A new docodont mammal from the Late Jurassic of the Junggar Basin in Northwest China

HANS-ULRICH PFRETZSCHNER, THOMAS MARTIN, MICHAEL W. MAISCH, ANDREAS T. MATZKE, and GE SUN

Pfretzschner, H.-U., Martin, T., Maisch, M.W., Matzke, A.T., and Sun, G. 2005. A new docodont mammal from the Late Jurassic of the Junggar Basin in Northwest China. *Acta Palaeontologica Polonica* 50 (4): 799–808.

Fieldwork in the early Late Jurassic (Oxfordian) Qigu Formation of the Junggar Basin in Northwest China (Xinjiang Autonomous Region) produced teeth and mandibular fragments of a new docodont. The new taxon has a large "pseudotalonid" on the lower molars, and by retention of crest b-g exhibits closer affinities to *Simpsonodon* and *Krusatodon* from the Middle Jurassic of Europe than to the other known Asian docodonts *Tashkumyrodon*, *Tegotherium*, and *Sibirotherium*. It differs from the *Haldanodon–Docodon*-lineage by the "pseudotalonid" and large cusps b and g. A PAUP analysis based on lower molar characters produced a single most parsimonious tree with two main clades. One clade comprises *Docodon, Haldanodon,* and *Borealestes*, and the other *Dsungarodon, Simpsonodon,* and *Krusatodon* plus the Asian tegotheriids. Analysis of the molar occlusal relationships using epoxy casts mounted on a micromanipulator revealed a four-phase chewing cycle with transverse component. The molars of the new docodont exhibit a well developed grinding function besides cutting and shearing, probably indicating an omnivorous or even herbivorous diet. A grinding and crushing function is also present in the molars of *Simpsonodon, Krusatodon*, and the Asian tegotheriids, whereas *Borealestes, Haldanodon,* and *Docodon* retain the plesiomorphic molar pattern with mainly piercing and cutting function.

Key words: Docodonta, *Dsungarodon*, occlusion, Jurassic, Qigu Formation, Junggar Basin.

Hans-Ulrich Pfretzschner [hans-ulrich.pfretzschner@uni-tuebingen.de] and Michael W. Maisch [michael.maisch@uni-tuebingen.de], Institut für Geowissenschaften, Universität Tübingen, Sigwartstraße 10, 72076 Tübingen, Germany;
Thomas Martin [tmartin@senckenberg.de], Forschungsinstitut Senckenberg, Senckenberganlage 25, 60325 Frankfurt am Main, Germany;
Andreas T. Matzke [matzkea@si.edu], Department of Paleobiology, Smithonian Institution, National Museum of Natural History, PO Box 37012 MRC 121, Washington, D.C. 20013-7012, USA;
Ge Sun [sunge@jlu.edu.cn], Research Center of Paleontology, Jilin University, 6, Xi-Minzhu Street, Changchun 130026, China.

Introduction

A long time docodonts were regarded as a small group of Mesozoic mammals restricted to the Jurassic of Europe and North America (e.g., Simpson 1928, 1929; Kühne and Krusat 1972; Kron 1979; Krusat 1980; Kermack et al. 1987; Lillegraven and Krusat, 1991). The first Asian docodont reported was *Tegotherium gubini* from the Late Jurassic of Shar Teg in Mongolia, that originally was described as an unusual symmetrodont (Tatarinov 1994). Nessov et al. (1994) announced a badly damaged possible upper docodont molar from the Middle Jurassic Balabansai Formation of Kalmakerchin in Kyrgyzstan which could not be determined at the specific or generic level. Prasad and Manhas (2001) assigned an upper premolar and a fragmentary lower molar from the supposedly Lower–Middle Jurassic Kota Formation of India to docodonts of Laurasian affinity ("*Haldanodon* grade"). Maschenko et al. (2003) described three incomplete dentaries of an Early Cretaceous docodont, *Sibirotherium rossicus* from the Shestakovo locality in Western Siberia. The first unquestioned docodont from Central Asia was reported by Martin and Averianov (2004) based on a lower molar from the Middle Jurassic Balabansai Svita near Tashkumyr in Kyrgyzstan. Here we present dental remains of a new Late Jurassic docodont which were collected in 2001 at Liuhuanggou in the valley of the Toutunhe river southwest of Urumqi during field work of the Sino-German cooperation between the Jilin University (Changchun) and the Eberhard-Karls-Universität (Tübingen).

The Junggar Basin is one of the largest sedimentary basins in Xinjiang Autonomous Region and contains a continuous succession from the Permian to the Late Cretaceous that is largely covered by Cenozoic sediments. In the center of the basin the sedimentary infill approaches 16,000 m of which about 6,000 m represent fluvio-lacustrine Mesozoic deposits. The locality at Liuhuanggou, 40 km southwest of the city of Urumqi and west of the Toutunhe river, is highly fossiliferous in several levels in the Toutunhe and Lower Qigu Formations. The Toutunhe Formation is dated as Callovian and the Qigu Formation, which is at the locality 731 m thick, as Oxfordian, based on spores and palynomorphs (Ashraf et al. 2004). About 470 m above the Toutunhe/Qigu boundary a bonebed was discovered during field work in 2000. This bonebed has yielded numerous mainly isolated bones and teeth of hybodontid sharks, actinopterygians, temnospondyles, turtles, crocodiles, dinosaurs and mammals (haramyids and docodonts) that appeared in lenses in a series of greenish siltstones and fine sandstones (Maisch et al. 2001, 2003, 2004; Martin and Pfretzschner 2003). The docodont remains are described in this study.

Material and methods

About 20 to 30 kg of sediment from the bonebed were screenwashed at a mesh size of 0.5 mm and the remaining concentrate was picked under a stereomicroscope. For biomechanical experiments epoxy casts of the docodont teeth were made using CAF 3 (Rhône-Poulenc) for moulding and Araldit M and hardener HY 956 for casting. Subsequently the teeth were mounted on SEM-stubs with acetone-soluble conductive mount and sputtered with gold for SEM study. The cast of the upper molar was mounted on a metal axis that could be rotated freely, whereas the cast of the lower molar was mounted on a Narishige micromanipulator which allowed precise positioning of the tooth in all three dimensions of space. This arrangement was used to study all stages of the occlusal relationships during the chewing cycle under a stereomicroscope. From each stage a digital photograph was taken and 25 to 47 images of one chewing cycle were combined to a movie sequence at the computer (available on the APP website at http://app.pan.pl/acta50/app50-799SM.htm).

Although the cusp homology of docodont molar teeth with that of other mammals has not yet been established, we follow the terminology proposed by Butler (1988, 1997) for practical reason and because we think that this homology is likely to be correct (Fig. 1). The purely descriptive cusp terminology of Kermack et al. (1987) and Sigogneau-Russell (2001, 2003) is more unbiased but has proven rather cumbersome for the morphological descriptions. The docodont wear facet terminology is after Jenkins (1969). We follow the stem-based definition of Mammalia, proposed by Luo et al. (2002) and Kielan-Jaworowska et al. (2004), which is equivalent to the Mammaliaformes of Rowe (1988) and McKenna and Bell (1997).

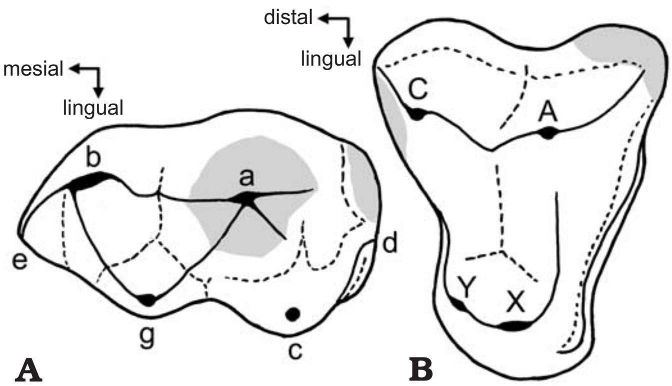

Fig. 1. Restoration of right lower (**A**) and upper (**B**) molar of the new docodont with designation of cusps (occlusal view). Reconstructed broken areas are shaded. Cusp designation follows Butler (1988).

Institutional abbreviations.—The holotype and referred specimens are deposited in the Sino-German Project collection (SGP/2001/21–26), currently housed at the Institute for Geosciences (IFG), University of Tübingen, Germany. The collection remains property of the People's Republic of China and will be transferred to a public Chinese collection after the scientific studies are finished. The final repository will be announced in an internationally accessible journal.

Other abbreviations.—L, length; W, width; asterisk * indicates preserved length or width in incomplete specimens.

Systematic palaeontology

Mammalia Linnaeus, 1758

Docodonta Kretzoi, 1946

Docodontidae Simpson, 1929

Genus *Dsungarodon* nov. Pfretzschner and Martin

Derivation of the name: Named after the Junggar Basin (formerly Dsungar) and οδο*ν*, stem of οδούς (Greek) tooth. *Dsungarodon* (masculine), tooth from the Junggar Basin.

Type species: *Dsungarodon zuoi* sp. nov.

Diagnosis.—Upper molar characters: (1) cusp X hook shaped and recurved buccally; (2) basin developed between cusps A-C-Y-X; (3) cusps A and C high and slender and considerably higher than cusps X and Y; (4) buccal crests forming a cutting edge; (5) lingual portion mesial to the A-X-crest is reduced; (6) distal margin C-Y of the lingual portion of the tooth not deeply indented; (7) strong ectoflexus; (8) outline of the tooth crown triangular.

Lower molar primitive (–) and derived (+) characters: (1) cusp e and f reduced (+); (2) crest b-e well developed (–); (3) crest b-e protruding to the mesial end of the tooth (+); (4) crest e-g missing (–); (5) crest b-g well developed (–); (6) enlarged anterior basin (pseudotalonid) (+); (7) cusp g enlarged, similar in height to cusp c (+); (8) region distal to cusps a and c reduced (+).

Differential diagnosis.—The upper molar of the new taxon differs from those of *Haldanodon exspectatus* by the following characters: (1) cusp X hook-shaped and recurved buccally; (2) basin developed between cusps A-C-Y-X; (3) cusps A and C high and slender; (4) buccal crests forming a cutting edge; (5) lingual portion mesial to the A-X-crest reduced; (6) distal margin C-Y of the lingual portion of the tooth not deeply indented; (7) strong ectoflexus. *Dsungarodon* differs from *Simpsonodon oxfordensis* by the following upper molar characters: (1) buccal cusps A and C much more slender and considerably higher than cusps X and Y; (2) lingual part of the tooth more narrow and more constricted; (3) outline of the tooth crown more triangular.

At the lower molars, the new taxon differs from *Tegotherium*, *Sibirotherium*, and *Tashkumyrodon* by exclusion of

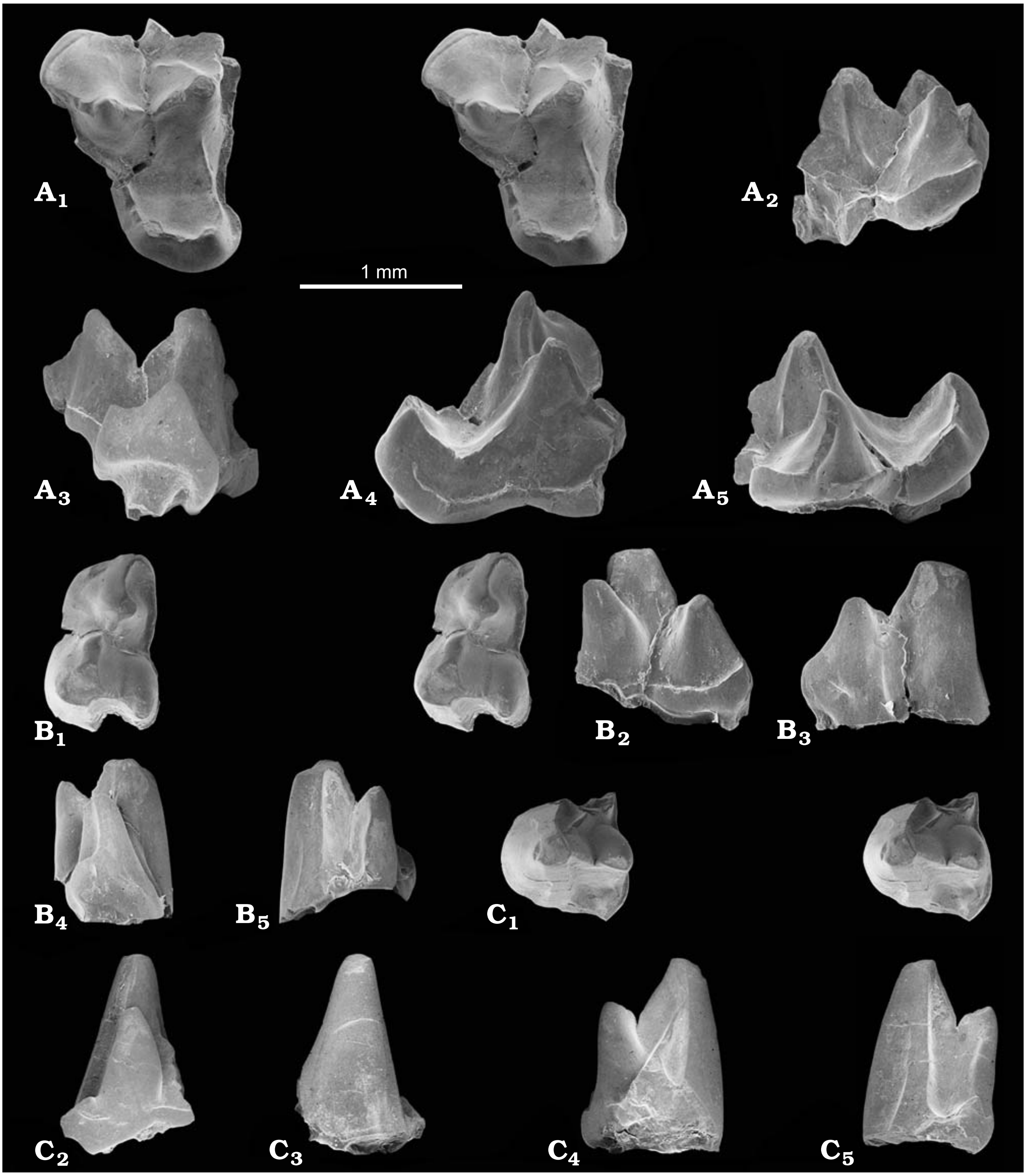

Fig. 2. SEM prints of upper molar and lower deciduous premolars of *Dsungarodon zuoi* gen. et sp. nov., Liuhuanggou, early Late Jurassic (Oxfordian). **A**. SGP 23, upper right molar, in occlusal (A_1, stereo-pair), buccal (A_2), lingual (A_3), occluso-mesial (A_4), and distal (A_5) views. **B**, **C**. Lower left deciduous premolars. **B**. SGP 24. **C**. SGP 25; in occlusal (B_1, C_1, stereo-pairs), lingual (B_2, C_2), buccal (B_3, C_3), mesial (B_4, C_4), and distal (B_5, C_5) views.

cusp e from the border of the "pseudotalonid" and by retaining a well developed crest b-g. From *Docodon*, *Haldanodon*, and *Borelalestes* it differs by reduction of cusps f, presence of a large anterior basin ("pseudotalonid"), reduction of a c-d crest, large cusp b, and cusps c and g being of equal height. From *Simpsonodon* it differs by a straight, mesio-lingually oriented crest b-e that is accompanied by a straight transversal valley between the crests b-g and b-e. Furthermore, the pattern of enamel ridges in the region distal to cusp a and c is less complex. *Dsungarodon* is clearly distinct from *Krusatodon* by the following characters: (1) crest b-e runs straight forward in a mesio-lingual direction; (2) a distinct cusp e is not developed;

(3) crest b-g is straight and not S-shaped; (4) cusp g does not bulge more lingually than cusp c; (5) crest c-d is almost straight; (6) a distinct cusp f is not developed.

Distribution and stratigraphical range.—Upper part of Qigu Formation at Liuhuanggou, 40 km southwest of Urumqi in the Junggar Basin (Xinjiang Autonomous Region, NW China). Early Late Jurassic (Oxfordian).

Dsungarodon zuoi, sp. nov. Pfretzschner and Martin

Figs. 1–3.

Derivation of the name: The species in named in honour of Prof. Zuo Xue-Yi, head of the Information Division of the Geological Bureau of Xinjiang in Urumqi, at the time director of the Xinjiang Geological Survey No. 1, for his long-term support of our fieldwork in the Junggar Basin.

Holotype: SGP 21, a right lower molar (L = 1.49 mm; W = 0.95 mm) (Fig. 3A).

Attributed material. SGP 23, a right upper molar (L* = 1.34 mm; W* = 1.58 mm) (Fig. 2A); SGP 24, a fragmentary left lower deciduous premolar (L* = 1.09 mm; W* = 0.71 mm) (Fig. 2B); SGP 25, a fragmentary left lower deciduous premolar (L* = 0.79 mm; W* = 0.79 mm) (Fig. 2C); SGP 26, a right lower premolar (L = 0.76 mm; W = 0.38 mm) (Fig. 3C); SGP 22, a right lower molar (L = 1.28 mm; W = 0.87 mm) (Fig. 2B).

Diagnosis.—As for the genus.

Description

Upper molar.—Specimen SGP 23 (Fig. 2A) is a right upper molar probably from a middle position in the tooth row. Four cusps can be identified. On the buccal side of the tooth two cusps, A and C, are preserved. Cusp B is broken off. Of the two remaining buccal cusps the mesial cusp A is slightly higher than the more distal cusp C. The lingual projection of the triangular tooth crown bears two cusps, a large cusp X and a smaller cusp Y. All cusps are convex on their lingual side and concave on the buccal flank. On the concave buccal flanks of cusps A and C a smooth vertical ridge is developed.

Cusp A is slender and of conical shape. Its tip is slightly bent towards the buccal side and is worn. On the mesial side of cusp A, a well developed crest runs in a mesio-buccal direction where the broken cusp B was located. On the distal side of cusp A a crest descends into the deep notch between cusps A and C. Both crests bear well developed wear facets that are facing lingually. A third crest originates at the lingual base of cusp A and connects it with cusp X. This crest does not exhibit any wear facets but has a knotty edge.

Cusp C is bucco-lingually slightly compressed. As in cusp A, its tip is bent towards the buccal side, but is not worn. A crest that runs down its mesial flank bears along its entire length a well developed wear facet, inclined towards the lingual side. In occlusal view the crests between cusps A and C form an obtuse angle that points lingually. The wear facets of the two crests are not fused. On the distal flank of cusp C a disto-buccal crest also has a well developed lingually inclined wear facet over its entire length. The wear facet exhibits a faint striation in a bucco-lingual direction. All four buccal crests of cusps A and C form a continuous cutting edge.

Cusp X is strongly bent to the buccal side and has a hook-like appearance. Its tip bears a steeply inclined wear facet that faces in buccal direction. On the mesial side of cusp X, a crest originates at its tip and bends soon in buccal direction to meet the lingual crest of cusp A. The two crests form the mesial border of a basin. At the distal side of cusp X, a second crest connects cusp X with cusp Y. On the distal side of cusp Y, a crest runs in buccal direction. It does not meet cusp C, but continues as a distal cingulum at the base of cusp C. The distalmost part of the cingulum is broken off.

One striking feature of the upper molar is the wide buccal shelf with a strongly developed ectoflexus. The mesial corner of this shelf is broken off. The shelf forms a shallow trough which is bordered by a sharp rim.

At the mesial base of cusp X, a well developed mesial cingulum originates which runs buccally and probably met the buccal shelf at the bucco-mesial corner of the tooth; now parts of the cingulum are broken off.

The buccal flange of cusp X is steeply inclined and forms the lingual border of the basin. Both the mesial and the distal borders of the basin are deeply notched. Buccally the basin is bordered by the tall cusps A and C. These buccal cusps are twice as high as cusp X.

Lower deciduous premolars.—Both lower deciduous premolars (Fig. 2B, C) are fragmentary and are from the left side. The teeth are molariform but differ from permanent lower molars by being laterally more compressed and mesio-distally elongated. In the more complete specimen SGP 24 cusps a, b, and c are preserved. Cusp a is the largest and bears three crests, crest a-c, crest a-b and a distal crest. Its tip is strongly worn and the dentine core is exposed. Cusp c has a recurved tip that is slightly worn and is connected to cusp a by crest a-c. Cusp b forms the mesial portion of the tooth. Besides crest b-a, a second crest originates at the mesial side of cusp b. It runs in mesial direction and meets a prominent mesio-lingual ledge at the mesial end of the tooth. The tip of cusp b is worn and the dentine is exposed. As there is neither a cusp g developed nor a crest connecting cusp b and c there is no basin present on the tooth crown.

The second specimen SGP 25 is a fragment with only cusps a and c preserved. Both cusps are strongly worn with the dentine exposed. The morphology of the tooth fragment corresponds in all details with the more complete specimen.

Lower premolar.—The right lower premolar SGP 26 (Fig. 3C) is double rooted with the anterior root broken off. Its crown is laterally compressed and the triangular main cusp is slightly recurved and has a small linguo-distally oriented wear facet on its tip. A crest runs down on its distal side and ends half way down. A small notch separates this crest from a small cuspule on the distal side of the main cusp. Distal to this cuspule a second crest continues the cutting edge and ends in a small enamel tip on the distal ledge. This ledge extends far anteriorly at the base of the lingual side. However,

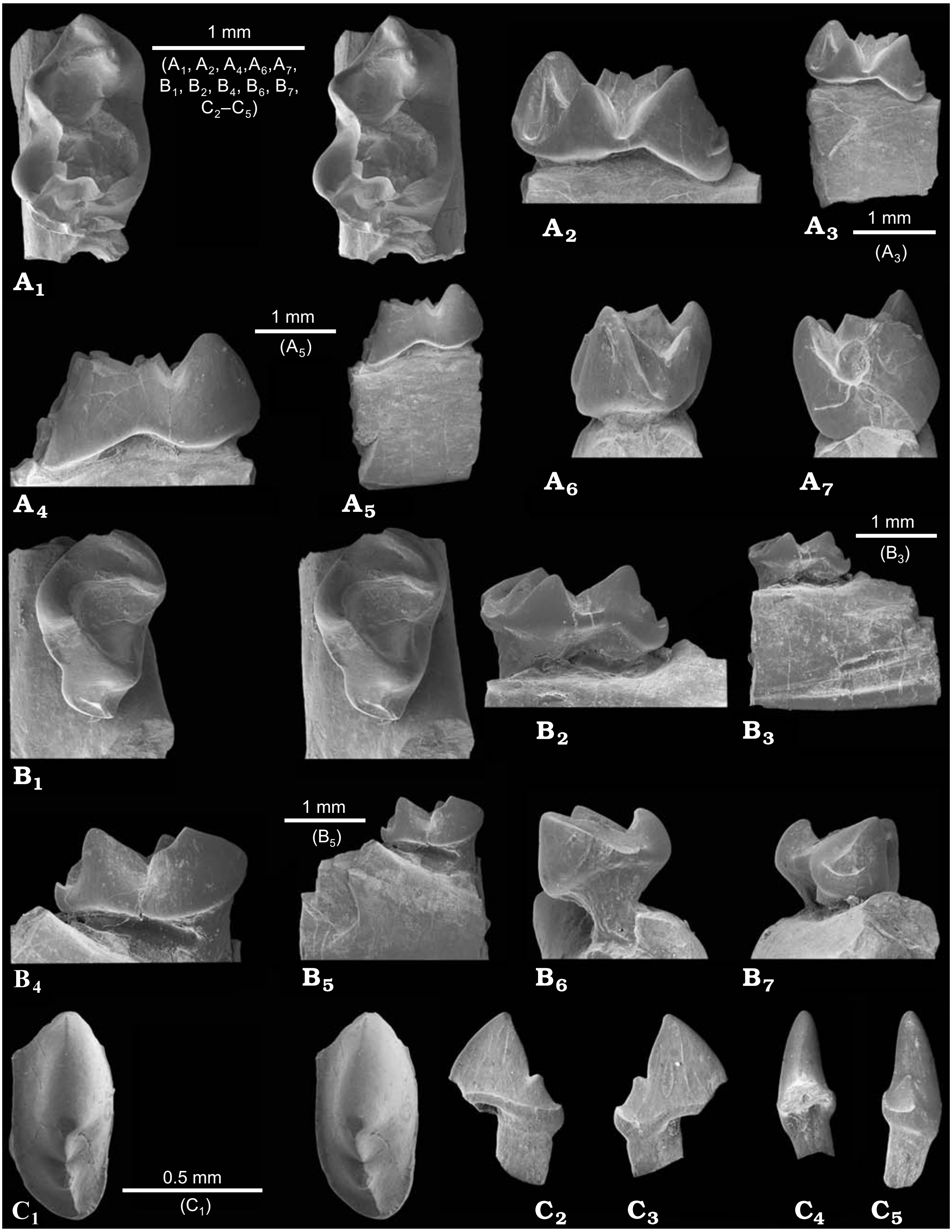

Fig. 3. SEM prints of lower molars and premolar of *Dsungarodon zuoi* gen. et sp. nov., Liuhuanggou, early Late Jurassic (Oxfordian). **A**. SGP 21, right molar (holotype), in occlusal view (A_1, stereo-pair), lingual (A_2, A_3), buccal (A_4, A_5), mesial (A_6), and distal (A_7) views. **B**. SGP 22 right ultimate molar, in occlusal (B_1, stereo-pair), lingual (B_2, B_3), buccal (B_4, B_5), mesial (B_6), and distal (B_7) views. **C**. SGP 26, right premolar, in occlusal (C_1, stereo-pair), lingual (C_2), buccal (C_3), mesial (C_4), and distal (C_5) views.

the most mesial part of the tooth is broken off together with the anterior root. On the buccal side a cingulum is developed that fades in the middle of the tooth crown.

Lower molars.—The holotype SGP 21 is a right lower molar preserved in a fragment of the mandible (Fig. 3A). Its position cannot be determined precisely, but it is definitely not the last of the tooth row as is evident from the presence of a partially preserved alveolus distal to it. The tooth is double rooted and is slightly wider than the preserved madibular fragment. The crown bears five cusps that can be identified as a, b, c, d, and g. Cusps e and f are not developed as distinct cusps.

The tooth crown is dominated by large cusp a, of which the upper portion is broken off. Cusp a is located disto-buccally and at its base four crests can be identified. A short crest runs on its mesial side towards cusp b. It has a well developed wear facet on the buccal side. A second crest without wear facets is located on the mesio-lingual side connecting cusps a and g. Crest a-c is only weakly developed and fades at the base of cusp c; it does not exhibit any wear facets. At the distal side a crest runs obliquely in lingual direction and stops at the base of cusp c.

The second highest cusp is cusp b which is situated in the mesio-buccal corner of the tooth crown. Three crests, a-b, b-g, and a mesial crest run down from the blunt apex of cusp b which is worn. Crest b-g is well developed and forms the mesial border of the anterior basin between cusps a, b, and g, corresponding to the situation in *Simpsonodon* and *Krusatodon*. The mesial crest runs slightly curved to the mesio-lingual end of the crown where in other docodonts cusp e is situated. In SGP 21 no distinct cusp e is developed. Between the mesial crest and crest b-g a straight valley runs perpendicularly to the long axis of the tooth.

Cusp g is the lowest of the main cusps and forms part of the margin of the mesial basin ("pseudotalonid"). It sits in a lingual position and is connected by a crest to cusp a as well as to cusp b. The tip of cusp g is bluntly worn and next to it crest g-b bears an elongated, mesially facing wear facet.

Cusp c is slightly higher than cusp g and is located in the disto-lingual corner of the tooth; it bulges somewhat over the lingual margin of the crown. The tip of cusp c is slightly bent disto-buccally and is bluntly worn. Besides the already mentioned low crest a-c a second crest runs from the distal side of cusp c in a disto-buccal direction towards cusp d. Cusp d forms part of of a ledge around the disto-lingual corner of the tooth crown. In contrast to other docodonts, in *Dsungarodon* no distinct cusp f is developed in the disto-lingual corner. It is not clear whether the distal ledge originally extended to the buccal side since this area of the tooth is slightly damaged.

Lower molar SGP 22 (Fig. 3B) is almost completely preserved and is still sitting in a fragment of the dentary. In lingual aspect (Fig. 3B$_3$), the dentary exhibits the anteriormost part of the postdentary trough and the origin of Meckel's groove; the mandibular foramen is not preserved. SGP 22 is the last molar of the tooth row as is evident from the preserved base of the ascending coronoid process. The tooth exhibits a simplified morphology as is characteristic for the ultimate molar (Krusat 1980) and is double-rooted. It is considerably smaller than the holotype and some of the cusps are reduced. Only three cusps are present that can be identified as cusps a, b, and g. Cusp a forms the distal portion of the tooth crown and is somewhat reduced in size; therefore it is no longer the highest cusp. The region distal to this cusp is reduced to a narrow ledge. Two crests originate at cusp a and run respectively mesio-lingually (crest a-g) and mesio-buccally (crest a-b). The two crests form the V-shaped distal border of the basin a-b-g. Cusp b is the largest of these three cusps. Three crests extend from cusp b: a-b, b-g, and a crest that runs in a lingual direction along the mesial border of the tooth crown (equivalent of crest b-e of the docodonts where cusp e is developed). As in the holotype, a straight valley lies between the mesial crest ("b-e") and crest b-g, which is oriented transversely to the long axis of the tooth. Cusp g is the most lingually situated cusp on the tooth and bulges over the lingual border of the dentary. It is connected by two crests with cusps a and b.

Discussion

Phylogenetic relationships of *Dsungarodon*.—The upper molar at first glance shows similarities with tribosphenic or pseudotribosphenic teeth, such as the molars of *Shuotherium* (Sigogneau-Russel 1998; Wang et al. 1998). Especially the triangular shape, the presence of a large "pseudoprotocone" and of a "pseudotrigon basin" lead to this impression. However, the "pseudoprotocone" (= cusp X) possesses wear facets only at its buccal side and none at its lingual side. This wear pattern is confined to an occlusal mode in which the "pseudoprotocone" occludes lingually of the lower molar. In contrast to this situation the protocone in tribosphenic teeth fits during occlusion into the talonid basin of the corresponding lower molar and therefore wear facets (numbers 5 and 6) develop only on the lingual side of the protocone (Crompton 1971). A similar situation is met in *Shuotherium*, where the pseudoprotocone occludes into the center of the mesially situated pseudotalonid basin and possesses well developed wearfacets (numbers 5' and 6') only on the lingual side (Wang et al. 1998). Although a buccal wear facet is not present on the pseudoprotocone of *Shuotherium shilongi*, it was inferred by the authors as a small facet ?7' from the presence of a small facet 7 on the lower molar of *Shuotherium dongi* (Wang et al. 1998). As docodonts are the only known mammals with an occlusal mode where the "pseudoprotocone" (cusp X) fits lingually to the corresponding lower molars producing buccally facing wear facets (numbers 5, 6, and 7 in docodonts after Crompton and Jenkins 1968; Butler 1997), the attribution of upper molar SGP 23 to Docodonta (and *Dsungarodon*) is justified. The precise occlusal fit between the larger of the two lower molars (SGP 21) and the upper molar (SGP 23) (Martin and Pfretzschner 2003) is strong evidence that these two teeth belong to the same taxon. The ultimate lower molar, although exhibiting a simplified morphology, closely corresponds to the other specimen. It therefore is also attributed to the same taxon. The fragmentary lower deciduous premolars are characterised by a lingually bulging and considerably recurved cusp c that is typical for *Dsungarodon*. The isolated premolar possesses a strongly developed lingual cingulum which is characteristic for docodonts. Therefore it is here tentatively attributed to the new taxon.

To assess the phylogenetic position of *Dsungarodon*, we performed a PAUP 4.0b10 analysis based on lower molar characters. Exhaustive search with all characters unordered and of equal weight resulted in one most parsimonious tree (Fig. 4). In this tree, *Dsungarodon zuoi* appears as sister taxon of *Simpsonodon oxfordensis*. Synapomorph characters of the two taxa are: reduction of cusp e, reduction of crest c-d, cusps c and g of equal size, cusp f lost, anterior basin ("pseudotalonid") enlarged and bordered mesio-lingually by crest b-g. This sister-group relationship indicates certain faunal interrelations between Central Asia and Europe in Middle to Late Jurassic times.

Krusatodon kirtlingtonensis appears as sister taxon of the clade that includes *Dsungarodon* and *Simpsonodon*. Synapomorphies of all three taxa are reduction of crest c-d, cusps c and g of equal size and anterior basin ("pseudotalonid") enlarged and bordered by crest b-g. Compared to *Simpsonodon* and *Dsungarodon*, *Krusatodon* is more plesiomorphic in retaining a distinct cusp e at the mesial end and a cusp f at the distal end of the lower molar.

Sister group of the clade comprising *Krusatodon*, *Dsungarodon*, and *Simpsonodon* is the clade formed by *Borealestes*, *Haldanodon*, and *Docodon*, a very stable group that was recognised in an earlier analysis (Martin and Averianov 2004). Synapomorph character of the clade formed by *Borealestes, Haldanodon*, and *Docodon* is the reduction of cusp e, which is not included in a crest towards b. Differing from the results of Martin and Averianov (2004), the Tegotheriidae appear as a

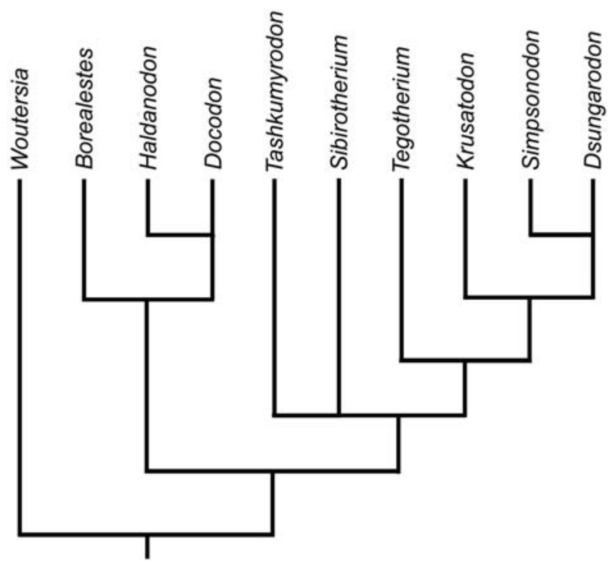

Fig. 4. Phylogenetic relationships of Docodonta based on lower molar characters. Single most parsimonious tree resulting from analysis (exhaustive search) of data matrix shown in Table 1. Tree length = 11, consistency index = 0.727, retention index = 0.850, rescaled consistency index = 0.618.

Table 1. Data matrix for the cladistic analysis of Docodonta, based on lower molar characters: 1, cusp b small, approximated to cusp a (0), larger, well separated from cusp a by notch (1); 2, cusp g small (0), large, almost equal to cusp c (1); 3, cusp e present, unreduced (0), reduced, or lost (1); 4, cusp f absent (0); present (1); 5, pseudotalonid absent (0), present and bordered mesiolingually by crest b-g (1), present and bordered mesiolingually by crest e-g (2); 6, crest b-e present (0), absent (1); 7, crest b-g absent (0), present (1).

Taxon	Characters						
	1	2	3	4	5	6	7
Woutersia	0	0	0	0	0	0	0
Borealestes	0	0	1	1	0	0	1
Haldanodon	0	0	1	1	0	1	1
Docodon	0	0	1	1	0	1	1
Simpsonodon	1	1	1	0	1	0	1
Tashkumyrodon	1	0	0	1	2	0	0
Sibirotherium	1	0	0	1	2	0	0
Tegotherium	1	1	0	1	2	0	0
Krusatodon	1	1	0	1	1	0	1
Dsungarodon	1	1	1	0	1	0	1

paraphyletic assemblage with *Tegotherium* forming the sister-taxon of the clade consisting of *Krusatodon, Simpsonodon*, and *Dsungarodon*. Tegotheriids share an enlarged pseudotalonid that is bordered by crest e-g (character 5 in Table 1) as a synapomorph character. This ambiguity certainly is due the limited number of characters available for phylogenetic analysis (lack of upper molars). The node of *Sibirotherium* and *Tashkumyrodon* is unresolved, both taxa appear in a more distant position and separated from the clade formed by *Tegotherium* plus *Krusatodon*, *Simpsonodon*, and *Dsungarodon*. Our analysis does not support the phylogeny of docodonts (based on lower molars) proposed by Sigogneau-Russell (2003: fig. 9), where *Borealestes* and *Haldanodon* appear as sister taxa of a clade comprising *Simpsonodon*, *Krusatodon*, and *Tegotherium*.

Experimental analysis of the chewing cycle.—The larger of the lower molars (SGP 21) and the upper molar (SGP 23) were used to study the occlusal relationships and the chewing cycle (Fig. 5). As the two teeth fit together very precisely, they probably were antagonistic teeth in the living animal. The whole occlusal cycle can be divided into four successive phases starting with the initial occlusal contact between the buccal cusps and their connecting crests in the first phase. As cusp a is broken off, only the occlusal function of cusp b could be observed in the experiment. Cusp b has its initial contact to the lingual side of cusp A in the upper molar. During this initial stage of the occlusion the buccal crests a-b-e in the lower and and A-C in the upper molar work as antagonistic cutting edges, with crest a-b-e passing crest A-C on the lingual side. As cusp a obviously was considerably higher than cusp b, it would first come into contact with the upper molar. However, occlusional experiments combining *Haldanodon* lower molars with the *Dsungarodon* upper molar

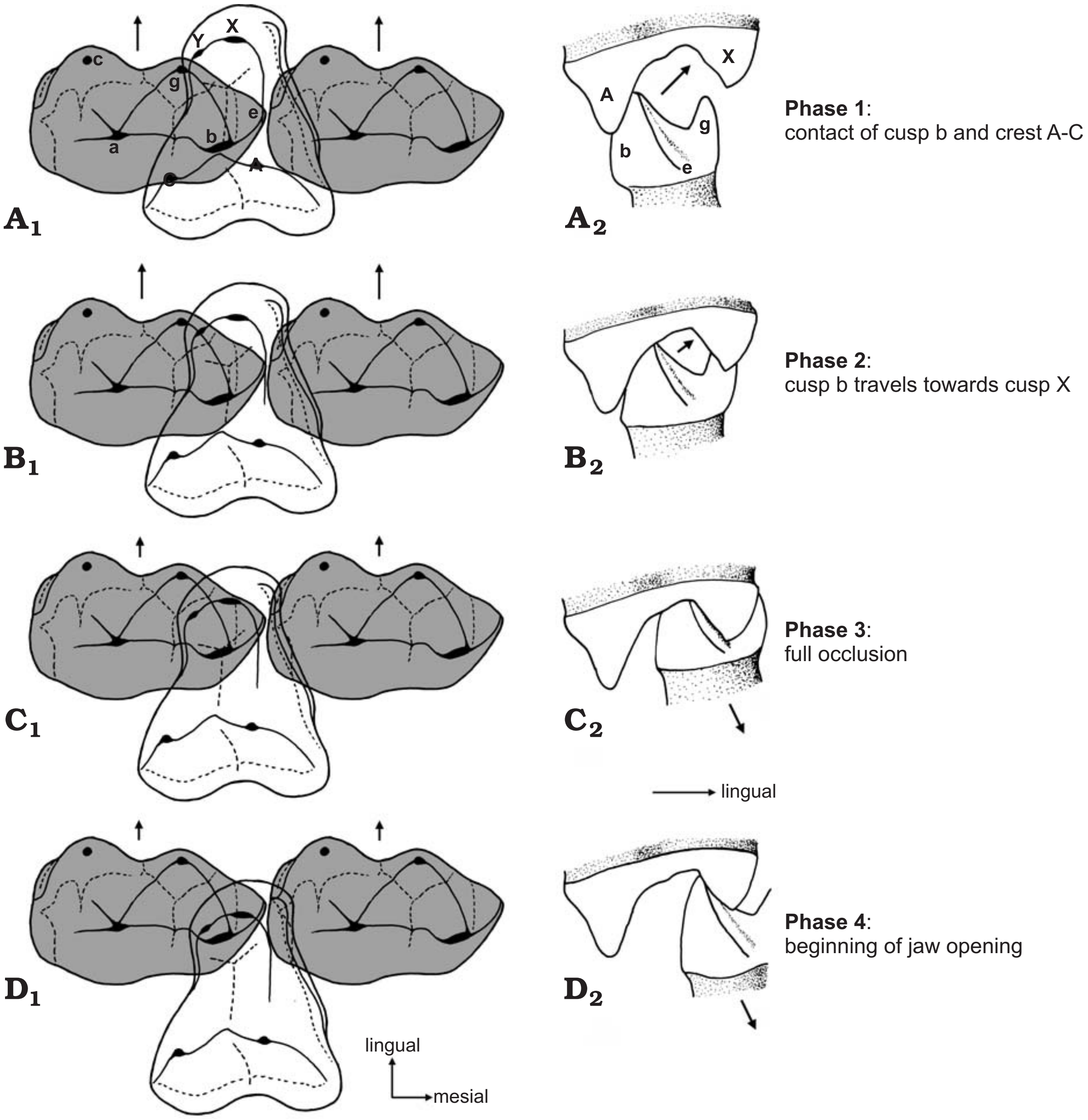

Fig. 5. Occlusion of lower and upper molars during the chewing cycle (four phases) in superposition (A_1–D_1, left) and mesial aspect (A_2–D_2, right). In the superposition, the upper molar is drawn as if it were transparent. The phases of the chewing cycle were drawn after an experimental study with high precision epoxy casts. Arrows indicate direction of movement of lower molars. **A**. Initial contact. Cusp b of the lower molar contacts ridge A-C and moves dorso-medially towards the center of the upper molar (Phase 1). **B**. During this stage of the power stroke the volume between cusp b and cusps X-Y is compressed. A wear facet is produced at the buccal side of cusp b (Phase 2). **C**. Maximum occlusion. Cusp b fits snuggly into the deepest point of basin A-C-Y-X. Crest a-b fits into the deep valley of the distal margin of the upper molar between cusp Y and C. The inclined buccal side of cusp X meets the straight valley e-b-g (Phase 3). **D**. This stage of the power stroke reopens the jaws by a ventro-medial movement of the lower molar. Cusp X grinds along the straight valley e-b-g. This valley controls the movement of the lower molar and restricts it to a straight, transversal direction (Phase 4).

indicated, that cusp a in *Dsungarodon* must have been considerably lower than in *Haldanodon* and its allies. During this cutting stage the lingually facing wear facets on the buccal crest A-C and the corresponding buccal facing facets on crest a-b are formed.

After this initial cutting contact of the buccal crests, the lower molar ascends into the maximum occluding position. During these second and third phases of the chewing cycle the food item is squashed in the "pseudotrigon" basin A-C-Y-X of the upper molar. The latter functions as a mortar and cusp b as a pestle, which is worn blunt accordingly. Such a close approximation of lower and upper molars during occlusion of cusp b into the basin A-C-Y-X requires cusp a to be considerably lower than it is in *Haldanodon*. Although cusp a is broken off in the type specimen of *Dsungarodon*, it can be inferred that it was similar to those of *Krusatodon* and *Simpsonodon*. During the upward movement of the lower jaw the food is compressed between cusps b and crest X-Y. In order to intensify this function cusp b is slightly elongated mesiodistally. As crest X-Y crosses crest b-g, a wear facet is formed on the lingual half of crest b-g. Correspondingly crest X-Y and cusp Y experience considerable wear. However, a distinct wear facet is not developed on crest X-Y. Maximum occlusion is attained, when cusp b fits into the deepest point of the "pseudotrigon" basin A-C-Y-X. In this position crest X-Y crosses crest b-g exactly in its lowest point. Similarly the crest distal to Y crosses crest a-b at its notchlike incision.

In the fourth phase of the chewing cycle the jaws begin to open again, with the lingual side of cusp b moving along the buccal side of crest X-Y without producing distinct wear facets. However, during this movement food may be ground between cusp b and crest X-Y. At the same time cusp X is grinding along the straight valley between crests b-g and b-e at the mesial end of the lower molar, which produces the well developed wear facet at the lingual tip of cusp X. This grinding function of cusp X requires a straight and transversely oriented valley e-b-g. Another grinding function can be observed on the distal end of the tooth. Crest X-A moves across the shortened portion of the lower molar distal to cusps a and c that shows wear facets on the c-d crest and the crest distal to a. Crest X-A is only slightly worn. The facet on the distally bent tip of cusp c lies in the same plane as the other distal wear facets. The last phase of the chewing cycle is the recovery stroke of the lower jaw without occlusal contact between upper and lower molars.

Jenkins (1969) studied the occlusal movement in *Docodon* on the basis of wear facets and assumed only a small transversal component. He also proposed a slightly foreward directed component during jaw closure in *Docodon*, which was denied by Gingerich (1973), who deduced from striations on the teeth a backward component. In the case of *Dsungarodon* the occlusal experiments have confirmed the existence of a considerable transverse component in the chewing stroke during jaw closure and jaw opening as postulated by Butler (1988). The chewing stroke after maximum occlusion also seems to be restricted to the transverse plane by the orientation of the valley e-b-g. When cusp X grinds along this valley in the third phase of the chewing stroke, no additional forward or backward component is possible.

Altogether the molars of *Dsungarodon* exhibit cutting, crushing, and grinding functions during a chewing cycle. Compared to most other docodonts, *Dsungarodon* has a considerably elongated "pseudotrigonid" basin a-b-g. This is due to the large, elongated cusp b, which must be well separated from cusp a in order to function as a pestle for the mortar formed by basin A-C-Y-X in the upper molar. Additionally, the region anterior to the "pseudotalonid" basin is elongated by the mesially oriented crest b-e, which, however, lacks a distinct cusp e at its mesial end. This crest extends the buccal cutting edge of the lower molar mesially and, what is probably more important, allows the valley e-b-g to run straight and transversely across the lower molar to serve as a grinding device for cusp X. Together with the enamel ridges on the distal part of the lower molar the grinding function seems to be well established in *Dsungarodon* molars. A comparison with the other known docodonts reveals a considerable diversification of molar morphology and of dietary preferences in this non-holotherian mammalian group.

Haldanodon and *Docodon* are lacking a "pseudotalonid" basin which indicates that puncturing and cutting were the main functions of their molars whereas crushing or grinding were less important. Especially the very high cusp a was necessary to puncture the food item. Correspondingly, there is no real "pseudotrigon" basin A-C-Y-X developed in the upper molars of *Haldanodon,* but the lingual part of the crown is dominated by the very prominent crest A-X. The remaining Asian docodonts (*Tashkumyrodon*, *Sibirotherium,* and *Tegotherium*) all have well developed and enlarged "pseudotalonid" basins a-b-e-g in their lower molars which is evidence for some crushing function. *Simpsonodon* possesses a special grinding surface at the distal end of the lower molar formed by several wrinkled enamel ridges, and finally *Dsungarodon* has well developed crushing and grinding functions. In both taxa the grinding function is enhanced compared to the situation in *Krusatodon*. A crushing or squashing and grinding function is particularly effective for processing plant material or soft-bodied invertebrates, whereas a diet mainly based on chitinous arthropods would require a puncturing and cutting function. Whereas *Haldanodon* and *Docodon* probably mainly preyed on arthropods and other invertebrates, *Dsungarodon*, the other Asian docodonts, and *Simpsonodon* more likely preferred a mixed diet of plants and soft bodied invertebrates, although it is not possible to establish the exact diet on the base of the evidence available.

Conclusion

Together with the other discoveries of new docodonts in the last decade, *Dsungarodon* demonstrates that these basal mammals achieved a considerable diversity in the Jurassic and Early Cretaceous. Differences in molar structure and function indicate that the various docodont lineages had different dietary specialisations. Three different trends of molar structure and function can be distinguished. The first group including *Borealestes*, *Haldanodon*, and *Docodon* from Europe and North America has a comparatively plesiomorphic molar pattern, that mainly allowed piercing and cutting of food items. These docodonts probably preyed on arthropods and other invertebrates of various kind. Some Asian docodonts such as *Tashkumyrodon*, *Sibirotherium*, and *Tegotherium* developed two large basins in the lower molars for a crushing function (best-developed in *Tegotherium*). As such a broadening and change to crushing function in the molars of modern insectivors indicates either a diet of armoured insects, such as beetles, or a more omnivorous diet, as in the case of the European hedgehog (*Erinaceus*), similar conditions may be proposed for these Asian docodonts. Finally, both the European *Simpsonodon* and the Asian *Dsungarodon* developed extensive grinding functions in their molars, probably due to an increased share of plant material in their diet (to a lesser extent also present in *Krusatodon*). This phylogenetic and ecologic diversity and wide geographic distribution stands in contrast to the classical view of docodonts as a small group of basal mammals. Future studies may show, that docodonts were even more widespread and important faunal elements in Jurassic and Cretaceous ecosystems.

Acknowledgements

We thank Prof. Zuo Xue-Yi, head of the Information Division of the Geological Bureau of Xinjiang in Urumqi, at the time director of the Xinjiang Geological Survey No. 1, for his extensive technical support of our fieldwork. The paper greatly benefited from constructive reviews by Alexander O. Averianov (Zoological Institute, Russian Academy of Sciences, St. Petersburg), Percy M. Butler (School of Biological Sciences, Royal Holloway, University of London, London), and Zhe-Xi Luo (Carnegie Museum of Natural History, Pittsburgh). Wolfgang Müller (Institut für Geowissenschaften, Freie Universität, Berlin) assisted at the SEM and provided the photographical prints. This study has been funded by a technical grant to HUP (Pf 219/13) and a Heisenberg grant (Ma 1643/5-2) to TM by the Deutsche Forschungsgemeinschaft (DFG).

References

Ashraf, A.R., Sun, Y.-W., Li, J., Sun, G., and Mosbrugger, V. 2004. Palynostratigraphic analysis of the Huangshanjie-, Haojiagou-, Badaowan-, Sangonghe- and Xishanyao Formation (Upper Triassic–Middle Jurassic) in the Southern Junggar Basin (NW China). *In*: G. Sun, V. Mosbrugger, A.R. Ashraf, and Y.-W. Sun (eds.), *Proceedings of Sino-German Cooperation Symposium on Paleontology, Geological Evolution and Environmental Changes of Xinjiang, China*, 41–44. Urumqi.

Butler, P. M. 1988. Docodont molars as tribosphenic analogues (Mammalia, Jurassic). *In*: D.E. Russell, J.P. Santoro, and D. Sigogneau-Russell (eds.), Teeth Revisited: Proceedings of the VIIth International Symposium on Dental Morphology. *Mémoirs du Muséum national d'Histoire naturelle C* 53: 329–340.

Butler, P.M. 1997. An alternative hypothesis on the origin of docodont molar teeth. *Journal of Vertebrate Paleontology* 17: 435–439.

Crompton, A.W. 1971. The origin of the tribosphenic molar. *In*: D.M. Kermack and K.A. Kermack (eds.), Early Mammals. *Zoological Journal of the Linnean Society, London* 50 (Supplement No. 1): 65–87.

Crompton, A.W. and Jenkins, F.A. 1968. Molar occlusion in Late Triassic mammals. *Biological Reviews* 43: 427–458.

Gingerich, P.D. 1973. Molar occlusion and function in the Jurassic mammal *Docodon*. *Journal of Mammalogy* 54: 1008–1013.

Jenkins, F.A. 1969. Occlusion in *Docodon* (Mammalia, Docodonta). *Postilla* 139: 1–24.

Kermack, K.A.., Lee, A.J., Lees, P.M., and Mussett, F. 1987. A new docodont from the Forest Marble. *Zoological Journal of the Linnean Society* 89: 1–39.

Kielan-Jaworowska, Cifelli, R. L., and Luo, Z.-X. 2004. *Mammals from the Age of Dinosaurs. Origins, Evolution, and Structure*. xv + 630 pp. Columbia University Press, New York.

Kretzoi, M. 1946. On Docodonta, a new order of Jurassic Mammalia. *Annales Historico-Naturales Musei Nationalis Hungarici* 39: 108–111.

Kron, D.G. 1979. Docodonta. *In*: J.A. Lillegraven, Z. Kielan-Jaworowska, and W.A. Clemens (eds.), *Mesozoic Mammals: The First Two-thirds of Mammalian History,* 91–98. University of California Press, Berkeley.

Krusat, G. 1980. Contribuição para o conhecimento da fauna do Kimeridgiano da Mina de Lignito Guimarota (Leiria, Portugal). IV Parte. *Haldanodon exspectatus* Kühne & Krusat 1972 (Mammalia, Docodonta). *Memórias dos Serviços Geológicos de Portugal* 27: 1–79.

Kühne, W.G. and Krusat, G. 1972. Legalisierung des Taxon *Haldanodon* (Mammalia, Docodonta). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1972: 300–302.

Lillegraven, J.A. and Krusat, G. 1991. Cranio-mandibular anatomy of *Haldanodon exspectatus* (Docodonta; Mammalia) from the Late Jurassic of Portugal and its implications to the evolution of mammalian characters. *Contributions to Geology, University of Wyoming* 28: 39–138.

Linneaus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol 1: Regnum animale. Editio decima, reformata*. 824 pp. Laurentii Salvii, Stockholm.

Luo, Z.-X., Kielan-Jaworowska, Z., and Cifelli, R.L. 2002. In quest for a phylogeny of Mesozoic mammals. *Acta Palaeontologica Polonica* 47: 1–78.

Maisch, M.W., Matzke, A. T., Ye, J., Pfretzschner, H.-U., and Sun, G. 2001. The fossil vertebrate faunas of the Toutunhe and Qigu Formations of the Southern Junggar Basin and their biostratigraphical and palecological implications. *In*: G. Sun, V. Mosbrugger, A.R. Ashraf, and Y.D. Wang (eds.), *The Advanced Study of Prehistory Life and Geology of Junggar Basin, Xinjiang, China*, 83–94. Urumqi.

Maisch, M.W., Matzke, A.T., Pfretzschner, H.-U., Sun, G., Stöhr, H. Grossmann, F. 2003. Fossil vertebrates from the Middle and Upper Jurassic of the Southern Junggar Basin (NW-China)—results of the Sino-German expeditions 1999–2000. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 2003: 297–313.

Maisch, M.W., Matzke, A.T., Grossmann, F., Stöhr, H., Pfretzschner, H.-U., and Sun, G. 2004. The first haramiyid mammal from Asia. *Naturwissenschaften* 92: 40–44.

Martin, T. and Averianov, A.O. 2004. A new docodont (Mammalia) from the Middle Jurassic of Kyrgyzstan (Central Asia). *Journal of Vertebrate Paleontology* 24: 195–201.

Martin, T. and Pfretzschner, H.-U. 2003. Functional morphology and evolution of docodont molars (Mammalia) from the Middle Jurassic of Junggar Basin (NW China). *Journal of Vertebrate Paleontology* 23 (Supplement to No. 3): 76A.

Maschenko, E.N., Lopatin, A.V., and Voronkevich, A.V. 2003. A new genus of the tegotheriid docodonts (Docodonta, Tegotheriidae) from the Early Cretaceous of West Siberia. *Russian Journal of Theriology* 1: 75–81.

McKenna, M.C. and Bell, S. 1997. *Classification of Mammals Above the Species Level*. xii + 631 pp. Columbia University Press, New York.

Nessov, L.A., Kielan-Jaworowska, Z., Hurum, J.H., Averianov, A.O., Fedorov, P.V., Potapov, D.O., and Frøyland, M. 1994. First Jurassic mammals from Kyrgyzstan. *Acta Palaeontologica Polonica* 39: 315–326.

Prasad, G.V.R. and Manhas, B.K. 2001. First docodont mammals of Laurasian affinity from India. *Current Science* 81: 1235–1238.

Rowe, T. 1988. Definition, diagnosis, and origin of Mammalia. *Journal of Vertebrate Paleontology* 8: 241–264.

Sigogneau-Russell, D. 1998. Discovery of a Late Jurassic Chinese mammal in the Upper Bathonian of England. *Comptes Rendus des Séances de l'Academie des Sciences, sciences de la terre et des planètes* 327: 571–576.

Sigogneau-Russell, D. 2001. Docodont nature of *Cyrtlatherium*, an upper Bathonian mammal from England. *Acta Palaeontologica Polonica* 46: 427–430.

Sigogneau-Russell, D. 2003. Docodonts from the British Mesozoic. *Acta Palaeontologica Polonica* 48: 357–374.

Simpson, G.G. 1928. *A Catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum*. x + 215 pp.Trustees of the British Museum, London.

Simpson, G.G. 1929. American Mesozoic Mammalia. *Memoirs of the Peabody Museum* 3: 1–171.

Tatarinov, L.P. 1994. On an unusual mammalian tooth from the Mongolian Jurassic [in Russian]. *Paleontologičeskij žurnal* 2: 97–105.

Wang, Y.-Q., Clemens, W.A., Hu, Y.-M., and Li, C.-K. 1998. A probable pseudo-tribosphenic upper molar from the Late Jurassic of China and the early radiation of the Holotheria. *Journal of Vertebrate Paleontology* 18: 777–787.