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New interpretation of dentition in Early Cretaceous docodontan *Sibirotherium* based on micro-computed tomography

Alexander O. Averianov[1] · Alexey V. Lopatin[2] · Sergey V. Leshchinskiy[3]

Abstract

A tegotheriid docodontan *Sibirotherium rossicum* from the Early Cretaceous of Western Siberia, Russia, was considered to have six lower premolars, as in the tegotheriids *Agilodocodon* and *Microdocodon* from the Middle Jurassic of China. The micro-computed tomography of two dentary specimens with a supposed submolariform ultimate deciduous premolar (dp6) revealed absence of a replacing tooth germ in this locus. Also, the morphology of the roots of this tooth is more consistent with that of molariform teeth. Based on the new data, we interpret *Sibirotherium* to possess five lower premolars rather than six and that the supposed dp6 might in fact be better interpreted as the first molariform (m1). The results of our phylogenetic analysis suggest that this is a plesiomorphic condition for Docodonta and, under slow character optimization, for Tegotheriidae, with the number of premolars reduced to three to four in Docodontidae (*Haldanodon*, *Docodon*, and *Docofossor*).

Keywords Mammaliaformes · Docodonta · *Sibirotherium* · Dentition · MicroCT

Introduction

Docodonta is an early-diverging branch of mammaliaforms that achieved a considerable taxonomic and ecomorphological diversity in the Middle Jurassic – Early Cretaceous of Laurasia (Kielan-Jaworowska et al. 2004; Martin 2018) and possibly persisted into the early Late Cretaceous of Gondwana (Martin et al. 2022). The clade includes taxa with ecomorphological specializations including for semiaquatic, fossorial, and arboreal lifestyles (Martin 2005; Ji et al. 2006; Luo et al. 2015; Meng et al. 2015). The molariform teeth of docodontans are strikingly similar to those of tribosphenic mammals in having the enlarged lingual cusps on the upper teeth grinding against the basins on the lower teeth. The docodontan molariform teeth were capable of more complex shearing and crushing functions compared with other contemporaneous Mesozoic mammaliaforms, suggesting more efficient food processing (Schultz et al. 2019). The middle ear bones in docodontans were still attached to the dentary, as in other stem mammals (Kielan-Jaworowska et al. 2004).

The decline of docodontans in the Early Cretaceous may have been related to the emergence and dispersal of tribosphenic mammals, which have (among other features) similar shearing and crushing dentition, but their middle ear bones detached from the dentary, providing a wider range of hearing capabilities. However, to date, the fossils of tribosphenic mammals have not been found in the Early Cretaceous of Siberia, and docodontans appear to have persisted. The docodontans *Khorotherium yakutense* and *Sibirotherium rossicum* are among the most commonly found mammals in the Early Cretaceous faunas of Yakutia and Western Siberia, respectively (Maschenko et al. 2003; Lopatin et al. 2009, 2020; Averianov et al. 2018).

Lopatin et al. (2009) suggested *Sibirotherium rossicum* possessed six lower premolars, similar to other docodontans such as *Agilodocodon scansorius* and *Microdocodon gracilis* from the Middle Jurassic Tiaojishan Formation of Inner Mongolia, China (Meng et al. 2015; Zhou et al. 2019).

✉ Alexander O. Averianov
dzharakuduk@mail.ru

Alexey V. Lopatin
alopat@paleo.ru

Sergey V. Leshchinskiy
sl@ggf.tsu.ru; mammothfauna@gmail.com

[1] Zoological Institute, Russian Academy of Sciences, Universitetskaya Nab. 1, Saint Petersburg 199034, Russia

[2] Borissiak Paleontological Institute, Russian Academy of Sciences, Profsouznaya Ul. 123, Moscow 117647, Russia

[3] Laboratory of Mesozoic and Cenozoic Continental Ecosystems, Tomsk State University, Pr. Lenina 36, Tomsk 634050, Russia

In *Castorocauda lutrasimilis*, also from the same formation (Ji et al. 2006), and in *Borealestes serendipitus* from the Middle Jurassic Kilmaluag Formation of Scotland, United Kingdom (Waldman and Savage 1972; Panciroli et al. 2019, 2021), there are five lower premolars, and the remaining docodontan taxa for which the tooth row is known, *Docodon*, *Haldanodon*, *Dsungarodon*, and *Docofossor*, have three to four lower premolars (Kielan-Jaworowska et al. 2004; Schultz et al. 2019). The dental formula count in *S. rossicum* was based on the interpretation of the first lower molariform tooth as a partially molarized ultimate deciduous premolar (dp6). Here we present results of the micro-computed tomography of two specimens of *S. rossicum* indicating absence of the replacing permanent premolar in this locus, and discuss implications of this discovery for the interpretation of dental formula and phylogenetic affinities of this docodontan.

Institutional abbreviations LMCCE, Laboratory of Mesozoic and Cenozoic Continental Ecosystems, Tomsk State University, Tomsk, Russia; PM TGU, Paleontological Museum of Tomsk State University, Tomsk, Russia.

Materials and methods

The cusp nomenclature of docodontan teeth follows that of Averianov et al. (2010: fig. 1), which was modified from Luo and Martin (2007). The nomenclature differs from Luo and Martin (2007) in the addition of cusp bb on the lower molariform teeth and that the cusp df on lower molariform teeth is labelled as cusp dd.

Two specimens of *Sibirotherium rossicum*, the holotype PM TGU 16/5–22 and PM TGU 120/9–34, were CT scanned at the Saint Petersburg State University Research Centre for X-ray Diffraction Studies (Saint Petersburg, Russia) using the CT model SkyScan 1172. They were imaged at 100 kV and 0.1 mA, generating a resolution of 2.07 μm and 3.45 μm of isotropic voxel size and output of 3024×2436 and 1928×1928 pixels per slice. The CT scan data were imported to the software Avizo Lite 2019.1 (FEI-VSG Company) for segmentation and reconstruction of three-dimensional surface files.

For the phylogenetic analysis, we used a data matrix focused on Docodonta presented by Zhou et al. (2019) with some modifications. First, we excluded *Tikitherium* and *Gondtherium* from the matrix because they are not docodontans (Averianov et al. 2010; Zhou et al. 2019). Second, we changed the scorings for *Borealestes* and *Sibirotherium* on the number of premolar or premolar positions (character 49) from unknown to five premolars (character state 2) following Panciroli et al. (2019) and this study. Third, we changed scorings for *Haldanodon* and *Docofossor* for the same character (number of premolars or

premolar positions) from four premolars (state 1) to three premolars (state 0) following Krusat (1980), Martin and Nowotny (2000), and Luo et al. (2015). All characters were treated as unordered. The parsimony analysis was run on the TNT software (v. 1.5) (Goloboff and Catalano 2016). The implicit enumeration search produced six most parsimonious trees of 143 steps with a consistency index of 0.55 and a retention index of 0.83. The strict consensus tree, tree statistics, and character distribution and optimization were obtained using WinClada v. 1.00.08 (Nixon 2002). The fast and slow character optimizations of Winclada correspond to ACCTRAN and DELTRAN optimizations, respectively, of PAUP (Swofford 2002).

Systematic paleontology

Mammaliaformes Rowe, 1988
Docodonta Kretzoi, 1946
Tegotheriidae Tatarinov, 1994
Sibirotherium rossicum Maschenko et al., 2003
Figures 1–4
Sibirotherium rossicus Maschenko et al., 2003: p. 77, figs. 1–4 (original description).
Sibirotherium rossicus Maschenko et al., 2003: Averianov 2004: fig. 1D.
Sibirotherium rossicum Maschenko et al., 2003: Lopatin et al. 2009: p. 454, figs. 2–6, pl. 12 (emended spelling).

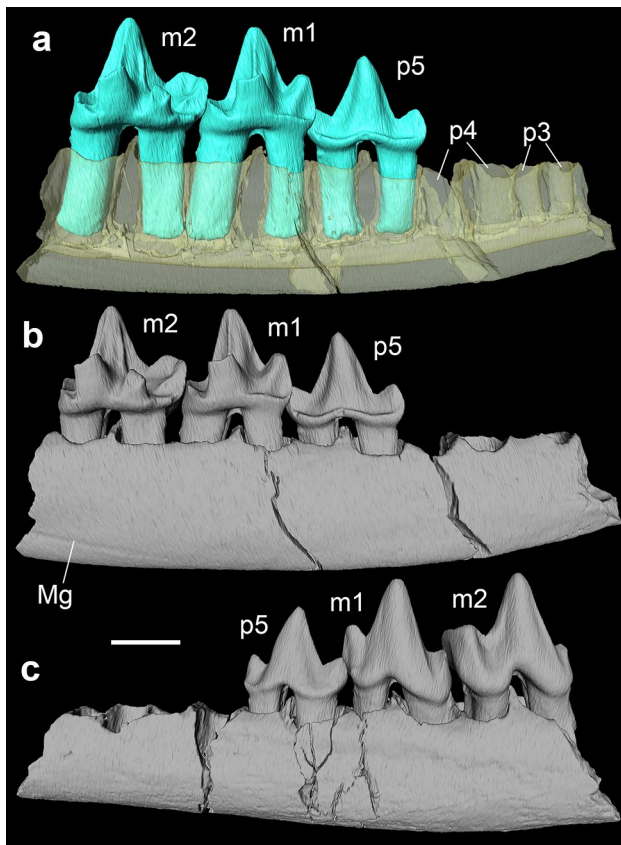**Holotype**. PM TGU 16/5–22, left dentary fragment with p5, m1-2, and alveoli for p3-4.

Type locality and horizon. Shestakovo 1 locality (55° 54′ 36.4" N, 87° 56′ 53.6" E), Chebula raion, Kemerovo oblast, Russia. Ilek Formation, Lower Cretaceous (Aptian).

Referred specimens. Maxillary and dentary fragments, isolated upper and lower teeth; see Lopatin et al. (2009) for the list of specimens. A lower molar LMCCE 005/127 from the Ilek Formation (Barremian?) at Bol'shoi Kemchug 3 locality, Krasnoyarsk krai, Russia may belong to a different species and was identified as *Sibirotherium* sp. (Lopatin et al. 2020).

Description. See Lopatin et al. (2009).

Results

The micro-computed tomography of the holotype of *S. rossicum* and dentary fragment PM TGU 120/9–34 reveal no tooth germs for replacing permanent teeth in these specimens (Figs. 1a, 2a). This suggests that what Lopatin et al. (2009) identified as an ultimate deciduous premolar lacking the cusp g is more likely to be the first molariform tooth (m1), and the rest of the premolars represent

Fig. 1 PM TGU 16/5–22, holotype of *Sibirotherium rossicum*, left dentary fragment with p5, m1-2, and alveoli for p3-4. **a**. Segmented surface visualization of permanent teeth (blue) and dentary (translucent yellow), lingual view. **b**, **c**. Surface rendering based on high-resolution X-ray computed tomography scans, lingual (**b**) and labial (**c**) views. Shestakovo 1, Kemerovo oblast, Russia; Ilek Formation, Lower Cretaceous (Aptian). Abbreviations: **m**, molar; **Mg**, Meckelian groove; **p**, premolar. Scale bar equals 1 mm

the permanent generation (Fig. 3). This re-interpreted m1 has long and robust roots similar to the rest of the molars, in contrast with slightly shorter and slender roots of the premolars (Fig. 2a), a feature also seen in the holotype PM TGU 16/5–22 (Fig. 1a). We therefore reinterpret the lower dental formula of *S. rossicum* as including five premolars (Figs. 3 and 4).

On the strict consensus tree obtained in the TNT analysis (Fig. 5), the family Docodontidae (*Haldanodon*, *Docodon*, and *Docofossor*) is the basalmost clade of Docodonta. The most deeply nested clade is the family Tegotheriidae, including *Krusatodon*, *Agilodocodon*, *Sibirotherium*, *Tegotherium*, *Microdocodon*, and *Hutegotherium*. Tegotheriidae is defined here as a stem clade including all docodontans more closely related to *Tegotherium* than *Docodon* or *Simpsonodon*. This analysis does not support Simpsonodontidae sensu Averianov et al. (2010) (including *Simpsonodon* and *Dsungarodon*). *Simpsonodon* is a sister

taxon to the Tegotheriidae and *Dsungarodon* is clustered with *Tashkumyrodon* and *Castorocauda*.

The resulting consensus tree differs in a number of details from the single most parsimonious tree produced by the PAUP analysis in Zhou et al. (2019). *Tashkumyrodon*, *Dsungarodon*, and *Borealestes* are not included in the Docodontidae but are more deeply nested within the cladogram and a position closer to Tegotheriidae. *Castorocauda* is not the basalmost docodontan but clusters with *Tashkumyrodon* and *Dsungarodon* outside of Docodontidae. Within the Tegotheriidae, *Microdocodon* is the sister taxon to *Hutegotherium* rather than to *Tegotherium*.

Discussion

The holotype of *S. rossicum* was interpreted as having two deciduous premolars (dp3-4?) and first molariform tooth (m1) in the original description (Maschenko et al. 2003). The alveoli of two more anterior teeth were attributed to the anterior deciduous teeth (dp1-2?). The dental formula of *S. rossicum* was estimated as including four lower premolars and at least six lower molariforms. The interpretation of the anterior teeth in this specimen as deciduous was based on their similarity with the teeth on the single known specimen of *Peraiocynodon inexpectatus* Simpson, 1928 from the Lower Cretaceous (Berriasian) Purbeck Limestone Group of England (Simpson 1928), proposed to be deciduous teeth by Butler (1939) and synonymized with *Docodon* (later supported by Kielan-Jaworowska et al. 2004, though maintained as a distinct taxon by Sigoneau-Russell 2003). The latter is certainly a juvenile specimen, with a tooth erupting posterior to the fourth preserved tooth. The presumed ultimate deciduous premolar in *P. inexpectatus* and *S. rossicum* has only one lingual cusp (c), while molariform teeth have two lingual cusps (c and g). According to Averianov (2004), all known deciduous lower premolars of docodontans lack the cusp g. Butler's interpretation of the teeth on the holotype of *P. inexpectatus* was accepted by a number of authors (see review in Averianov 2004), but alternatively, these teeth have been interpreted as m1-4 (Simpson 1928) or p1, dp2-3, and m1 (Krusat 1980). According to Sigogneau-Russell and Kielan-Jaworowska (2002) and Sigogneau-Russell (2003), the last preserved molariform tooth on the holotype of *P. inexpectatus* is m1 whereas as some of the anterior teeth could be deciduous premolars.

Our tomographic data reveal that in PM TGU 120/9–34, there are five premolars with simple crowns between the large two-rooted canine and a molariform tooth with a single lingual cusp (c) (Figs. 2 and 3). The latter tooth was considered a deciduous premolar (dp6) by analogy with the holotype, while all the anterior premolars are permanent. Thus, the dental formula of *S. rossicum* was estimated as including
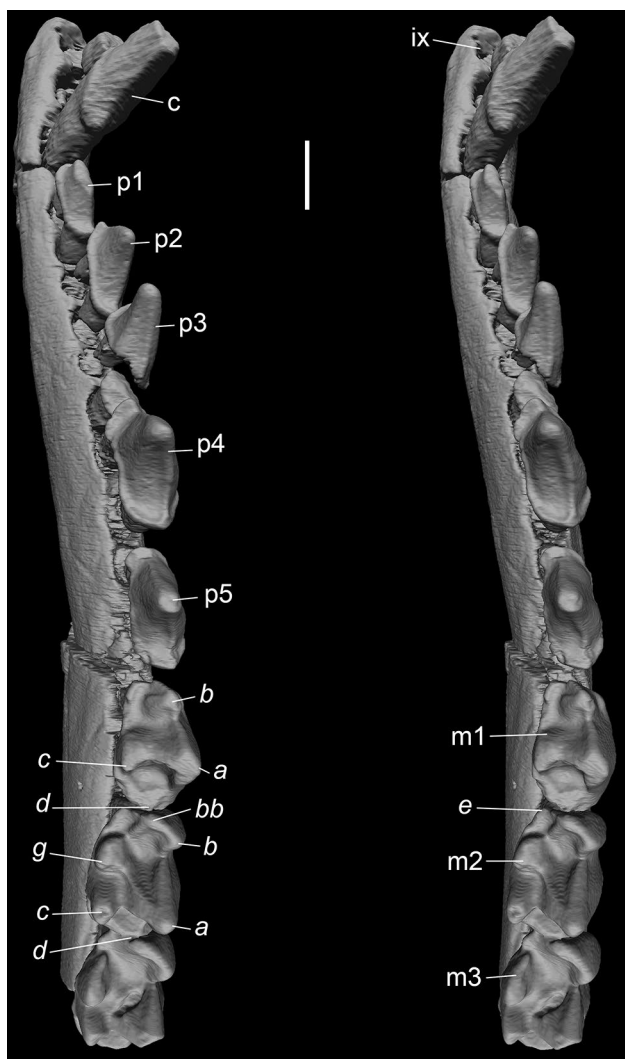
Fig. 2 PM TGU 120/9–34, *Sibirotherium rossicum*, right dentary fragment with c, p1-5, m1-3, and root of ix. **a**. Segmented surface visualization of permanent teeth (blue) and dentary (translucent yellow), lingual view. **b**, **c**. Surface rendering based on high-resolution X-ray computed tomography scans, lingual (b) and labial (c) views. Shestakovo 1, Kemerovo oblast, Russia; Ilek Formation, Lower Cretaceous (Aptian). Abbreviations: **c**, canine; **i**, incisor; **m**, molar; **Mg**, Meckelian groove; **p**, premolar. Scale bar equals 1 mm
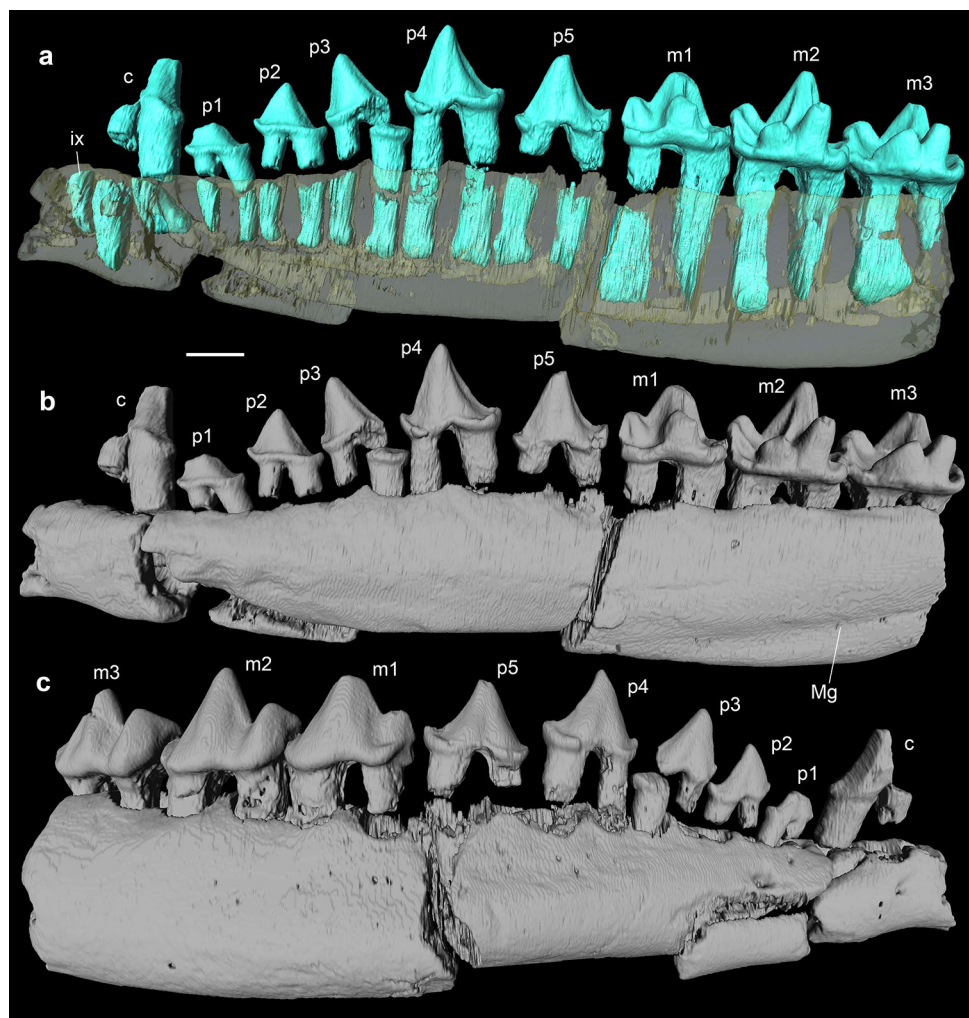
six lower premolars. Such a high number of lower premolars is known for *Agilodocodon* and *Microdocodon* (Meng et al. 2015; Zhou et al. 2019), as well as stem mammal *Kuehneotherium* and australosphenidan *Bishops* (Kermack et al. 1968; Rich et al. 2001; Martin 2018). Therefore, a dental formula with six premolars of *Sibirotherium* did not seem unusual. Nevertheless, the micro-computed analysis of the relevant specimens of *Sibirotherium* presented herein suggests that this taxon had only five lower premolars based on the absence of any developing replacement teeth. Among docodontans, five lower premolars are also present in *Borealestes* and *Castorocauda* (Fig. 5). Under fast (ACCTRAN) optimization, having five premolars is plesiomorphic for docodontans (Fig. 5a). In this model the number of premolars would be reduced to three-four in Docodontidae and increased to six in the clade *Simpsonodon* + Tegotheriidae with a reversal to five in *Sibirotherium*. Under slow optimization (DELTRAN), having five premolars is also plesiomorphic for docodontans, with a parallel increase in the
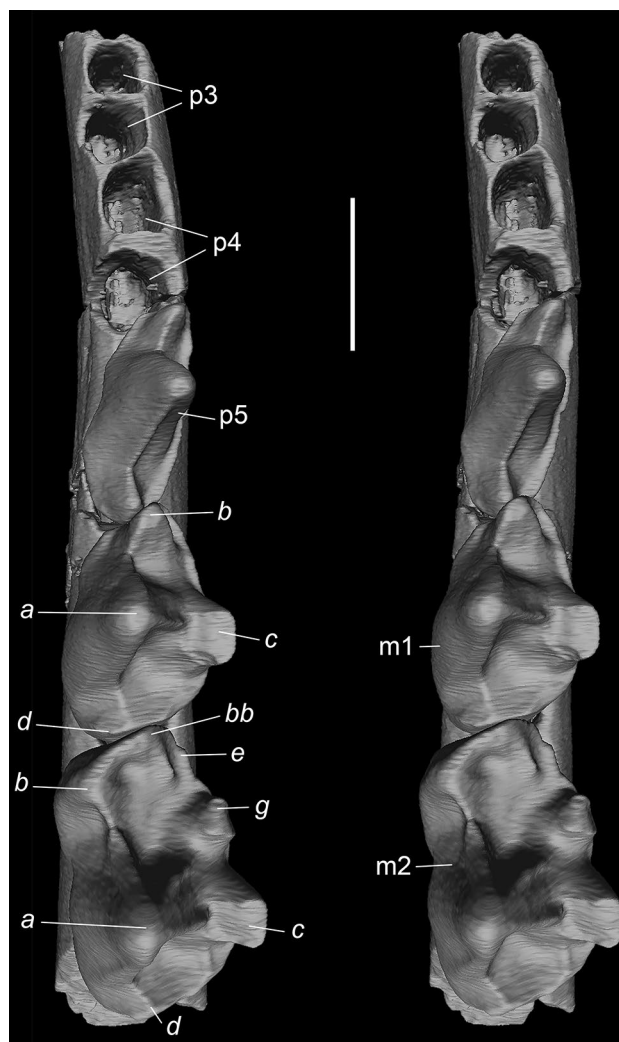
number of premolars to six in *Agilodocodon* and *Microdocodon* (Fig. 5b).

There is some morphological variation between the ultimate permanent lower premolars (p5) in the holotype of *S. rossicum* and PM TGU 120/9–34 (Figs. 1, 2, 3 and 4). On the holotype, the p5 has more pronounced mesial and distal accessory cusps and complete lingual cingulid in contrast with PM TGU 120/9–34 where the accessory cusps are smaller and the lingual cingulid is incomplete. In absence of a larger sample, we do not know the significance of this variation. The deciduous premolars are currently unknown for *S. rossicum*. In *Haldanodon expectatus* from the Upper Jurassic (Kimmeridgian) Guimarota Beds of Portugal, the ultimate deciduous premolar (dp4) is submolariform with a lingual cusp c and without a lingual cusp g, and is replaced by a p3 with a simple crown (Krusat 1980; Martin and Schultz 2023). A similar pattern is observed in the last premolar locus (p4) in *Docodon* spp. from the Upper Jurassic (Kimmeridgian-Tithonian) of the USA (Schultz et al. 2019:

Fig. 3 PM TGU 120/9–34, *Sibirotherium rossicum*, right dentary fragment with c, p1-5, m1-3, and alveolus for ix. Surface rendering based on high-resolution X-ray computed tomography scans, occlusal view (stereopair). Shestakovo 1, Kemerovo oblast, Russia; Ilek Formation, Lower Cretaceous (Aptian). Abbreviations: **c**, canine; **i**, incisor; **m**, molar; **Mg**, Meckelian groove; **p**, premolar. Cusps designated on m1-2. Scale bar equals 1 mm

Fig. 4 PM TGU 16/5–22, holotype of *Sibirotherium rossicum*, left dentary fragment with p5, m1-2, and alveoli for p3-4. Surface rendering based on high-resolution X-ray computed tomography scans, occlusal view (stereopair). Shestakovo 1, Kemerovo oblast, Russia; Ilek Formation, Lower Cretaceous (Aptian). Abbreviations: **m**, molar; **p**, premolar. Cusps designated on m1-2. Scale bar equals 1 mm

fig. 8). Schultz et al. (2019) interpreted the anterior cusp in the ultimate deciduous premolar in *Docodon* as a cusp g, which would not fit the pattern suggested for molariform ultimate premolars in docodontans, so we reinterpret this as variation in the development of the lingual cusp c. In *Agilodocodon* the ultimate lower permanent premolar (p6) has a submolariform crown, with lingual cusp c and lacking a cusp g (Meng et al. 2015: figs. 2F, J and S3), which is congruent with the ultimate deciduous premolar of *Haldanodon* and our interpretation of *Docodon* (above), or in the first molariform of *Sibirotherium* (m1). The similarity of the first molariform tooth of *Sibirotherium* with the ultimate

deciduous premolar in some docodontans in lacking the cusp g could be explained by loss of replacement at the distal premolar position. This implies an ancestral condition with six premolars for *Sibirotherium*, which is postulated under the accelerated character transformation on our phylogenetic tree (Fig. 5a). However, this hypothesis is weakened by the fact that the first molariform tooth lacks cusp g in *Agilodocodon*, which have six lower premolars (Meng et al. 2015). Applying the same mechanism to *Agilodocodon* suggests that its ancestors had seven lower premolars, which is unknown for any of the docodontans. More data is needed to reconstruct the dental replacement pattern and tooth homology in Docodonta.

Fig. 5 Strict consensus of six most parsimonious trees produced by TNT implicit enumeration search showing distribution of character 49 (premolars number) among Docodonta and outgroup taxa. **a**. fast optimization; **b**. slow optimization. Abbreviations: **D**, Docodontidae; **T**, Tegotheriidae
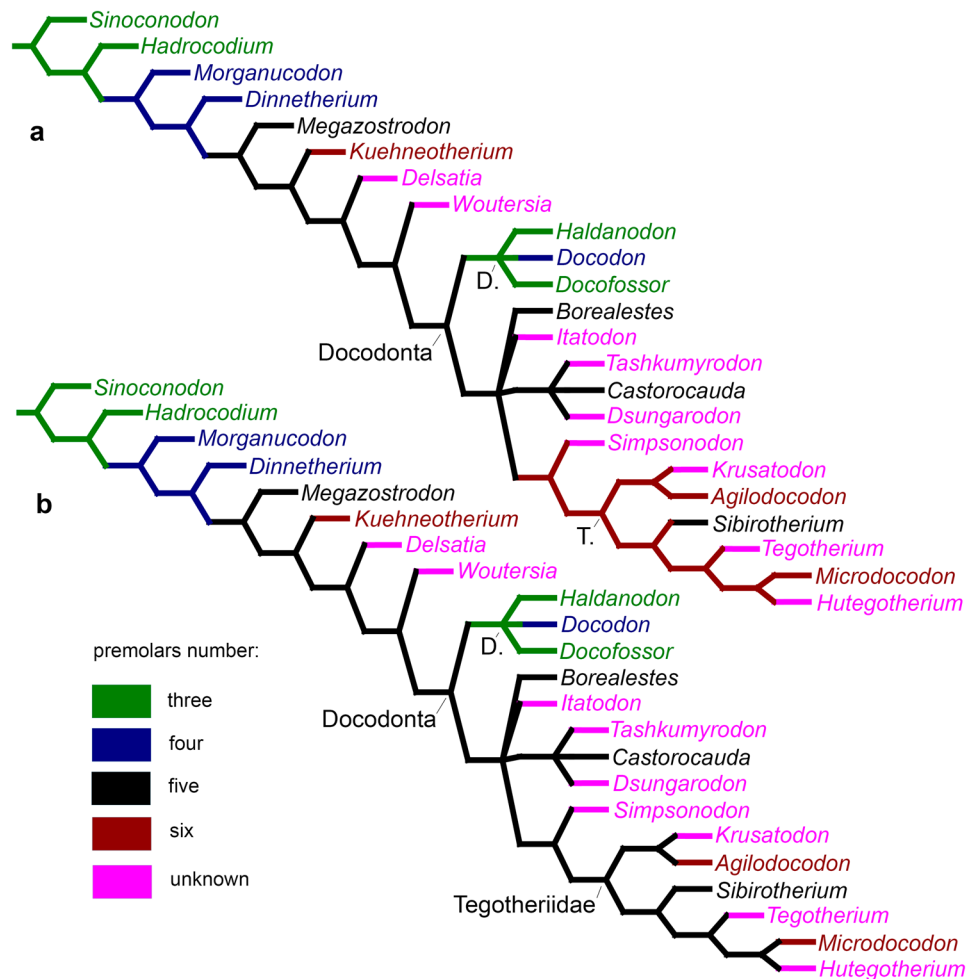
Authors' contributions AA designed the research, acquired funding, segmented and reconstructed 3D surface files from the CT data, and prepared Figs. 1, 2, 3, 4 and 5. AA and AL wrote the main manuscript text. SL organized the fieldwork and curated the specimens. All authors reviewed the manuscript.

Availability of data and materials The fossil specimens have been accessioned into a recognized public collection, where it is available for study. Virtual models of the specimens available upon request.

Declarations

Competing interests The authors declare no competing interests.

References

Averianov AO (2004) Interpretation of the Early Cretaceous mammal *Peraiocynodon* (Docodonta) and taxonomy of some British Mesozoic docodonts. Russ J Theriol 3:1–4. https://doi.org/10.31610/trudyzin/2010.314.2.121

Averianov AO, Lopatin AV, Krasnolutskii SA, Ivantsov SV (2010) New docodontans from the Middle Jurassic of Siberia and reanalysis of Docodonta interrelationships. Proc Zool Inst RAS 314:121–148

Averianov AO, Martin T, Lopatin AV, Skutschas PP, Schellhorn R, Kolosov PN, Vitenko DD (2018) A high-latitude fauna of mid-Mesozoic mammals from Yakutia, Russia. PLoS One 13:e0199983. https://doi.org/10.1371/journal.pone.0199983

Butler PM (1939) The teeth of the Jurassic mammals. Proc Zool Soc Lond 109:329–356. https://doi.org/10.1111/j.1096-3642.1939.tb00719.x

Goloboff PA, Catalano SA (2016) TNT version 1.5, including a full implementation of phylogenetic morphometrics. Cladistics 32:221–238. https://doi.org/10.1111/cla.12160

Ji Q, Luo Z-X, Yuan C-X, Tabrum AR (2006) A swimming mammaliaform from the Middle Jurassic and ecomorphological diversification of early mammals. Science 311:1123–1127. https://doi.org/10.1126/science.112302

Kermack DM, Kermack KA, Mussett F (1968) The Welsh pantothere *Kuehneotherium praecursoris*. J Linn Soc Lond Zool 47:407–423. https://doi.org/10.1111/j.1096-3642.1968.tb00519.x

Kielan-Jaworowska Z, Cifelli RL, Luo Z-X (2004) Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure. Columbia University Press, New York

Kretzoi M (1946) On Docodonta, a new order of Jurassic Mammalia. Ann Hist-Nat Mus Nat Hung 39:108–111

Krusat G (1980) Contribução para o conhecimento da fauna do Kimeridgiano da mina de lignito Guimarota (Leiria, Portugal). IV Parte. *Haldanodon exspectatus* Kühne & Krusat 1972 (Mammalia, Docodonta). Mem Serv Geol Port 27:1–79

Lopatin AV, Averianov AO, Kuzmin IT, Boitsova EA, Saburov PG, Ivantsov AY, Skutschas PP (2020) A new finding of a docodontan (Mammaliaformes, Docodonta) in the Lower Cretaceous of Western Siberia. Doklady Earth Sci 494:667–669. https://doi.org/10.1134/S1028334X20090123

Lopatin AV, Averianov AO, Maschenko EN, Leshchinskiy SV (2009) Early Cretaceous mammals from Western Siberia: 2. Tegotheriidae. Paleontol J 43:453–462. https://doi.org/10.1134/S0031030109040157

Luo Z-X, Martin T (2007) Analysis of molar structure and phylogeny of docodont genera. Bull Carnegie Mus Nat Hist 39:27–47

Luo Z-X, Meng Q-J, Ji Q, Liu D, Zhang Y-G, Neander AI (2015) Evolutionary development in basal mammaliaforms as revealed by a docodontan. Science 347:760–764. https://doi.org/10.1126/science.1260880

Martin T (2005) Postcranial anatomy of *Haldanodon exspectatus* (Mammalia, Docodonta) from the Late Jurassic (Kimmeridgian) of Portugal and its bearing for mammalian evolution. Zool J Linn Soc 145:219–248. https://doi.org/10.1111/j.1096-3642.2005.00187.x

Martin T (2018) Mesozoic mammals – early mammalian diversity and ecomorphological adaptations. In: Zachos FE, Asher RJ (eds) Mammalian Evolution, Diversity and Systematics. De Gruyter, Berlin, Boston, pp 199–299

Martin T, Goin FJ, Schultz JA, Gelfo JN (2022) Early Late Cretaceous mammals from southern Patagonia (Santa Cruz Province, Argentina). Cret Res 133:105127. https://doi.org/10.1016/j.cretres.2021.105127

Martin T, Nowotny M (2000) The docodont *Haldanodon* from the Guimarota mine. In: Martin T, Krebs B (eds) Guimarota – a Jurassic Ecosystem. Verlag Dr. Friedrich Pfeil, Munich, pp 91–96

Martin T, Schultz JA (2023) Deciduous dentition, tooth replacement, and mandibular growth in the Late Jurassic docodontan *Haldanodon exspectatus* (Mammaliaformes). J Mamm Evol. https://doi.org/10.1007/s10914-023-09668-2

Maschenko EN, Lopatin AV, Voronkevich AV (2003) A new genus of the tegotheriid docodonts (Docodonta, Tegotheriidae) from the Early Cretaceous of West Siberia. Russ J Theriol 1:75–81. https://doi.org/10.15298/rusjtheriol.01.2.01

Meng Q-J, Ji Q, Zhang Y-G, Liu D, Grossnickle DM, Luo Z-X (2015) An arboreal docodont from the Jurassic and mammaliaform ecological diversification. Science 347:764–768. https://doi.org/10.1126/science.1260879

Nixon KC (2002) WinClada version 1.00.08. Software published by the author, Ithaca, NY. Available on-line at www.cladistics.org

Panciroli E, Benson RBJ, Fernandez V, Butler RJ, Fraser NC, Luo Z-X, Walsh SL (2021) New species of mammaliaform and the cranium of *Borealestes* (Mammaliformes: Docodonta) from the Middle Jurassic of the British Isles. Zool J Linn Soc 192(4):1323–1362. https://doi.org/10.1093/zoolinnean/zlaa144

Panciroli E, Benson RBJ, Luo Z-X (2019) The mandible and dentition of *Borealestes serendipitus* (Docodonta) from the Middle Jurassic of Skye, Scotland. J Vert Paleontol 39:e1621884. https://doi.org/10.1080/02724634.2019.1621884

Rich THV, Flannery TF, Trusler P, Constantine A, Kool L, Klaveren NA, van, Vickers-Rich P (2001) A second tribosphenic mammal from the Mesozoic of Australia. Rec Queen Victoria Mus 110:1–9

Rowe TB (1988) Definition, diagnosis, and origin of Mammalia. J Vert Paleontol 8:241–264. https://doi.org/10.1080/02724634.1988.10011708

Schultz JA, Bhullar B-AS, Luo Z-X (2019) Re-examination of the Jurassic mammaliaform *Docodon victor* by computed tomography and occlusal functional analysis. J Mamm Evol 26:9–38. https://doi.org/10.1007/s10914-017-9418-5

Sigogneau-Russell D (2003) Docodonts from the British Mesozoic. Acta Palaeontol Pol 48:357–374

Sigogneau-Russell D, Kielan-Jaworowska Z (2002) Mammals from the Purbeck Limestone Group of Dorset, southern England. Spec Pap Palaeontol 68:241–255

Simpson GG (1928) A Catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum. British Museum (Natural History), London

Swofford DL (2002). PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0. Sunderland, Sinauer Associates.

Tatarinov LP (1994) On an unusual mammalian tooth from the Mongolian Jurassic. Paleontol Zh 2:97–105 [In Russian]

Waldman M, Savage RJG (1972) The first Jurassic mammal from Scotland. J Geol Soc 128:119–125. https://doi.org/10.1144/gsjgs.128.2.0119

Zhou C-F, Bhullar B-AS, Neander AI, Martin T, Luo Z-X (2019) New Jurassic mammaliaform sheds light on early evolution of mammal-like hyoid bones. Science 365:276–279. https://doi.org/10.1126/science.aau934