it to cusp d. Cusp d is small in SGP 2001/22 and is pointed and poorly individualized in SGP 2004/7. These rudimentary structures on the distal side of the ultimate tooth are without functional significance and are undoubtedly highly variable. Both teeth have a short lingual cingulid distal to cusp g, which is better developed in SGP 2001/22 than in SGP 2004/7. The distal root is much shorter than the mesial root.

The dentary fragment SGP 2001/22 was originally described as exhibiting "the anteriormost part of the postdentary trough and the origin of Meckel's groove," but it was mentioned that "the mandibular foramen is not preserved" (Pfretzschner et al. 2005, p. 804). However, the mandibular foramen should open at the anterior end of the postdentary trough, which cast doubt on the identification of the groove above the Meckelian groove as the postdentary trough. A similar and rather long additional groove of uncertain function above the Meckelian groove is present in a new species of Simpsonodon from West Siberia (Averianov et al. in preparation). There it is separated by a ridge from the more posterior postdentary trough with a mandibular foramen. The postdentary trough and the mandibular foramen in the new species of Simpsonodon, as well as in other docodontans, is situated well posterior to the ultimate molar, and this portion of the dentary is not preserved in SGP 2001/22.

Measurements: SGP 2004/39: L of lingual portion = 0.94; SGP 2005/15: L of lingual portion = 1.02;SGP 2004/ 9: L=1.32, W=0.74; SGP 2004/19: L=1.22*, W=0.73; SGP 2004/18: p: L=0.56; W=0.28; SGP 2005/6: L=1.14, W= 0.49; SGP 2004/24: L=1.12*, W=0.77; SGP 2004/7: L= 1.18; W=0.82;

Tegotheriidae Tatarinov, 1994 *Tegotherium* Tatarinov, 1994

1994 Tegotherium, Tatarinov, p. 104

Type species: Tegotherium gubini Tatarinov, 1994

Revised diagnosis: Referred to Tegotheriidae and differs from all other docodontans by a pseudotalonid that is bordered by crests a-g, a-b, b-e, and g-e. Among tegotheriids, it differs from Tashkumyrodon Martin and Averianov, 2004 by a strong a-d crest and lack of a c-d crest (in Tashkumyrodon, the c-d crest is strong, and crest a-d is absent); it differs from Krusatodon Sigogneau-Russell, 2003a by the lack of additional crests in the distal portion of the crown of the lower molars; it differs from both Tashkumyrodon and Krusatodon by a complete lingual cingulid; it differs from Sibirotherium Maschenko et al., 2003 by a stronger crest e-g and much weaker distal cingulid (crest d-dd). Further, it differs from Krusatodon and Sibirotherium by the presence of two (X and Y) rather than three (X, Y, and Z) lingual cusps on the upper molars. **Included species:** Type species and *Tegotherium* sp.

Distribution: Late Jurassic of Asia (Mongolia and northwest China).

Tegotherium sp., Figs. 8-12

2005 *Dsungarodon zuoi* [partim], Pfretzschner et al., fig. 2A, C 2007 cf. *Tegotherium*, Martin et al., fig. 2A, B

Referred specimens: SGP 2001/23 and SGP 2005/7, right upper molars missing the mesiolabial lobe; SGP 2004/ 32, a right upper molar lacking the distal side; SGP 2004/23, SGP 2004/25, and SGP 2004/34, right upper molar labial fragments; SGP 2005/13, SGP 2004/30, and SGP 2004/26, right upper molar lingual fragments; SGP 2004/20, a right dentary fragment with the last three broken molars; SGP 2004/11, a left dentary fragment with two molars; SGP2005/8, a left dentary fragment with alveoli for three posterior molars; SGP 2004/3, a right lower molar; SGP 2004/29, a right lower molar missing the pseudotalonid; SGP 2001/25, a fragmentary left lower molar; SGP 2004/26, SGP 2004/27, SGP 2004/35, and 2004/37 left lower molar distal fragment; SGP 2004/28, a right lower molar

Fig. 8 Upper molar fragments of Tegotherium sp., with explanatory schematic drawings of Sibirotherium upper molars in occlusal views with the preserved parts shaded (redrawn after Lopatin et al. 2009). Liuhuanggou locality, 40 km southwest of Urumqi, Xinjiang. Upper part of the Late Jurassic Oigu Formation (Oxfordian). a. **b** SGP 2004/32, right upper molar lacking the distal portion: occlusal (a, stereopair) and mesial (b) views, c-e SGP 2004/ 23, right upper molar labial fragment in occlusal (c, stereopair), lingual (d), and labial (e) views. ec Ectocingulum, mc mesial cingulum



fragment; SGP 2004/5, a right ultimate lower molar; SGP 2004/13, a right ultimate lower molar.

Description: There are three, mostly complete upper molars (SGP 2001/23, 2004/32, and 2005/7) and several labial and lingual fragments. SGP 2001/23 was previously described in detail by Pfretzschner et al. (2005, p. 802, fig. 2A). Other teeth are very close in size and structure to the latter. A labial tilt of the published occlusal view of SGP 2001/23 (Pfretzschner et al. 2005, fig. 2A₁) exaggerates its labial shelf. In reality, there is almost no difference in the width of the labial shelf between the known specimens. Strictly speaking, the labial shelf as a flat area between the

ectocingulum and the bases of labial cusps is not developed in SGP 2005/7 and is very narrow in SGP 2001/23. All specimens have a peculiar fourth crest at cusp A, not mentioned by Pfretzschner et al. (2005), that extends labially and somewhat distally towards the ectocingulum but does not reach the ectocingulum.

The mesiolabial corner of the tooth is completely preserved in SGP 2004/32 and 2004/23 (Fig. 8a–b and c–e, respectively) and exhibits a different structure in both specimens. In 2004/32, the mesiolabial lobe projects labially and mesially, forming a deep ectoflexus along the labial crown side. In SGP 2004/23, it projects mostly mesially and

Fig. 9 SGP 2005/7, right upper molar of *Tegotherium* sp. lacking the mesial corner, with explanatory schematic drawing of *Sibirotherium* upper molar in occlusal view with the preserved part *shaded* (redrawn after Lopatin et al. 2009), Liuhuanggou locality, 40 km southwest of Urumqi, Xinjiang. Upper part of the Late Jurassic Qigu Formation (Oxfordian), in occlusal (**a**, stereopair), lingual (**b**), labial (**c**), mesial (**d**), distal (**e**) views



only a little labially, forming a very shallow ectoflexus and almost straight labial side of the crown. In SGP 2004/23, the mesial crest of cusp A connects to the ectocingulum somewhat posterior to cusp B, with a cusp-like eminence at the contact. Cusp B is a cingular cusp distinctly smaller than cusp C. There is an additional poorly defined smaller cusp E immediately lingually to cusp C (Luo and Martin 2007, fig. 1), continuing lingually into the mesial cingulid. In SGP 2004/32, there is a cusp-like eminence at the contact of crest A–B and the mesial cingulum. After this crest, A–B continues to the small cingular cusp B. In contrast to SGP 2004/23, cusp B is not connected to the mesial cingulum.

These two types of mesiolabial lobe can be observed in the other, less complete specimens: SGP 2001/23 and SGP 2004/25 have a mesiolabially projecting lobe with deep ectoflexus, while in SGP 2005/7 (Fig. 9) and 2004/34, this lobe is mesially projecting and the ectoflexus is shallow, most certainly due to the positional variation within the tooth series (the ectoflexus possibly deepens towards the posterior end of the series).

On the lingual side, cusp X is much larger (more than twofold larger) than cusp Y (the size difference between the two cusps is smaller in the teeth attributed to *Dsungarodon*, see above). The lingual side of the crown is convex or only slightly concave between the two cusps in most specimens (more deeply concave in *Dsungarodon*). Crest A–X is as strong as crest C–Y and extends from the apex of cusp A mesiolabially. It then turns labially towards the base of cusp A but does not reach the apex of cusp A. The crests A–X, X-Y, and C–Y delimit a relatively wide "talon" basin, the deepest part of which is at the bases of the lingual cusps. Crest C–Y extends labially along the base of cusp C as the distal cingulum and labially contacts the crest extending distally from cusp C. The mesial cingulum is strong but relatively narrow. Its lingual end extends onto the crown towards cusp X but ends far beneath the apex of the cusp X.

The lower penultimate molars are represented by one complete isolated tooth, two dentary fragments with two and three incomplete teeth, respectively, and several isolated tooth fragments. The teeth show little variation. The crowns have a unilateral hypsodonty, as in other docodontans, in which the labial crown side extends downwards to a greater extent than the lingual crown side. The crown has nearly an "eight shape" in occlusal view and is dominated by a high cusp a, which occupies the distal and central part of the crown. Distolingual cusp c is distinctly lower than cusp a, and mesiolingual cusp g is distinctly lower than cusp c. Cusp c is slightly curved backward, and cusp g is directed mesiolingually. Mesiolabial cusp b is well separated from cusp a and is similar in height to cusp g. Longitudinal crests a-b and a-d are strong and usually worn. The transverse crest a-d is similarly strong and forms a kind of carnassial notch (Fig. 10; Pfretzschner et al. 2005, fig. 2C_{4, 5}). This crest is worn in all specimens. In SGP 2004/3, crest a-g is very weak, with

Fig. 10 Right lower molars of *Tegotherium*. **a**–**e** SGP 2004/3, *Tegotherium* sp. from Liuhuanggou locality, 40 km southwest of Urumqi, Xinjiang. Upper part of the Late Jurassic Qigu Formation (Oxfordian), in occlusal (**a**, stereopair), lingual (**b**), labial (**c**), mesial (**d**), distal (**e**) views. **f**–**h** *Tegotherium gubini* from the Late Jurassic of Shar Teeg, Mongolia, in occlusal (**f**), lingual (**g**), labial (**h**) views. **f**–**h** courtesy of L. P. Tatarinov



a short robust arm at the apex of cusp g that is very faint, almost indistinguishable, on cusp a. In other, less complete specimens, this crest seems to be better developed. The pseudotalonid occupies about one third of the crown length and is bordered by crests a–b, a–g, g–e, and b–e. Cusp e is merely the meeting point of the two later crests and the mesial cingulid. The mesial cingulid extends between cusp e and the base of cusp g and forms a mesiolingual projection ("cusp" ee). The posterior basin is a deep triangular vertical valley between the ridges a–d, a–c, and c–dd. The posterior basin has half the size of the pseudotalonid basin. Cusp dd is an additional cuspule just distal to the base of cusp c and connected with the apex of the latter cusp by a vertical crest (it is designated as df? in Luo and Martin 2007, fig. 3 for *Tegotherium*). It is unclear if this cusp is homologuous to cusp dd of the distal cingulid (see Hu et al. 2007, fig. 1). This cusp is consistently present in all available specimens, but it is variable in size. It is connected by the distal crest with the distal cingulid lingual to cusp d. The wear facet along crest a–d extends downwards into a groove between the two cusps on the labial side. The lingual cingulid is well developed in all specimens, sometimes with weakening or partial interruption at the bases of the lingual cusps g and c. The roots of Fig. 11 Right lower ultimate molars of *Tegotherium* sp. Liuhuanggou locality, 40 km southwest of Urumqi, Xinjiang. Upper part of the Late Jurassic Qigu Formation (Oxfordian). \mathbf{a} -e, SGP 2004/13, in (\mathbf{a} , stereopair) occlusal, (\mathbf{b}) lingual, (\mathbf{c}) labial, (\mathbf{d}) mesial, and (\mathbf{e}) distal views; \mathbf{f} - \mathbf{j} , SGP 2004/5, in (\mathbf{f} , stereopair) occlusal, (\mathbf{g}) lingual, (\mathbf{h}) labial, (\mathbf{I}) mesial, and (\mathbf{j}) distal views. Abbreviations: *mcd*, mesial cingulid; *licd*, lingual cingulid



the penultimate lower molars are roughly equal in mesiodistal length and are widely separated.

The ultimate molars of *Tegotherium* sp. are easily distinguishable from those of *Dsungarodon* by a less-reduced distal portion of the crown with the rudimentary cusp c distolingual to cusp a (distal in *Dsungarodon*), a crest-like cusp b, which is lower than cusp g (cusp-like and taller than cusp g in *Dsungarodon*), and a complete lingual cingulid (extremely short in *Dsungarodon*). Most of the crown is occupied by the triangular pseudotalonid basin, bordered by crests a–b, a–g, and the mesiolingual co cusp b.

Although cusp e is not individualized, this pattern is intermediate between the a–b, a–g, and g–b pseudotalonid rim of non-tegotheriid and a–b, a–g, g–e, and e–b rim of the tegotheriid molars. The mesial cingulid is confined lingually and forms and arc-like projection analogous to cusp ee found on the molars of other docodonts. The difference in height between cusp a and the remaining cusps is much larger than in *Dsungarodon*, and crests a–g and a–c are stronger and reach almost the apex of cusp a. Cusp c is more rudimentary in SGP 2004/13 (Fig. 11a–e) than in SGP 2004/5 (Fig. 11f–j) and cusp d is poorly individualized in both. The most striking difference between the two specimens is the

Fig. 12 Dentary fragments of Tegotherium sp. Liuhuanggou locality, 40 km southwest of Urumqi, Xinjiang. Upper part of the Late Jurassic Qigu Formation (Oxfordian). a-c SGP 2004/ 20, right dentary fragment with three ultimate molars, in occlusal (a, stereopair), lingual (b), and labial views (c), d-f, SGP 2004/11. left dentary fragment with two molars, in occlusal (d, stereopair), lingual (e), and labial (f) views, g-h SGP 2005/8, left dentary fragment with alveoli of three ultimate molars, in occlusal (g) and lingual (h) views. Mgr Meckel's groove, *pdt* postdentary trough



construction of the distal side of the crown. In SGP 2004/3 there are strong crests a–d and a–c and a deep vertical groove between them (Fig. 10). A short distal crest directing from cusp c towards cusp d does not reach the latter and both cusps are separated by a deep transverse groove, which is confluent with the above mentioned vertical groove. In SGP 2004/13 there is a strong crest a–c but crest a–d is not present and the stronger crest c–d connects these cusps without a groove in between (Fig. 11a–e). However, a high variation is to be expected for this side of the ultimate molar which has no functional significance due to a lack of occlusion with its upper counterpart (see Jenkins 1969:

fig. 2C). The lingual cingulid is very weak (SGP 2004/5) or interrupted (SGP 2004/13) at the base of cusp g. The mesial root is about 15% longer (mesiodistally) than the distal root.

The horizontal ramus of the dentary is relatively shallow, only slightly higher than the molars, and even more decreasing in height posterior to the tooth row (Fig. 12). The Meckelian groove is very short, not extending anteriorly beyond the penultimate tooth. It markedly widens backwards. In the posterior portion, the Meckelian groove contacts a flattened area which is apparently the ventrolateral floor of the mandibular canal. The mandibular canal is seen on the posterior broken side of the specimens, but the mandibular foramen itself is not preserved; it should be in a more posterior portion of the dentary. There is no additional groove above the Meckelian groove as in *Dsungarodon* and *Simpsonodon* (see above).

Measurements: SGP 2005/7: L=1.28*, W=1.69; SGP 2004/32: L=1.10*, W=1.46; SGP 2004/23: L of labial portion = 1.50*; SGP 2004/3: L=1.36, W=0.82; SGP 2004/13: L=1.09; W=0.68; SGP 2004/5: L=1.07; W=0.69; SGP 2004/20: anteriormost molar: L=1.38; W=0.83; middle molar: L=1.32; W=0.75*; SGP 2004/11: anterior molar: L=1.23; W=0.76; posterior molar: L=1.20; W=0.76;

Comments: *Tegotherium* sp. from Liuhuanggou is very similar to *T. gubini* from Shar Teeg, Mongolia. The only differences between the two are that the Chinese form is a little larger (by approx. 8%) and has a somewhat better developed additional cusp immediately distal to the cusp c (dd?). A larger sample of *T. gubini*, known currently from a single molar (Fig. 10), is needed to confirm these differences between species and to clarify the taxonomic position of the Chinese form.

Docodonta indet.

2005 Dsungarodon zuoi [partim], Pfretzschner et al., fig. 3C

Referred specimens: SGP 2004/10, a right upper canine; SGP 2001/26, a right lower or left upper premolar.

Description: SGP 2004/10 is identified as an upper canine because the wear facet at the tooth apex is on the lingual side of the tooth (should be on the labial side in a lower canine). The tooth structure is typical for docodontans (compare with Haldanodon; Krusat 1980, fig. 16; Luo and Martin 2007, fig. 5D–F). The crown is massive and distally curved. It is subtriangular in cross section, with mesial, distal, and distolingual edges. There are complete lingual and distal cingula, but no labial cingulum. The lingual cingulum is stronger distally than mesially. There is no distal cusp. The enamel surface is sculptured by fine striations on the labial side and on the mesial half of the lingual side. The tooth is double rooted. The mesial root is missing for most of its length but was apparently somewhat longer (mesiodistally) than the distal root. The distal root has a longitudinal groove along its mesial side and a bumplike expansion at the end, as in other docodontans.

For a description of the premolar SGP 2001/26, see Pfretzschner et al. (2005, pp. 802, 804).

Comments: The upper canine SGP 2004/10 may belong to *Dsungarodon* as it seems to be similar in size with the partially preserved lower canine in the dentary fragment SGP 2004/18 referred to that taxon (see above). However, we cannot completely rule out its attribution to *Tegotherium* sp. described here.

Interpretation of the premolar SGP 2001/26 is difficult. It was originally described as a lower premolar of *Dsungarodon* (Pfretzschner et al. 2005), which is reasonable because a similar ultimate premolar with a small distal cusp and the labial cingulid is known for *Simpsonodon* (Kermack et al. 1987), a close relative of *Dsungarodon*. However, on the other hand, it seems to be too small for *Dsungarodon*. Premolar SGP 2005/6, which has been attributed above to *Dsungarodon*, is larger and has only a short labial cingulid restricted to the posterior end of the crown. SGP 2001/26 may actually be a lower premolar of *Tegotherium* sp. described above. Another possibility is that it is an upper premolar of either *Dsungarodon* or *Tegotherium*.

Eutriconodonta Kermack, Mussett and Rigney, 1973 Eutriconodonta indet., Figs. 13a–c

Referred specimen: SGP 2005/4, a right lower molar missing the mesial end (Fig. 13a–c).

Description: The tooth has a large main cusp a, a comparatively large distal cusp c of about half the height, and a small but distinct more distal cusp d. The anterior side of the crown is missing. Cusp a is somewhat curved distally, and its apex is missing. Cusp c is sharp with dorsally directed apex. Cusp d is not cingular as it is well separated from the cingulid. The distal end of the crown is sharply pointed, and there is no distinct distal cingulid, while the lingual and labial cingulids extend to the pointed distal end of the tooth. On both sides, the cingulids are confined only to the posterior part of the crown and do not extend mesially beyond cusp c. The lingual cingulid is about twofold longer than the labial cingulid. The crown is slightly asymmetrical on the posterior side in occlusal view, with the lingual side more expanded, but it is more symmetrical on the anterior side. The enamel surface is sculptured by very fine striations. The tooth was doublerooted, with a large space between the roots; however, the roots are not preserved.

Measurements: SGP 2005/4: L=1.07*, W=0.54.

Comments: The tooth is likely a lower tooth as the wear facet at the apex of cusp c slopes on the labial side (should be on the lingual side in an upper tooth). Additional support for this interpretation comes from the poorly developed labial cingulum which should be stronger in an upper tooth. It is more likely to be a molar than a premolar because cusp c appears to be too large for a premolar and because it possesses a complex posterior end with non-cingular cusp d. Although the mesial end of the crown is missing, it is likely that the mesial cusp b, if present at all, was not large. The important size difference between cusps a and c suggests attribution of this specimen to an amphilestid-grade eutriconodontan. A possible small size or even absence of cusp b would make it similar to the first lower

Fig. 13 Molars of Eutriconodonta indet. and Nanolestes mackennai sp. nov. Liuhuanggou locality, 40 km southwest of Urumqi, Xinjiang. Upper part of the Late Jurassic Qigu Formation (Oxfordian). a-c SGP 2005/4, right lower molar of Eutriconodonta indet. in occlusal (a, stereopair), lingual (**b**), and labial (**c**) views. d-h SGP 2004/4, right upper molar (Holotype) of N. mackennai sp. nov. in occlusal (d, stereopair), lingual (e), labial (f), mesial (g), and distal (h) views. mc Metacone, ms metastyle, pa paracone, pc paracrista, ps parastyle, st stylocone; see other figure captions for remaining abbreviations



molar tooth of gobiconodontids or to the lower molars of klameliids (Martin and Averianov 2007). This specimen certainly lacks the imbricating interlocking characteristic of klameliids, exemplified by the parallelogram shaped molars, but it is not fully symmetrical in occlusal view, distantly approximating the parallelogram shape. The fine striations of its crown also suggest affinities with klameliids. However, this specimen currently cannot be identified beyond Eutriconodonta indet.

Cladotheria McKenna, 1975 Stem-lineage of Zatheria McKenna, 1975 "Amphitheriidae" Owen, 1846 Nanolestes Martin, 2002

Type species: Nanolestes drescherae Martin, 2002.

Diagnosis: The original generic diagnosis of *Nanolestes* (Martin 2002, p. 333) is amended here after reinterpretation of Gui Mam 1005 (Martin 2002, fig. 4A–C) as m1, and not as a deciduous premolar as interpreted by Lopatin and Averianov (2006): Trigonid comparatively short (angle 50°) and metaconid in line with protoconid, not shifted posteriorly in molars distal to m1.

Fig. 14 Left lower molars of N. mackennai sp. nov. Liuhuanggou locality, 40 km southwest of Urumqi, Xinjiang. Upper part of the Late Jurassic Qigu Formation (Oxfordian). a-e SGP 2005/2, in occlusal (a, stereopair), lingual (b), labial (c), mesial (d), and distal (e) views, f-j SGP 2004/14, in occlusal (f, stereopair), lingual (g), labial (h), mesial (I), and distal (i) views. dmc Distal metacristid, med metaconid, pad paraconid, pcd precingulid, prd protoconid



Included species: Type species, *N. krusati* Martin, 2002 and *N. mackennai* sp. nov.

Distribution: Late Jurassic to Early Cretaceous of Europe (Portugal) and Late Jurassic of Asia (Northwest China).

Comments: *Amphitherium* from the Bathonian Taynton Limestone Formation of England, known only from lower dentitions, was considered by Butler and Clemens (2001) to represent a lineage different from stem zatherians due to a different interlocking lower molar arrangment. However, cusp f is clearly present in *Amphitherium*, and the talonid fits between the paraconid and cusp f of the following tooth

(Sigogneau-Russell 2003b, fig. 11; see also Martin 2002; Sigogneau-Russell 1999), as in many specimens of *Palae-oxonodon* and in *N. mackennai* sp. nov. "Amphitheriidae" are considered here as a possible paraphyletic group of Middle Jurassic to Early Cretaceous stem zatherians (*Amphitherium* de Blainville, 1838; *Palaeoxonodon* Freeman, 1976; *Kennetheredium* Sigogneau-Russell, 2003b; *Amphibetulimus*, Lopatin and Averianov 2007; *Nanolestes* Martin, 2002; *Chunnelodon* Ensom and Sigogneau-Russell, 1998; *Arguimus* Dashzeveg, 1979) with unicuspid talonid with or without an incipient basin, with the metacone labial to the paracone, and without a lingual cingulum on the upper molars (a short lingual cingulum is present on P5 of *Nanolestes* (Martin 2002, fig. 9I). This group shows progressive reduction of the molar count from six to seven in *Amphitherium* to five in *Nanolestes* and four in *Arguimus*. In early zatherians, as exemplified by the Early Cretaceous *Peramus* Owen, 1871, there are three molars, a bicuspid basined talonid, a metacone positioned distally to the paracone, and a lingual cingulum on the upper molars.

Nanolestes mackennai sp. nov., Figs. 13 d-h and 14

2007 cf. Nanolestes, Martin et al. (fig. 2C,D)

Etymology: After Professor Malcolm Carnegie McKenna (1930–2008) in recognition of his contribution to our understanding of Mesozoic mammals.

Holotype: SGP 2004/4, a right upper molar (Fig. 13d-h).

Referred specimens: SGP 2004/41, a right upper molar lacking the parastylar lobe (lost); SGP 2004/33, a heavily worn right upper molar; SGP 2005/2, a fragmented left lower molar; SGP 2005/14, a fragmented right lower molar; SGP 2004/14, a right lower molar lacking the talonid.

Diagnosis: Differs from *N. drescherae* Martin, 2002 by the lack of cingular cusps on the ectocingulum; differs from *N. krusati* Martin, 2002 by the presence of an additional metacrista cusp C^1 .

Description: The crown of the upper molars is triangular in occlusal view, even heart-shaped because of the deep labial ectoflexus. The lingual paracone is the largest and tallest of the crown cusps. Its apex is somewhat deflected labially. The paracone is greatly convex labially and concave lingually between the paracrista and metacrista. There is no median ridge on the paracone between these two crests. The paracrista is straight with two paracrista cusps. The lingual one is about twofold longer than the labial one. The paracrista extends labially towards a large stylocone (its apex is broken off in the holotype). The parastylar lobe is prominent and mesially projecting. The parastyle is large (broken in the holotype) and connects to the subvertical lingual ridge ("preparastyle"). There is a short longitudinal ridge between the stylocone and parastyle. The ectocingulum is well developed, without cingular cusps. The metacrista is longer than the paracrista and somewhat convex distally. It bears four cusps, decreasing in size labially: metacone, metacrista cusp C, additional metacrista cusp C^1 , and metastyle. The cusps along the metacrista are separated by deep V-shaped notches. The "trigon" basin is triangular in shape, quite shallow, and slightly concave. It is confined mesially because the slopes of the metacrista cusps are much longer than those of the paracrista cusps. The upper molars have three roots. The mesial labial root is somewhat longer mesiodistally than the distolabial root. The lingual root is wider labiolingually than the labial roots.

SGP 2004/41 had a deeper ectoflexus and a more prominent metastyle compared to the holotype.

The lower molars are represented by three specimens, all missing the talonid. The trigonid is short, with the trigonid angle 33° and 36° (SGP 2005/2, Fig. 14a-e and 2004/14, Fig. 14f-j) or approximately 46° (SGP 2005/14). The protoconid (completely preserved in SGP 2004/14) is distinctly higher than the metaconid, with a cusp-like eminence on the protocristid accentuating the "carnassial" notch of the protocristid. The protocristid is straight, while the paracristid is somewhat convex mesiolabially. The metaconid is compressed mesiodistally. The base of the paraconid is similar in size to that of the metaconid (none of the specimens preserves the complete paraconid). The bases of the paraconid and metaconid are closely spaced closing the trigonid basin lingually. There is a long, prominent precingulid (=mesiolabial cusp f, =anterobasal cingulum of Martin 2002). The mesiolingual cusp e is absent. There is a faint distal metacristid (best seen in SGP 2004/14) extending vertically towards the protocristid notch. The shape of the talonid, evident from its remnant in SGP 2005/2, was similar to the talonid shape found in N. drescherae.

Measurements: SGP 2004/4: L=1.01, W=0.99; SGP 2005/2: L=0.96, W=0.76, talonid length = 0.32; SGP 2004/14: L=0.72, W=0.77.

Comments: The new species is referred to *Nanolestes* because it exhibits isolated cusps along the paracrista. In the Middle Jurassic *Palaeoxonodon*, which has an upper dentition that is similar to that of *Nanolestes*, there are no paracrista cusps (cusp-like structures may be present in some specimens: Sigogneau-Russell 2003b, fig. 14B, C). Martin (2002) distinguished *N. drescherae* and *N. krusati* by the structure of the talonid, which is not known for *N. mackennai*. The absent cusp e (=anterobasal cuspule of Martin 2002) may potentially distinguish *N. mackennai* sp. nov. from *N. drescherae*, where it is present in some lower molars.

The para- and metacrista cusps are variable in *N. drescherae*. In Gui Mam 1033 (Martin 2002, fig. 9A, B) there are three paracrista cusps, with the middle cusp being the largest. In Gui Mam 1023/2 (Martin 2002,fig. 9C, D), there are two paracrista cusps: a lingual very small cuspule and a labial long cusp. In *N. mackennai* sp. nov., the situation is the opposite: of two paracrista cusps, the lingual one is much longer. In Gui Mam 1033 (Martin 2002, fig. 9A, B), there are four metacrista cusps decreasing in size labially, with the metacone immediately labial to the paracone, as in SGP 2004/4 and 2004/41. In Gui Mam 1023/2 (Martin 2002, fig. 9C, D), there are five cusps on the metacrista, with two small cuspules inserted between paracone and metacone.

Discussion

Five mammalian taxa have been identified from the Late Jurassic (Oxfordian) Qigu Formation of Junggar basin (Table 1). At the present time, this is the most diverse Late Jurassic mammalian assemblage in Asia (see review in Kielan-Jaworowska et al. 2004). There are only two other Late Jurassic mammal sites in Asia: Shar Teeg in Mongolia with the single docodontan Tegotherium gubini (Tatarinov 1994) and the Shishugou Formation in the Central Junggar basin (Laoshangou and Wucaiwan area) with the eutriconodontan Klamelia zhaopengi and the docodontan Dsungarodon (Acuodulodon) sunae (Chow and Rich 1984; Hu et al. 2007). The Shilongzhai site (Upper Shaximiao Formation) in the Sichuan Province of China, with two species of Shuotherium (Chow and Rich 1982; Wang et al. 1998) is most likely Middle Jurassic in age because Shuotherium is present in the well-dated Bathonian of Kirtlington in England (Sigogneau-Russell 1998; see also Averianov et al. 2005).

The Liuhuanggou mammal assemblage shares similarities with both these Late Jurassic mammal assemblages: *Tegotherium* is present at Liuhuanggou and Shar Teeg, and *Dsungarodon (Acuodulodon) sunae* from the Shishugou Formation is very similar to *Dsungarodon zuoi* from the Qigu Formation at Liuhuanggou. The Liuhuanggou mammal assemblage also shares similarities with the wellknown Bathonian Forest Marble assemblage of England (Butler and Hooker 2005; Freeman 1976, 1979; Kermack et al. 1987, 1998; Kielan-Jaworowska et al. 2004; Martin et al. 2007; Martin and Averianov 2010; Sigogneau-Russell 1998, 2003a, b). Both assemblages share eleutherodontid allotherians, simpsonodontid, and tegotheriid docodontans, and stem-lineage zatherians. While the Qigu and Forest Marble eleutherodontids are different enough, the differ-

 Table 1
 List of mammals from the Late Jurassic (Oxfordian) Qigu
 Formation in Junggar Basin, northwestern China

Allotheria
Eleutherodontidae
Sineleutherus uyguricus gen. et sp. nov.
Docodonta
Docodontidae
Dsungarodon zuoi
Tegotheriidae
Tegotherium sp.
Eutriconodonta
Eutriconodonta indet.
Stem Zatheria
Amphitheriidae
Nanolestes mackennai sp. nov.

ences between the Oigu Dsungarodon and Nanolestes and Forest Marble Simpsonodon and Palaeoxonodon are quite subtle. The only structural differences between Palaeoxonodon and Nanolestes are the presence of the incipient talonid basin in the former and isolated paracrista cusps in the latter. Nanolestes was known previously from the Late Jurassic (Kimmeridgian) of the Guimarota coal mine and the Late Jurassic or earliest Cretaceous (Tithonian-Berriasian) of the Porto Pinheiro (or Dinheiro) locality in Portugal (Krusat 1969; Martin 2002). With the exception of Nanolestes, the Qigu and Guimarota mammal assemblages are quite different. The Guimarota assemblage is dominated by dryolestidans (five genera) and various multituberculates (several genera) (Martin 2001), which are absent in the Qigu assemblage. The only docodontan from Guimarota, Haldanodon, belongs to a different family, the Docodontidae. The Early Cretaceous mammal assemblages of Asia are dominated by multituberculates, gobiconodontid eutriconodontans, symmetrodontans, and eutherians (Kielan-Jaworowska et al. 2004). The earlier Late Jurassic mammal assemblages of Asia, including the Qigu assemblage, are essentially Middle Jurassic in composition. The faunal turnover, leading to the mammalian communities characteristic of the Early Cretaceous, probably occurred in Asia sometime after the Oxfordian, possibly during the Kimmeridgian.

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