
Supplementary information

A Jurassic mammaliaform swimmer and transformation of the mammalian pharynx

In the format provided by the
authors and unedited

Supplementary Information
for
A Jurassic Mammaliaform Swimmer and Transformation of the Mammalian Pharynx
(Nature Ms. 2026-04-10515B)

Yikun Li¹, Peishu Li², April I. Neander³, Honggang Zhang⁴, Chang-Fu Zhou^{5,*}, Thomas Martin^{7,*}, & Zhe-Xi Luo^{3,*}

1- College of Paleontology, Shenyang Normal University, Shenyang, Liaoning Province, 110034, China

2 - Department of Biomedical Sciences, Heritage College of Osteopathic Medicine, Ohio University, Athens, OH 45701 USA

3- Department Organismal Biology and Anatomy, The University of Chicago, Chicago, IL 60637 USA

4 – Paleontological Museum of Liaoning, Shenyang Normal University, Shenyang, Liaoning Province, 110034, China

5- College of Earth Science and Engineering, Shandong University of Science and Technology, Qingdao, Shandong Province 266590 China

6 - Bonner Institut für Organismische Biologie, Abteilung Paläontologie, Universität Bonn, 53115 Bonn, Germany

*Co-Corresponding Authors:

Professor Chang-Fu Zhou (zhoucf528@sdust.edu.cn)

Professor Thomas Martin (tmartin@uni-bonn.de)

Professor Zhe-Xi Luo (zxluo@uchicago.edu)

Supplementary Information Guide
Table of Contents

- (1) Acknowledgement
- (2) Systematic Paleontology (including stratigraphy)
- (3) Differential Diagnosis and Comparison to Mammaliaforms
Body Mass Estimates
- (4) Description of Teeth
- (5) Interpretation of Dental Occlusion and Inference of Feeding Function
- (6) Hyoids Apparatus and Palato-pharyngeal Anatomical Reconstruction
- (7) Preliminary Description of Postcranial Skeleton

Forelimb and Manus

Humerus

Ulna and Radius

Carpals, Metacarpals and Phalanges

Vertebrae, Ribs and Ribcage

Vertebrae and Dorsal Ribs

Hemal Arches (Chevron bones) in Caudal Vertebral Column –

Thoracic Ribcage Reconstruction

Imbricated Costal Rib Plates

Re-interpretation of the Plated Ribs of *Castorocauda*

Comparative Morphology of Ribcages of Monotremes

Osteological Reconstruction of the Pelvis

Composite Pelvis Reconstruction

- Acetabulum, Obturator Foramen and Pelvic Symphysis
- Comparison on General Pelvic Features
- Ilium, Ischium and Epipubis
- Pelvic Musculoskeletal Reconstruction
 - (1) Iliopsoas Muscle
 - (2) Psoas minor Muscle
 - (3) Pectineus Muscle
 - (4) Ambiens Muscle
- Reconstruction of Soft Tissue and Muscular Features of the Tail
 - Interpretation of Soft Tissue Features of the Tail
 - Tail Shape
 - Interpretation of Muscle Attachments
- Hindlimb and Pedal Osteology
 - Femur, Tibia and Fibula
 - Interpretation of Tibia and Fibula Muscle Attachment
- Astragalus, Calcaneum and Upper Ankle Joint
 - Astragalus
 - Calcaneus
 - Astragalus-Calcaneus Size and Position
 - Other Tarsal Bones and Os calcaris
 - Cuboid Functional Morphology
 - Metatarsals, Phalanges and Digit-Rays
 - Hindlimb Posture
 - Posture of Knee Joint
 - Pedal Posture
 - Mobility of the Upper Ankle joint
- (8) Functional Interpretation of Musculoskeletal Morphology for Swimming
 - Tail Morphology
 - Implications for Tail Function
 - Pelvic Girdle Functional Interpretation
 - Implications for Pedal Function
 - Hindlimb and Pedal Function in Swimming
 - Dual Fossorial–Semiaquatic Function of Docodontans
 - Limitation of Inference
- (9) Phylogenetic Character List for Analysis of *Megacauda* among Docodontans
- (10) Phylogenetic Matrix: Nexus file
- (11) Maximum Parsimony and Bayesian Analyses: Comments & Summary
- (12) PAUP Search Log, Branch Support Summary; Bayesian Analysis Consensus Tree
- (13) References cited in Supplementary Information

Supplementary Videos

Video S1: *Megacauda sungei* gen et sp. nov. (Mammaliaformes; Docodonta) skull, mandibles, middle ear, hyoid bones and palato-pharyngeal structures.

Video S2: Anatomical restoration of pelvic structure of the docodontan *Megacauda*.

(1) Acknowledgement

Foremost we are indebted to Professors Sun Ge, Ning Tian and the leadership of the Paleontological Museum of Liaoning (PMOL) and Shenyang Normal University (Shenyang, Liaoning, China) for proposing the research collaboration on this fossil. For assistance with X-Ray Fluorescence imaging of the soft tissue preservation of this fossil, we would like to thank Professor Quanguo Li of China University of Geosciences-Beijing. For CT scanning of the fossil specimens, we are indebted to Professor Qingfang Fang of China University of Geosciences (Beijing) for his meticulous work to scan the fossil specimen.

Research work by Changfu Zhou (SDUST) was supported by funding from the National Natural Science Foundation of China (42161134003), Taishan Scholar Program of Shandong Province (tstp20240514). Research by Thomas Martin (Uni-Bonn) was supported by Deutsche Forschungsgemeinschaft (DFG). CT scanning of comparative specimens in Zhe-Xi Luo Lab was supported by National Science Foundation (US-NSF) (NSF BRS-TCN 1702421), comparative studies on mammalian hyoids was supported by NSF (NSF-IOS 2315501). Peishu Li was supported by National Science Foundation (NSF-IOS 2315501) and by Ohio University Heritage College of Osteopathic Medicine. For access to comparative specimens of extant mammals at the Field Museum of Natural History (Chicago), we are grateful for the support of Drs. Bruce Patterson, Lawrence Heaney, Adam Ferguson. We also thank Profs. Qing-Jin Meng and Yugang Zhang, and Dr. Di Liu for us to examine the fossil mammals of National Natural History Museum of China (Beijing).

We would like to thank Prof Diying Huang for his discussion with us about Daohugou geological section and stratigraphy, Dr Elsa Panciroli for discussion on postcranial anatomy of docodontans, Prof Jia Jia for discussion about Xiayingzhi locality and field geology. During this work, we benefited from extensive discussion on mammalian cranial and hyoid structures with Professors Callum F. Ross (UChicago), Bhart-Anjan S. Bhullar (Yale), on morphologies of fossil docodontans with Dr. Elsa L. Panciroli (National Museum of Scotland, UK) and Dr. Julia A. Schultz (Universität Bonn), on phylogenetic relationships of Mesozoic mammaliaforms, with Professor Guillermo W. Rougier (University of Louisville) and Professor Alexander O. Averianov (Russian Academy of Sciences). We are very thankful for Professors Susan Hand, Rebecca German, and two anonymous reviewer for constructive feedbacks and suggestions for improvement. However, we emphasize any potential weakness or errors of the manuscript remain to be responsibilities of the authors.

Institutional Abbreviations

BMNH – Beijing Museum of Natural History (Beijing, China)
FMNH – Field Museum of Natural History (Chicago, USA)
IVPP – Institute of Vertebrate Paleontology and Paleoanthropology (Beijing, China)
PMOL – Paleontological Museum of Liaoning (Shenyang, China)
SDUST – Shandong University of Science and Technology (Qingdao, China)

(2) Systematic Paleontology (Expanded)

Clade Mammaliaformes (emended from Ref-71 Rowe 1988)

Clade (Order) Docodonta (Ref-72 Kretzoi 1946, emended by Ref-1 Kielan-Jaworowska et al. 2004)

Family Megacaudidae familia nov.

Zoobank LSID: urn:lsid:zoobank.org:act:20A95F1F-F06A-49B3-8DD8-6701704AD5D5

Type Genus: *Megacauda* gen. nov.

Diagnosis: Docodontans with sectorial posterior lower premolars and anterior lower molars; lower premolars and m1 with tall, trenchant and recumbent primary cusp a on bilaterally compressed crowns, middle molars with hypertrophied V-notch between cusps b and a. Upper premolars and M1 with triangular crown base and tall and trenchant cusp A that is also recumbent posteriorly in lateral view. Molars 2-4 with quadrotubercular crown characterized by a V-shaped notch between Cusps A and C, and a posterolingual Cusp Y and a constricted waist between Cusps C and Y. Postcranial skeletal apomorphies include wide proximal caudal vertebrae with bifurcate transverse processes, and bilaterally wide and dorsoventrally compressed caudal vertebrae in mid region of tail, and a widened soft-tissue outline of the tail.

Included genera: In addition to the type genus, *Castorocauda* Ji, Luo, Yuan and Tabrum 2006, from the Middle Jurassic of the Inner Mongolia Region of China.

Comments. Megacaudidae is recognized as a family because the two included genera are distinct, characterized by a list of synapomorphies of the lower dentition (as listed in the diagnosis). The included genera possess a list of derived skeletal apomorphies: an elongate hind foot relative to femur and tibia; pes with elongated lateral digit rays and digit rays asymmetrical due to elongation; widened caudal vertebrae related to the broad and flattened tail, all features related to swimming locomotion. The likely sister taxon of the Megacaudidae is *Dsungarodon zuoi* from western China (Xinjiang) according to our phylogenetic analysis. *Dsungarodon* is recovered in our phylogenetic analysis to be closely related to the Megacaudidae (*Megacauda* and *Castorocauda*), by its apomorphic molar features: an enlarged cusp b, a prominent V-notch between cusps b and a, and a reduced distal part of the ultimate lower molar. However, the published information for *Dsungarodon* (“*Acuodulodon*” Ref-73 Hu et al. 2007, synonymized to *Dsungarodon* by Ref-74 Martin et al. 2010) is limited to isolated teeth (Ref-73 Hu et al. 2007; Ref-74 Martin et al. 2010), and a partially preserved mandible (Ref-73 Hu et al. 2007), the skull and postcranial material of this fossil have not been described. The putative sister-group relationship of *Dsungarodon* needs to be tested by more complete fossils of *Dsungarodon* (= “*Acuodulodon*”).

Megacauda gen. nov.

Zoobank LSID: urn:lsid:zoobank.org:act:858D78B8-9973-4C95-8286-CA05B77EFBBC

M. sungei sp. nov.

Zoobank LSID: urn:lsid:zoobank.org:act:E1D7A965-E547-4705-8696-E63F672564ED

Etymology: Generic name “*Megacauda*” in reference to the broad tail and widened caudal vertebrae. Species name “*sungei*” in honor of Professor Sun Ge, for his contribution in paleontology, and for his support of studies of Mesozoic mammals.

Holotype Specimen: PMOL-AM00026A/B of Paleontological Museum of Liaoning, Shenyang, Liaoning Province, China, a nearly complete skeleton including most of the skull, complete dentition, and preservation of fur and scales (**Fig. 1 and Extended Data Figs. 1-10**); the flattened skeleton, skull and associated soft tissue features are split into the part A (**Extended Data Fig. 1**) and counter-part B (**Extended Data Fig. 2**) preserved on two matching mudstone slabs. On the main-slab PMOL-AM00026A (Fig. 1 and Extended Data Fig. 1), the skull is compressed into the slab but its dorsal aspect (skull roof) is exposed on the bedding plane. On this slab, the thoracic ribcage and the associated dorsal vertebrae are compressed, and the right side of the skeleton is exposed laterally and also ventrolaterally. The sacral vertebrae, the pelvis, the two hindlimbs, and caudal vertebrae are mostly exposed ventrally. The counter-slab PMOL-AM00026B contains less bone materials than the main slab, but the counter-slab shows the matching outline of the preserved bones in XRF (X-Ray Fluorescence) photographs, which are helpful to supplement and corroborate the bones preserved on the main-slab. The holotype is a fully grown adult, characterized by adult permanent teeth and absence of any replacing teeth from the upper and lower jaws by CT scanning, by the closed root-tips of the lower m5 (ultimate molar) and upper M4 (ultimate upper molar), and by adult mandibular features (**Extended Data Figs. 3-4**).

Diagnosis: Dental formula Upper I5.C1.P4.M4/Lower i4.c1.p5.m5 (**Fig. 3; Extended Data Figs. 3 – 6**), characterized by the upper molars transversely widened with lingual cusps X, and Y (M2-4), by the lower molars with prominent lingual cingulid cusp g in addition to an alignment of primary cusps b, a and d on the buccal side of the crown, and by a triangulation of cusps b-a-c which is best developed on m3 and m4. This is a diagnostic (classic) cusp pattern originally recognized by Butler (Ref-20 Butler 1988, Ref-61 Butler 1997) as reviewed by Luo & Martin (2007) (Ref-17). Other typical docodontan characters are the anteriorly placed cusp g on molars, which is also enlarged on lower molar 3 (m3) of *M. sungei* holotype (**Extended Data Fig. 5, 6**). By these molar characters, *M. sungei* is distinct from non-docodontan mammaliaforms. *M. sungei* is unique among all mammaliaforms preserved with upper canines by a hypertrophied upper canine with three fully divided canine roots that has a posterior groove running from the crown to its posterior roots. Its upper and lower canines show over-erupted patterns in which about a half of the root height is exposed beyond the alveolar margin of the canine sockets according to Jones (2023) (Ref-23). More description of this dental pattern will be presented below). *M. sungei* is similar to *Castorocauda lutrasimilis* in development of sectorial crowns on its posterior premolars and the bilaterally compressed M1/m1. These sectorial teeth are characterized by a trenchant and recurved main cusp (cusp a) and a serrated posterior shearing crest formed by cusps a-c-d. Both *M. sungei* sp. nov. and *C. lutrasimilis* are distinguishable from all other docodontans and other mammaliaforms by the sectorialized ultimate premolars and anterior molars.

Megacauda sungei differs from *Castorocauda lutrasimilis* in a list of characters of premolars and molars (Supplementary Table 1; **Extended Data Fig. 6**) including the following: the ultimate premolar shows a single cusp c on the p5 posterior crest in *Megacauda* (p5 = ultimate premolar), in contrast to two cusps c1 and c2, on the p6 posterior crest in *Castorocauda* (p6 = ultimate premolar). Primary cusp a of p5 is taller and more reclined in *Megacauda* than in *Castorocauda* (**Extended Data Fig. 6-b**). For m1, *Megacauda* is characterized by a single cusp posterior to the primary cusp a, in

contrast to *Castorocauda* with two cusps (c1 and c2) (**Extended Data Fig. 6-c**). For m2: cusp g is large and distinct in *Castorocauda* but absent in *Megacauda* (related to a partial sectorialization of m2 of *Megacauda*); the m2 distal basin is well developed in *Castorocauda* but absent in *Megacauda* (**Extended Data Fig. 6-e**). For m3, cusps b and g are larger and more distinct in *Castorocauda*, than the reduced cusps b and g of the same tooth in *Megacauda*; the m3 distal basin is well developed in *Castorocauda* but absent in *Megacauda*. *Castorocauda* shows larger cusp c and the fully formed distal basin on m4 in contrast to reduced cusp c and absence of the distal basin on m4 of *Megacauda*. For the ultimate molar (m5), *Megacauda* shows a more laterally compressed distal half of m5, than in *Castorocauda* (**Extended Data Fig. 6 - e**). Among all molariform loci, the most prominent and consistent dental difference between *Megacauda* and *Castorocauda* is that the distal basins are well developed in molariforms of *Castorocauda* but these are absent or incompletely formed in corresponding molariforms of *Megacauda* (details in **Extended Data Figure 6 - e**).

Supplementary Table 1: Differences of Dental Characters of *Castorocauda* and *Megacauda* (illustrated in **Extended Data Fig. 6**)

Tooth Loci	Dental Characters	<i>Castorocauda</i>	<i>Megacauda</i>	illustration
Ultimate premolar	difference in posterior crest cusp(s)	double cusps c1 and c2 on p6 (ultimate premolar) [¶]	single cusp c on p5 (ultimate premolar) [¶]	ED Fig.6-b
	orientation of cusp a	more vertical	more reclined [§]	
m1	difference in posterior crest cusp(s)	double cusps c1 and c2 on m1 [¶]	single cusp c on m1	ED Fig. 6-c
	orientation of cusp a	more vertical	more reclined [§]	ED Fig. 6
m2	mesial end shape/outline	rectangular	bilaterally compressed [§]	ED Fig. 6
	cingular cusp g	present	absent [§]	ED Fig. 6
	cusp c	large	small [§]	ED Fig. 6
	distal occlusal basin	present [¶]	absent	ED Fig. 6
m3	cingulid cusp g	large	small [§]	ED Fig. 6
	entoflexus	narrow and distinct	wide and shallow [§]	ED Fig. 6
	distal occlusal basin	present [¶]	absent	ED Fig. 6
m4	cingulid cusp e	present and distinct	reduced [§]	ED Fig. 6
	entoflexus	narrow and distinct [¶]	wide and shallow	ED Fig. 6
	distal occlusal basin	present [¶]	absent	ED Fig. 6
	cusp c	large	reduced [§]	ED Fig. 6
m5	cusp e	present	reduced [§]	ED Fig. 6
	anterior	fully formed [¶]	incomplete	ED Fig. 6

¶ - Character state of *C. lutasimilis* is more derived in comparison to other mammaliaforms

§ - Character state of *M. sungei* is more derived, in comparison to other docodontans

M. sungei sp. nov. and *C. lutasimilis* also show proportional differences in cheek teeth and mandibles. *M. sungei* has a total of 10 postcanines (p5 and m5) in contrast to a total of 11 postcanines (p6 and m5) in *C. lutasimilis*. The lower jaw is 20% longer in *M. sungei* sp. nov. than in *C. lutasimilis*. Taken together the information on cheek count and jaw length, there is clearly a proportional difference of number of teeth and jaw length between *M. sungei* sp. nov. and *C. lutasimilis*. Given that the crowns are preserved only on the ultimate premolar (p6) and five molars in the single specimen of *Castorocauda*, a more informative taxonomic separation of *Castorocauda* from the new genus *Megacauda* will be based on the comparative differences of these teeth (Supplementary Table 1).

Fortunately we can demonstrate the different characters on each of these teeth. We interpret that differences in dental character are more than sufficient for establishing *Megacauda* as a new genus.

Furthermore, the diagnosis of *M. sungei* sp. nov. from *C. lutasimilis* is supported by several postcranial characters of caudal vertebrae and hindlimb that are distinctly different between these taxa: (1) In the caudal vertebral region (**Fig. 1**), *M. sungei* sp. nov. has one “butterfly-shaped” proximal caudal vertebra (Ca5) in which the paired anterior transverse processes are longer than the paired posterior processes. This is in contrast to *C. lutasimilis* that has two “butterfly-shaped” vertebrae (Ca5 and Ca6). These butterfly-shaped caudals with longer anterior transverse process and shorter posterior process are a prominent caudal vertebral type marking the vertebral transitioning from the pelvic caudals to post-pelvic caudals. (2) Caudals in Ca7-Ca9 positions show more distinct “transverse H-shaped” or “bifurcate” morphology with more gracile (and pointed) transverse processes in *Castorocauda*, than in *Megacauda*. In the latter, caudals in Ca6-Ca9 positions show more rounded transverse process (**Fig. 1**). (3) The parafibular process of the fibula (**Extended Data Fig. 8**) shows a distinctly rectangular outline, in contrast to the round outline of the parafibula of *Castorocauda* – the latter parafibular shape is more common in other docodontans (see *Agilodocodon* – **Extended Data Fig. 8-d**). Further skeletal differences of *Megacauda sungei* gen. et sp. nov. and *Castorocauda lutasimilis*, and their differences from other mammaliaforms will be presented below in full differential diagnosis and description of its skeleton.

Locality and Stratigraphy: The holotype specimen (PMOL-AM00026A/B) of *Megacauda sungei* gen. et sp. nov. was found at the Xiayingzi locality of the Daohugou Village area, Ningcheng County of Inner Mongolia Autonomous Region of China. The locality of *M. sungei* type specimen is about 1.7 km away from the locality of the *Castorocauda lutasimilis* type specimen at the Daohugou Fossil Museum (the Daohugou Museum Locality) (Ref-13 Ji et al. 2006) (**Supplementary Figure 1 on Stratigraphy**).

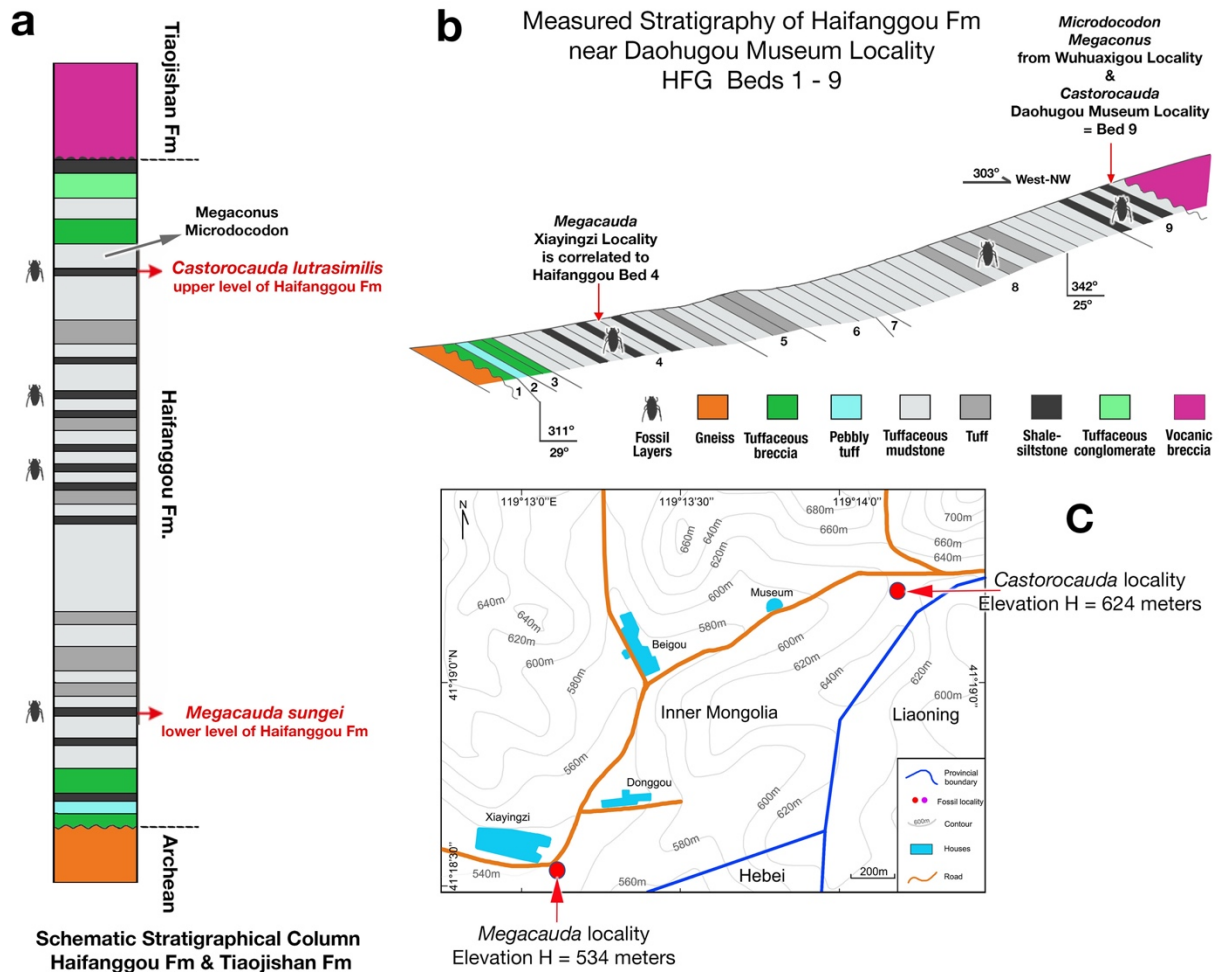
Rocks of the Daohugou Museum Locality and nearby areas are more fossiliferous and yielded several mammaliaform fossils, feathered dinosaurs, and abundant arthropod fossils. Thus the areas around Daohugou Museum were extensively excavated for fossil search. The more extensive rock outcrops are main basis for local stratigraphic correlation (Ref-16 Huang et al., 2016; Ref-75 Ren et al. 2002). The outcrops at the Xiayingzi Locality are mainly dark grey and dense laminated mudstones deposited in lacustrine environments (Ref-15 Huang et al. 2016; Ref-75 Ren et al. 2002; Ref-76 Huang 2019). The Xiayingzi Locality produced abundant salamander fossils (Ref-14 Jia et al. 2021) and relatively abundant anostracan arthropods (our team’s field observation) but is devoid of conchostracan fossils common at the Daohugou Museum Locality in higher stratigraphic levels of the Haifanggou Formation Beds.

Field geological observations by Ren et al. (2002) (Ref-75) and Huang et al. (2016) (Ref-16) suggest that the Xiayingzi outcrops (yielding *M. sungei* type specimen) are lower in the stratigraphic position, than the fossiliferous beds of the Daohugou Museum Locality (yielding *C. lutasimilis* type specimen) (**Supplementary Figure a**). This interpretation is also supported by Jia et al. (2021) (Ref-14) and by our team’s field geology work, on the basis of three lines of field evidence (**Supplementary Figure 1**):

(1) The fossil-bearing layers of the Haifanggou Formation (“Daohugou Beds”) have a general occurrence that is inclined to the north with 25°-29° dip angle (Ref-15 Huang et al. 2016; Ref-75 Ren et al. 2002). See our schematic illustration in **Supplementary Figure b** of the consensus of previous field

studies is that, given the dip angle and orientation of these beds inclined to the north (Ref-15 Huang et al. 2016; Ref-75 Ren et al. 2002), the sites in more southerly locations are geologically older than the more northerly locations (**Supplementary Figure 1-b**).

(2) By ground elevation, the outcrops at lower ground elevation, such as the Xiayingzi Site at elevation of 534 meters (H=534 or “Height” 534 meters of topographical elevation), are stratigraphically lower in the Haifanggou Formation sedimentary sequence, than the Daohugou Museum Site (at H=624, or “Height” 624 meters of topographical elevation; **Supplementary Figure 1-c**).



Supplementary Figure 1

Stratigraphical Separation of the *Megacaula* locality (Bed 4) and the *Castorocaula* Locality (Bed 9) by 60-meter thickness of section in the Haifanggou Formation by previous estimates (Ren et al. 2002 and Huang et al. 2016)

Our field observation marked on the schematic stratigraphical column (**1-a**), and on approximate geological section (**1-b**) summarized from Ren et al. (2002) (Ref-75) and Huang et al. (2016) (Ref-15). Both *Megacaula* locality and *Castorocaula* Locality marked on a simplified countour map (**1- c**)

(3) By lithological Differences: Rocks and fossils of the Xiayingzi locality and the Daohugou Museum locality show contrasting lithographical characteristics. The fossiliferous rocks of the Xiayingzi, which are assigned to Bed 4 of Haifanggou Formation, according to division of sediment beds of Huang et al.

(2016) (Ref-15), are harder mudstones-shales in thinner lamination. The soft tissue outline area of vertebrates (both salamanders and *Megacauda*) are black to dark grey (**Extended Data Figs 1 and 2**).

By contrast, the most fossiliferous beds at Daohugou Museum Locality belong to Bed 9 of Haifanggou Formation in the outcrops of the DHG Museum Locality. The laminated mudstone of Bed 9 in the outcrop of the Daohugou Museum site is softer with variegated colors from light grey to reddish brown. The preserved soft tissues of the *Castorocauda* type specimen are in grey outline, in which the carbonized hairs and scales are black to grey or brown in color. The specimens of the docodontans *Microdocodon gracilis* and *Megaconus mammaliaformis* from the Wuhuaxigou site are embedded in rocks of light grey color, and their soft tissue outlines are lighter in coloration than the surrounding rock. This color pattern is opposite to the patterns of *Megacauda* and *Castorocauda*.

In the geological outcrop near the Daohugou Museum Locality, Bed 4 (the lower “*Megacauda* horizon”) and Bed 9 (the higher “*Castorocauda* horizon”) are separated by over 60 meters of sediments, in comparison to the thickness of 90 meters of the entire Haifanggou Formation in the outcrops in Daohugou area (Supplementary Stratigraphy Figure b). We highlight the major stratigraphical difference of these two taxa.

The lithological difference is consistent with a moderately abundant presence of the anostracan arthropod fossils and the absence of any conchostracans in the Xiayingzi Locality outcrops (lower in geological section). This is in contrast to the common and abundant specimens of *Euestheria luanpingensis* in the outcrops of the Daohugou Museum Locality (higher in geological section), according to the studies of the sedimentology and field stratigraphy by Huang and colleagues (Ref-15 Huang et al. 2016; Ref-76 Huang 2019; Ref-77 Huang et al. 2015) and Wang et al. (2019) (Ref-78). By our field stratigraphical correlation, the holotype of *Megacauda* is from Bed 4 of the Haifanggou Formation (Ref-15 Huang et al., 2016). Bed 4 is below and separated by more than 60 meters of geological section, from Bed 9 of Haifanggou Formation that yielded the holotype of *Castorocauda* at the Daohugou Museum Locality. *Megacauda* is geologically older than *Castorocauda*.

The Xiayingzi locality (yielding *M. sungei* specimen) and the Daohugou Museum Quarry (yielding *C. lurasimilis* type specimen) are also separated respectively, by 10 to 11 kilometers, from the Wuhuaxigou site that yielded the docodontan *Microdocodon gracilis* (Ref-8 Zhou et al. 2019), and *Megaconus mammaliaformis* (Ref-79 Zhou et al. 2013). These three fossil sites are all parts of the Haifanggou Formation (Ref-14 Jia et al. 2021), or the Jiulongshan Formation (Ji et al. 2006). According to the interpretation by Huang (2019) (Ref-76), the Tiaojishan Formation is superpositional to the Haifanggou Formation (**Supplementary Figure 1-a**). We follow Huang et al (2016) (Ref 15) in treating Haifanggou and Tiaojishan as separate formation. However we are cognizant that the Haifanggou Formation and the Jiulongshan Formation were treated by some other workers as alternative names for the formations, dependent on the regional lithostratigraphic formation name preferred by the investigators. The fossil biota of the Daohugou Beds are broadly considered to be part of the Jurassic Yanliao Biotas of northeastern China (Ref-14 Ji et al. 2021; Ref-77 Huang et al. 2015; Ref-80 Xu et al. 2016).

Verification of Provenance and Field Stratigraphy: The specimen of *Megacauda sungei* was acquired from a third party by the Paleontological Museum of Liaoning at Shenyang Normal University. In 2015, the co-author Chang-Fu Zhou of this study and a team from the Paleontological

Museum of Liaoning investigated the provenance of the fossil. The team were able to re-trace the specimen to its source, and to confirm that the fossil is from an abandoned excavation well at the Xiayingzi site. By our team's firsthand fieldwork on the geological outcrops at Xiayingzi locality, we have now established that the Xiayingzi rock outcrops clearly belong to Bed 4 of Haifanggou Formation at the Daohugou Museum Locality according to the latest stratigraphy (Ref-15 Huang et al 2016) by both lithological similarity and the relatively abundant anostracan fossils (arthropods). In the geological section of Daohugou Museum locality (1.7 km away from Xiayingzi), Bed 4 of Haifanggou Formation is lower than the Bed 9 of the Haifanggou by more than 60 meters in stratigraphical thickness (Supplementary Stratigraphy figure a, b). Bed 9 at the Daohugou Museum site has so far yielded the *Castorocauda* holotype and possibly also the *Volaticotherium* fossil (**Supplementary Figure 1 b**). Here we interpret that the rock in the locality of *Megacauda* is geological much older than that of *Castorocauda*.

Geological Age: The “Daohugou” Beds of the Haifanggou Formation (= “Jiulongshan Formation” of some other authors) of the Daohugou area of Inner Mongolia are dated to be between 164 and 168 ma (mega annum) by Liu Yongqing and colleagues (Ref-81 Liu et al. 2006, Ref-82 Liu et al. 2012), which has been accepted by others (Ref-80- Xu et al. 2016). Elsewhere in the neighboring Beipiao area of Liaoning Province, the Haifanggou Formation has been dated to be 166.7 ± 1.0 Ma by $^{40}\text{Ar}/^{39}\text{Ar}$ dating of sanidines (Ref-83 Chang et al., 2014), or to be between 167.1 ± 0.9 Ma to 161.7 ± 1.9 Ma by U-Pb dating of zircons (Ref-76 Huang 2019). Based on these geochronology studies, we adopt an estimate that the holotype of *Megacauda sungei* to be about 165 million years old. The current consensus is that most of the Daohugou Beds are of Middle Jurassic (Callovian) Age (Ref-80 Xu et al. 2016).

Associated Vertebrate Fauna: The associated fossil vertebrates in the Xiayingzi locality are primarily specimens of the salamander *Neimengtriton daohugouensis* (Ref-14 Jia et al. 2021) in addition to *Megacauda sungei* gen. et sp. nov. So far, the *Megacauda* holotype is the first mammaliaform specimen from the Xiayingzi quarry. But in the area of the Daohugou Museum locality, a much larger assemblage of fossil vertebrates have been discovered from a higher stratigraphic level (the main fossiliferous beds of Ref-15 Huang et al. 2016). In addition to the docodontan *Castorocauda* (Ref-13 Ji et al. 2006), there are also the eutriconodontan *Volaticotherium* (Ref-84 Meng et al. 2006), and the pseudotribosphenid *Pseudotribos* (Ref-21 Luo et al. 2007) from the Daohugou Museum Locality.

The Xiayingzi Locality (yielding *M. sungei* specimen) and the Daohugou Museum Locality (yielding *C. lurasimilis* type specimen) are also separated respectively from the Wuhuaxigou site that yielded the docodontan *Microdocodon gracilis* (Ref-8 Zhou et al. 2019), and *Megaconus mammaliaformis* (Ref-79 Zhou et al. 2013). *Feredocodon chowi* reported by Mao et al (2024) (Ref-22) is likely also from Wuhuaxigou Locality by its lithology. The Wuhuaxigou Locality is either slightly higher stratigraphically than Daohugou Museum Locality, or about the same as Bed 9 (the “*Castorocauda*” horizon) (sensu Ref-15 Huang et al. 2016). These three sites (Xiayingzi, Daohugou Museum and Wuhuaxigou) are all parts of the Haifanggou Formation (Ref-14 Jia et al. 2021), or the Jiulongshan Formation (Ref-13 Ji et al. 2006), or the Tiaojishan Formation (Ref-77 Huang et al. 2015), depending on the regional lithostratigraphic formation name preferred by the investigators. The fossil biota of the Daohugou Beds in Ningcheng County of Inner Mongolia and in Jianchang County of Liaoning and Qinglong County of Hebei Province are broadly considered to be part of the Jurassic Yanliao Biotas of

northeastern China by all investigators (Ref-14 Jia et al. 2021; Ref-77 Huang et al. 2015; Ref-80 Xu et al. 2016; Ref-81 Liu et al. 2006, Ref-82 Liu et al. 2012).

(3) Full Differential Diagnosis and Comparison to Mammaliaforms

Megacauda sungei gen. et sp. nov. is distinguished from all Mesozoic mammaliaforms in possessing three fully divided roots of the upper canine. *Megacauda sungei* can be distinguished from the other two docodontans from the Middle Jurassic Daohugou sites: *Castorocauda lutasimilis* and *Microdocodon gracilis*. Among docodontans, *M. sungei* and *C. lutasimilis* are more similar to each other in their sectorial cheek teeth, thus different from other docodontans (**Extended Data Fig. 6**), and also from all other Mesozoic mammaliaforms, in development of a series of sectorial premolars and anterior molars. These teeth are bilaterally compressed, trenchant and recurved in lateral profile. Their crowns show a longer and more convex anterior crest and a shorter and straight posterior margin of the primary cusp a. Cusps a, c, and d are aligned to form a serrated posterior shearing crest on the sectorial crown (Extended Data Fig. 5). These features are unique among Mesozoic mammaliaforms, although known in Cenozoic mesonychia eutherians that are carnivorous ungulates.

The most prominent and consistent dental difference between *Megacauda* and *Castorocauda* is that the distal basin is well developed in molariforms (m2-m4) in *Castorocauda* but this basin is absent in corresponding molariforms of *Megacauda* (details in **Extended Data Figure 6 d and 6 e**). Overall, the molariforms are also more compressed bilaterally (smaller width-to-length ratio) in *Megacauda*, than in *Castorocauda*. *M. sungei* shows a much greater degree of reduction in the posterior part of the ultimate molar (m5) with a short and featureless slope posterior to cusp a, in contrast to the m5 of *C. lutasimilis* that still retains the distinctive lingual cingulid that wraps around to the distolingual side of the ultimate molar. *M. sungei* and *C. lutasimilis* are different in the premolar count. As mentioned above, the *M. sungei* holotype has five lower premolars on a jaw that is 20% longer, in contrast to the *C. lutasimilis* type specimen that has six premolars and five molars on a jaw that is 20% shorter, meaning that each lower postcanine of *Megacauda* is larger than its corresponding tooth of *Castorocauda*. Both *Megacauda sungei* holotype and *Castorocauda lutasimilis* holotype are adult specimens and neither is affected by reduction/loss of the anterior premolar(s) with ageing, a pattern known to affect other docodontans (Ref-25 Schultz et al. 2017; Ref-65 Panciroli et al. 2019; Ref-86 Martin and Schultz 2023), and other mammaliaforms (Ref-87 Parrington 1971; Ref-88 Luo et al. 2022).

For comparison with non-docodontan mammaliaforms, *M. sungei* differs from *Sinoconodon*, morganucodontans, *Hadrocodium*, kuehneotheriids, eutriconodontans, and spalacotherioids in the development of an anteriorly positioned cusp g on the hypertrophied lingual cingulid of the lower molars (best developed on m4 of *M. sungei* holotype), and in the widened anterior pseudotalonid structure on m3-m4, all common diagnostic features of docodontans (Ref-17 Luo and Martin 2007), including the Early Jurassic *Nujalikodon* (Ref-19 Patrocínio et al. 2025).

M. sungei gen. et sp. nov. is similar to the upper cusp pattern of many of docodontans with transversely widened upper crowns with four largest and defining cusps: labial cusps A and C and lingual cusps X and Y (Ref-1 Kielan-Jaworowska et al. 2004; Ref-2 Martin 2018; Ref-16 - Panciroli et al. 2024; Ref-66 Panciroli et al. 2021; Ref-86 Martin and Schultz 2023). *M. sungei* also shows a well-developed prestylar region and a constricted waist of the upper molars, distinctive features of

many (although not all) docodontans (Ref-66 Panciroli et al. 2021; Ref-18 Averianov et al. 2024). However, from these docodontans, *M. sungei* can still be distinguished by lower molar characters. *Megacauda sungei* shows a cusp triangulation of cusp b, primary cusp a, and posterolingual cusp c (“docodont trigonid” *sensu* Ref-61 Butler 1997, followed by most subsequent researchers, e.g. Ref-17 Luo and Martin 2007). In two features of this pattern of cusp arrangement, *Megacauda sungei* is distinctive: presence of a prominent V-notch between large cusp b and primary cusp a (**Extended Data Fig. 6**). The enlargement of the b-a V-notch is also developed to a varying extent in some other docodontans. In both b-a-c cusp triangulation, and the carnassial-like V-notch, *Megacauda sungei* is more similar to *Castorocauda*, *Dsungarodon* (=“*Acuodulodon*”), *Itatodon*, *Agilodocodon* and *tegotheriids*, than to other docodontans.

Megacauda is similar to *Castorocauda* but different from other docodontans and all non-docodontan mammaliaforms in having wide and flattened posterior thoracic ribs in their preserved skeletons. *Megacauda* and *Castorocauda* are similar to extant monotremes but different from all mammaliaforms and therian mammals in possessing broad plate-like costal ribs that are imbricated with each other (**Extended Data Figs. 1, 2, 10**). *Megacauda* and *Castorocauda* differ from other Mesozoic mammaliaforms preserved with pedal skeleton in possessing more elongate pedal digit rays 4 and 5 and a laterally asymmetrical pattern of the pedal digit-rays, in contrast to all other mammaliaforms that have symmetrical pedal digit rays characterized by shorter lateral digit 5 (or both digits 4 and 5) and shorter medial digits 1 and 2 on either side of longer digit 3, which is a plesiomorphic pattern (**Extended Data Fig. 8**) (Ref-54 Kielan-Jaworowska and Gambaryan 1994; Ref-89 Luo et al. 2016).

Megacauda and *Castorocauda* (Ref-13 Ji et al. 2006) also exhibit an elongation of the pedal phalanges and overall metatarso-phalangeal length relative to the femoral and tibial lengths (Figs. 4 and **Extended Data Fig. 8**), differing from those of other docodontans (Ref-8 Zhou et al. 2019; Ref-10 Meng et al. 2015; Ref-12 Luo et al. 2015; Ref-16 Panciroli et al. 2024;). In proportion to the femoral and tibial length the tarso-pedal and phalangeal length is even greater in *Megacauda* and *Castorocauda* (**Extended Data Fig. 8**), than the elongate distal parts of the hindlimbs of the arboreal docodontan *Agilodocodon* (**Extended Data Fig. 8**), and haramiyidans from the Jurassic (Ref-9 Meng et al. 2017; Ref-79 Zhou et al. 2013; Ref-85 Zheng et al. 2013; Ref-90 Bi et al. 2014; Ref-91 Luo et al. 2017). *Megacauda* is also unique in development of a vertical crest on ventral aspect of the calcaneal tubercle, adding a vertical depth of the tubercle (**Extended Data Fig. 9**). Its calcaneus shows a stronger ventral concave curvature, far more than the calcanei of other docodontans (Ref-10 Meng et al. 2015; Ref-89 Luo et al. 2016; Ref-8 Zhou et al. 2019; Ref-66 Panciroli et al. 2021, Ref-16 Panciroli et al. 2024).

Supplementary Table 2: *Megacauda* Skeletal Measurements and Comparison of *Megacauda* and vs *Castorocauda*

<i>Megacauda</i>		<i>Castorocauda</i>	
Humerus length	27.2 mm (estimate)		
Humerus distal width	15 mm (estimate)	n/a	
Radius (lf) length	26 mm (113%*)	23 mm	Radius (rt) length
Ulnar total length	36 mm	n/a	
Ulnar coronoid length	25.5 mm (111%*)	23 mm	Ulnar (rt) length
manus	28 mm (97%*)	29 mm	Hand -length (along digit ray 3)
Femur (lf) Length	31 mm (117%*)	26.5 mm	Femur (lf) Length

Femur (lf) width proximal	10 mm (154%*)	6.5 mm	Femur (lf) width proximal
Femur (lf) width mid-shaft	6.3 mm (180%*)	3.5 mm	Femur (lf) width mid-shaft
Femur (lf) width distal	9 mm (150%*)	6 mm	Femur (lf) width distal
Tibia (rt) length	38 mm (126%*)	30 mm	Tibia (lf) length
Tibia (rt) maximum breadth	10 mm (143%*)	7.5 mm	Tibia (lf) maximum proximal breadth
Fibula (rt) length	42 mm (131%*)	32 mm	Fibular (lf) length
Fibula (rt) maximum depth	13 mm (137%*)	9.5 mm	Fibular (lf) maximum depth
Pedal length (rt) calcaneo-fibular contact to terminal phalanx V (longest digit)	37 mm (100%*)	37 mm	Pedal length (lf) calcaneo-fibular contact to terminal phalanx of V (longest digit)
Pelvis width (measured at trans-level of iliosacral contact)	25 mm (104%*)	24 mm	
Pelage of tail widths◇			
at caudal 7	32 mm (91%*)	35 mm	
at caudal 8	32 mm (86%*)	37 mm	
at caudal 10	30 mm (100%*)	30 mm	
at caudal 12	30 mm		
at caudal 14	24 mm (104%*)	23 mm	
at caudal 16	22 mm		

* Percentage (%) of measurement of *Megacauda sungei* to *Castorocauda lutrasimilis*

◇ estimates at the preserved edge of soft-tissue pelages

<i>Megacauda</i>		<i>Castorocauda</i>	
Jaw length	60 mm (122%*)	49 mm	Jaw length
Skull length	80~81 mm	≥ 60 mm	Skull length estimate
Postcranio-tail tip length	43.5 mm (118%*)	37 mm	Postcranial length (to tail tip)
Rostro-Tail Tip length	51.5 cm (121%*)	42~42.5 cm	

Femur/Tibia length ratio (Or Tibia/Femur Ratio) and Pedal Length to Femoral Length Ratio

	Femur/Tibia Ratio (%)	Tibia/Femur Ratio (%)	Pedal Digit length/Femur length
<i>Megacauda</i>	84% (Rt)	119%(Rt)	119% (Rt pes digit 5)
<i>Castorocauda</i>	84% (Lf)	113% (Lf)	125% (Lf pes digit 5)
<i>Agilodocodon</i>	79% (Lf)	125% (Lf)	104% (Lf pes digit 3)
<i>Microdocodon</i>	75% (Lf)	133% (Lf)	N/A
	69% (Rt)	144% (Rt)	N/A
<i>Docofossor</i>	79%.	126%	N/A
<i>Ornithorhynchus</i>	68%	146%	
<i>Tachyglossus</i>	108%	92%	

Body Mass Estimates of *Megacauda*

The body mass estimates of the type specimen of *Megacauda sungei* gen. et sp. nov. range from 652 g (regression by mandibular length) to 1,491 g (regression by skull length of PMOL-AM00026). By comparison, the type specimen of *Castorocauda lutrasimilis* (Ref-13 Ji et al. 2006) is estimated to be 380 g (by mandibular length) to 518 g (by estimated skull length). Both the *Megacauda sungei* specimen and the *Castorocauda lutrasimilis* specimen are fully grown adults by their dental features. But *Megacauda* has a greater body length (length from rostrum to tail end is about 510 to 520 mm),

than *Castorocauda* with about 420 mm. By inference *Megacauda* has larger body mass than *Castorocauda*.

The body mass estimates by jaw length is based on the regression equation by Foster (Ref-92 Foster 2009) on a comparative dataset of mandibular length relative to body mass of placental eulipotyphlans and marsupials (Ref-92 Foster 2009). The equation for body mass estimate by skull length is adopted from Gingerich and Smith (1984) (Ref-93) on a large dataset of body mass and skull lengths of placental mammals.

Supplementary Table 3: Scaling of Body Size (Mass) with Jaw and Skull Lengths

Body mass Estimates	Anatomical Measurement	Scaling Equations Body Mass - g Length - mm	Comparative Taxa	Sources of equations
<i>Megacauda sungei</i>				
1,491 g	Skull length = 80 mm	$\text{LogBM} = 3.68 \times \text{Log}_{10}(\text{skull-length}) - 3.83$	Placental mammals	Ref-93 Gingerich and Smith 1984; Ref-13 Ji et al. 2006
652 g	Jaw length = 60mm	$\text{LnBM} = 2.9677 \times \text{Ln}(\text{Jaw Length}) - 5.6712$	Placental insectivores & marsupials	Ref-92 Foster 2009
<i>Castorocauda lutrasimilis</i>				
518 g	Skull length ~ 60 mm	$\text{LogBM} = 3.68 \times \text{Log}_{10}(\text{skull-length}) - 3.83$		as above
380 g	Jaw length ~ 50 mm	$\text{LnBM} = 2.9677 \times \text{Ln}(\text{Jaw Length}) - 5.6712$		as above

Megacauda and *Castorocauda* and extant platypus (*Ornithorhynchus*) have similar forelimbs, pelvis and hindlimbs, as well as caudal vertebrae and wide and flattened tails. Thus it would be meaningful to compare their body mass and length. On the basis of a recent summary of data on body mass and length of monotremes (Ref-94 Van Dyck et al. 2013), we can offer the following comparison. The *Megacauda* specimen, with its estimated range from 650 g to 1,491 g, is overlapping in the body mass range with adult male platypuses – the latter ranging from about 800 g (around 400 mm in rostrum to tail-end length) to 3,000 g (about 630 mm in rostrum to tail-end length). The *Castorocauda* holotype is estimated to range from 380 g to 518 g on a rostrum-tail length of 420 mm. This is lower than the body mass range of adult female platypuses, from 600 g (about 370 mm in length) to 1,700 g (about 550 mm in rostrum-tail length).

Megacauda and *Castorocauda* are specialized semiaquatic mammaliaforms (to be detailed below). One noteworthy character of the more specialized semiaquatic mammals is in their limb segment ratios. The stylopod (humerus and femur) is proportionally short in comparison to the zeugopod (radius/ulna and tibia/fibula) and their autopods (hands and feet) (Ref-49 Howell 1930; Ref-55 Rose and von Koenigswald 2005). The proportionally shorter humerus relative to the forelimb and shorter femur relative to the hind limb are specialized traits of semiaquatic mammals (Ref-55 Rose and von Koenigswald 2005). The humeral length and femoral length are generally useful metrics for scaling estimates of body mass for all tetrapods including mammals (Ref-95 Campione and Evans 2012). But our estimates by using the short humerus and femur lengths of *Megacauda* have resulted in unrealistically small body mass estimates. We interpret that humeral

and femoral length are biased to under-estimate the body mass for semiaquatic mammals because their disproportionately shorter humerus and femur are part of their swimming specialization.

(4) Description of Dentition

Dental formula: upper I5.C1.P4.M4/lower i4.c1.p5.m5 (**Figs. 3, Extended Data Figs 3 and 4**)

Upper Incisors - The upper I1, I2 and I3 are single-rooted and each has a simple, and slightly recurved tubular crown, and the apical part of the crown is conical. The right upper I4 has two completely divided roots, while the left upper I4 has a single root with root grooves on the lingual and labial side of the root, showing incomplete root division. Both left and right I5s have a single root with incomplete root division. The I4 crown and I5 crown have a bilaterally compressed primary cusp with a recurved outline in lateral (external) view, and a smaller posterior cingular cusp, although their crowns are widened in the posterior area that bears a cingular cusp. There are noticeable diastema between I3 and I4, between I4 and I5, and between I5 and the upper canine.

Upper Canine (Fig. 3) - The upper canine crown is hypertrophied, and strongly recurved and “hook-like”. The canine has three roots. The canine crown has a vertically oriented median groove on the posterior aspect of the crown, flanked by a vertically oriented posterolingual keel, and a vertical posterolabial keel. The vertical median groove starts at the level about 2/3 of the crown height; the groove continues dorsally along the crown through a notch of the crown-root junction. This vertical median groove further extends dorsally between the two posterior roots. This groove of the upper canine is open to some alternative hypotheses of its function. It could be hypothesized to be related to venomous function; or the groove and its flanking crests could also be hypothesized to be a structure to reinforce the strength of the tall crowns of the canines (more discussion below on dental function). The crown shows a weakly developed anterior carina (more visible in the distal half of the crown), and a well-defined crest of the posterolingual keel. The relatively flat anteromedial surface between the anterior carina and the sharp posterolingual keel of the upper canine is the main contact surface with the posterior keel and posterolabial facet on the lower canine (**Fig. 3e**). Corresponding to presence of the median posterior groove and its flank keels, the crown base appears to have a triangular outline in horizontal section but the apical 1/3 of the crown shows a slight bilateral compression. The canine has a prominent pattern of over-eruption of the roots (*sensu* Jones 2023). About half of the root length of the long canine roots is exposed below the margins of the alveoli, a canine growth pattern also known from other docodontans such as *Haldanodon* (Ref-17 Luo and Martin 2007; Ref-96 Huttenlocker et al. 2018; Ref-86 Martin and Schultz 2023), *Docofossor* (Ref-12 Luo et al. 2015), but absent in *Agilodocodon* (Ref-10 Meng et al. 2015), *Borealestes* (Ref-66 Panciroli et al. 2021) and *Krusatodon* (Ref-16 Panciroli et al. 2024). Over-eruption of the teeth (especially the canines) is common in carnivorous marsupials and has been interpreted to be a feature related to carnivory feeding function (Ref-23 Jones 2023).

Upper Premolars - All four upper premolars (P1, P2, P3 and P4) have two fully divided roots, and their crowns are slightly laterally compressed. The P1 and P2 are smaller with simpler crown, with a primary cusp but without a mesial cingular cusplule. The primary cusp (and the crown) are slightly recurved in labial view on P1 and P2. P3 and P4 are larger than P1 and P2. The upper P3 and P4 possess a large, recurved primary cusp, a small mesial cusplule and two well-developed distal cingular cusps: the posterolingual cusp, and the distal cusp (=cusp c). The primary cusp A has a more convex

and longer anterior crest compared to the shorter posterior crest. The cusp is positioned in the middle of the upper P3 and P4 crowns; these features contribute to the recurved and asymmetrical outlines of the upper premolars in *Megacauda*, unlike the more anterior position of the primary cusp A in other docodontans. The distinct posterolingual cuspule, which is interpreted to be a serial homologue to cusp X of the molars, is a major feature of the upper premolars because this cingular cuspule and the anteromedial cingulum form a flat wear facet on the mesiolingual aspect of the upper molar. This wear facet matches the recurved and sectorial cusp a of the posterior lower premolars. By the presence of a posterolingual cuspule (in addition to distal cusp c), the P4 crown takes on a molariform appearance, analogous to the “molarization” of the posterior premolars in eutherians. The P1 is separated by two large diastemata, respectively from the upper canine, and from P2. The diastema is also present between P3 and P4, although smaller.

Upper molars - *Megacauda sungei* gen. et sp. nov. has four upper molars. The primary character to distinguish the upper molars from premolars is that the molars are interlocked with each other, by the distal cingular cusp d of the preceding molar contacting the flat to concave cingular wall between cusps B and E of the succeeding upper molar. M1 is identified as a molar by the presence of a M1-M2 interlock, in contrast to the lack of such interlock between the ultimate premolar (P4) and M1. Molars also show more differentiation of the roots than premolars. M2-M4 have three fully divided roots. In M1, the anterior root is fully divided from its posterior root but the M1 posterior root shows a “dividing” groove on the posterior aspect of the root that extends more than 2/3 of the root length, in contrast to the simple posterior roots of the two-rooted upper premolars. The posterior root of M1 is interpreted to be partially divided. The posterior root tip is singular; therefore, M1 lacks the fully differentiated posterolingual root (as known as the “third” lingual root of the more posterior molars). The holotype of *Megacauda* is a full adult, and lacks any replacing teeth for the ante-molars in the CT scans, thus it is not possible to distinguish premolars from molars by deciduous tooth crown for premolar loci of the replacing tooth lamina.

M1 – The crown shows a triangular outline in occlusal view. Its crown is characterized by a large primary cusp A, and a small posterolabial cusp C, and a mesial cingular cusp B. The lingual lobe of the crown bears a small lingual cusp X. A well-developed shearing surface is developed along the pre-cingulum on the mesiolingual aspect of the crown between cusp B and lingual cusp X. This facet is similar to the mesiolingual facet of P4 and P3.

M2 - M4 – Crowns of these molars show the common cusp pattern of docodontan upper molars as seen in *Borealestes* and *Krusatodon* (Ref-65 Panciroli et al. 2019; Ref-66 Panciroli et al. 2021; Ref-16 Panciroli et al. 2024) and to lesser extent also in *Simpsonodon* (Ref-97 Kermack et al. 1987) and *Agilodocodon* (Ref-10 Meng et al. 2015) and *Dsungarodon* (Ref-98 Pfretzschner et al. 2005; Ref-99 Martin et al. 2010). The main labial cusps A and C are subequal in size and height. Cusp B is represented by a smaller cingular cusp, and cusp E is weakly developed, and positioned anterolingual to cusp B. Cusps B and E together form the prestylar lobe. The flat (or slightly concave) cingulum bearing cusps B-E in the prestylar region of M2 forms the interlock with the distal cingulum above cusp C of M1. In M2, the lingual lobe bears the main lingual cusp X, which is bulbous with a swelling wall. A smaller posterolingual cusp Y that is appressed to cusp X on M2, but to cusp Y on M4, is well-separated from cusp X and larger than its serial homolog on M2. The transverse A-X crest (Ref-17 Luo and Martin 2007) is low, developed in M2 through M4, but the C-Y crest is only present on M2 and M3 but absent in the ultimate upper molar M4. A clearly constricted waist is developed in M2

through M4, another typical docodontan upper molar feature, and this waist constriction is made more prominent by the expanded lingual lobe bearing both cusps X and Y. M3 is the largest of the upper molar series. M4 shows a closed root-tip of the distolabial root, indicating that the tooth had stopped growth/erupting process at the time of death.

Lower Incisors (Extended Data Fig. 4) – The lower incisor 1 (i1) is the longest incisor with tubular crown and pointed apex. This tooth is well-preserved in the right mandible, but on the left side i1 is broken. Both left and right lower i2 are broken at the apex, although this tooth appears to be shorter than i1. Incisor 3 has a bilaterally compressed crown with a lancet-outline in lateral view. The i3 root is bilaterally compressed with dividing grooves on the medial and lateral sides of the root. The crown of i3 is medio-distally the longest among all incisors. The i4 crown is also lancet-shaped in lateral view; this tooth has a single root. The i4 and i2 are estimated to have about the same in crown height and in mesio-distal length.

Lower Canine (Figs. 3 and Extended Data Fig 4) – The lower canine crown is well preserved in the right jaw but its crown is broken and missing in the left. The crown shows a trenchant and triangular outline in medial and lateral views, and is slightly recurved from the fully divided roots. Overall, the canine crown is bilaterally compressed, but its lateral aspect is slightly convex, and the medial side (especially posteromedial aspect) of the crown is noticeably concave. The anterior and posterior carinas of the crown are sharp crests; the anterior crest is straight and the posterior crest is slight concave in lateral view. The posterolateral aspect of the canine adjacent to the posterior carina shows a flat-to-concave surface, which is in contact with the anterior to anteromedial aspect of the upper canine during occlusion. When the lower canine is in full occlusion with the upper canine, the apex of the tall lower canine is accommodated by a deep canine pit on the premaxilla anteromedial to the lower canine. The lower canine also shows the pattern of over-eruption of roots, and above 1/3 of its long roots are exposed above the margins of the root alveoli.

Lower Premolars (Extended Data Fig 4) – Five premolars are present in the lower jaw and all have two fully divided roots. The premolar-molar boundary is based on the presence of molar interlock of m1 and on the lack of such interlock between the premolars. But otherwise the posterior premolars are similar to m1 in the bilaterally compressed tooth crown with a trenchant and recurved main cusp. The main cusp is asymmetrical in lateral and medial views with a longer and slightly convex anterior crest and a shorter and straight posterior crest. The lower p1, p2 and p3 together show a gradient of posteriorly increasing size. The p1 is the smallest premolar and it has the main cusp a and the posterior cusp c, but lacks a mesial cingulid cuspule (cusp b). By contrast, a mesial cingulid cuspule (cusp b) is present on p2 and through p5. The p3, p4, and p5 are all characterized by recurved primary cusp a on both left and right mandibles. The distal cusp d of p4 touches on, but does not interlock with the mesial end of p5 tooth crown. By comparison, the cusp d of p5 is contacting a concave area near the base of cusp b, on the mesial end of m1, forming the p5-m1 interlock. The lower p5 has one cusp c on the posterior crest. *Megacauda* is distinct from *Castorocauda* in the single cusp c from the “double cusps c1 and c2” of the latter (**Extended Data Fig. 6**).

Lower Molars – The lower m1 is a sectorial tooth with a recurved primary cusp on bilaterally compressed crown that is asymmetrical in lateral and medial views. The posterior cusp c is aligned with primary cusp a, in contrast to m2, where cusp c is in a postero-lingual angle to cusp a. Aside from the interlock between m1 and m2, the m1 crown is overall similar to those of p3-p5, all of which are

sectorial. The m1 crown of *Megacauda* is characterized by a posterior crest with a single cusp c. This is different from the two cusps (c1 and c2) of *Castorocauda* (**Extended Data Fig. 6**).

The distal part of the lower m2 has a typical docodontan-like molar morphology, but the mesial half of the m2 crown is more bilaterally compressed, than in other docodontan molars. The recurved primary cusp a is bilaterally compressed, and cusp g, which is a major characteristic of docodontan lower molars, is absent. Because of these features, the anterior part of m2 is simplified and more sectorialized. The lower m2 is halfway like a docodontan molar, and halfway like a sectorial crown like m1 and posterior premolars.

The lower m3 is a typical docodontan-like molar. The anterior pseudotalonid part of the molar is much longer and slightly wider than the posterior part of the molar. The primary cusp a is the tallest and largest cusp. The anterior cusp b is prominent and the V-shaped notch between cusp b and primary cusp a is also a prominent structure. Cusp g is small. At the mesial end m3 has a small concave surface to receive the distal cusp d of m2 for interlocking. The lower molar 4 is a typical docodontan-like molar, with a large cusp g (the most diagnostic feature of docodontan lower molars).

The lower m5 is shortened, as compared to m2-4. The part posterior to cusp a is greatly reduced to a simple slope, and it is so simplified that the typical posterolingual molar cusp c of other docodontans is absent in this tooth of *M. sungei*. The lower m5 and m4 have cusp g fully developed, but this cusp is reduced on m3 and absent on m2 and m1. This shows an anterior gradient of the cusp g reduction toward anterior molars. This gradient of reduction-to-loss of cusp g is related to great degree of bilateral compression and sectorialization of the anterior molars and posterior premolars. The CT scans show clearly that there is no further molar in the mandible, and m5 is the ultimate molar of this mammaliaform.

Note on revision of *Castorocauda* dental formula – We revised the dental formula of *Castorocauda lutasimilis* to lower i4/c1/p6/m5 from the previous dental formula i4/c1/p5/m6 (Ref-13 Ji et al. 2006), according to the new information from the more completely preserved teeth in closely related *Megacauda sungei* gen. et sp. nov. In *M. sungei*, the boundary of upper P4-M1 can be based on the absence of contact between P4-M1 and the development of a posterior root division in M1, and the presence of M1-M2 interlock. The lower premolar-molar boundary of *M. sungei* can also be defined by a clear interlock of the m1 distal cusp d into the small concave area in the mesial aspect of the base of cusp b of m2. We re-interpret here that the boundary of the lower p5-m1 for *Castorocauda lutasimilis* can also be based on the d-b interlock of m1 and 2. In light of this revision of p6-m1 bound, the dental formula of *C. lutasimilis* is changed to i4/c1/p6/m5.

We also note that in the *Castorocauda* type specimen, the lower canine crown is broken off from the roots in the mandible, but is still nearby. By the restoration of the canine, *Castorocauda* should also have a tall and trenchant lower canine, as seen in *Megacauda sungei*.

Castorocauda lutasimilis holotype is a fully grown adult, as evidenced by the ultimate molar (designated to be m5) positioned in front of the coronoid process of the mandible (**Fig. 3**) (Ref-13 Ji et al. 2006). This is the adult-state of a classic age-indicating character for docodontans (Ref-25 Schultz et al. 2017; Ref-65 Panciroli et al. 2019; Ref-86 Martin and Schultz 2023) and for other early mammaliaforms (Ref-87 Parrington 1971; Ref-88 Luo et al. 2022).

(5) Interpretation of Dental Occlusion and Inference of Feeding Function

Functional Interpretation of Canines – *Megacauda sungei* gen. et sp. nov. is highly distinctive in its three-rooted upper canine, and the posterior vertical groove flanked by crests along the crown height of the canine. The three roots are identical between the left and right canines. It can be ruled out as an individual variation.

The posterior longitudinal groove along the height of the canine can be explained by two alternative hypotheses: either the groove could be a venom delivery structure, as interpreted for grooved canines (or incisors) of some extinct eutherian mammals of the Cenozoic (Ref-100 Fox and Scott 2005, Ref-101 Fox and Scott 2020; Ref-102 Cuenca-Bescós and Rofes 2007; Ref-103 Furió et al. 2010), or the groove and its flanking crests are structures that reinforce the tooth crown (Ref-24 Orr et al. 2007; Ref-104 Folinsbee et al. 2007; Ref-105 Turvey 2010).

Hypothesis 1 - Canine groove was analogous to the venom groove on incisors/canines of some venomous eutherians. The posterior and vertical groove on the upper canine of *M. sungei* is similar to some degree to the canine groove of the Paleocene eutherian *Bisonalveus*, which has been hypothesized to be a venom-delivery structure (Ref-100 Fox and Scott 2005; Ref-101 Fox and Scott 2020). Another comparable example is the Pliocene-Pleistocene fossil shrew *Beremendia*, which also has lower incisors with longitudinal groove. *Beremendia* is interpreted to possess a venom delivery structure (Ref-102 Cuenca-Bescós and Rofes 2007; Ref-105 Turvey 2010; Ref-106 Rofes and Cuenca-Bescós 2009), so is another fossil shrew *Dolinasorex* (Ref-106 Rofes and Cuenca-Bescós 2009). The putative function of the grooves in canines/incisors in these fossil eutherians, however, has been questioned by other workers (Ref-24 Orr et al. 2007; Ref-103 Furió et al. 2010; Ref-104 Folinsbee et al. 2007; Ref-105 Turvey 2010).

The best examples for venomous mammals with grooved canines or caniniform incisors are *Solenodon paradoxus* (Ref-107 Dufton 1992; Ref-108 McDowell 1958) and possibly also *Solenodon (Apotogale) cubanus* (Ref-109 Nowak 1999; Ref-110 Pournelle, G. H. 1968), although the saliva toxicity has not been tested for *S. cubanus* (Dufton 1992). The extinct *Nesophontes paramicrus*, a close relative of *Solenodon*, also has grooved upper canines that could be interpreted to be related to envenomation (Ref-105 Turvey 2010), although it is not possible to be tested by toxicology for this extinct species (Ref-105 Turvey 2010).

The only synapsid example of a canine with ridges and groove is the Late Permian therocephalian *Euchambersia* (Ref-104 Folinsbee et al. 2007; Ref-111 Hotton 1991; Ref-112 Benoit et al. 2017; Ref-113 Liu and Abdala 2022). The vertical groove of the canine is known to extend into the root (Benoit et al. 2017), and has been hypothesized to be an envenomating groove (Ref-105 Folinsbee et al. 2007; Ref-111 Hotton 1991; Ref-112 Benoit et al. 2017). In this therocephalian, the canine bears resemblance of a snake-like tooth (Ref-105 Folinsbee et al. 2007). However, the upper canine groove connected to a fossa in the maxilla, which was previously suggested to be the location of a venom gland (Ref-105 Folinsbee et al. 2007), is now considered to be a structure related to the maxillary nerve branches. Benoit et al. (2017) (Ref-112) further noted that the upper incisors of *Euchambersia* have similar longitudinal grooves. These features have been invoked to support the notion that *Euchambersia* would be capable of delivering venom by a grooved canine (Ref-105 Folinsbee et al.

2007; Ref-112 Benoit et al. 2017). Because *Megacauda* is phylogenetically so far removed from the therocephalian *Euchambesia*, the presence of a longitudinal groove in both taxa is best considered as convergence.

Hypothesis 2 – Longitudinal groove and the associated ridges on canine of *M. sungei* are for reinforcement of canines. It has been interpreted that the groove-ridges structure can increase the surface area of the enamel, which is a harder tissue than dentine (Ref-105 Folinsbee et al. 2007), or the slender canines can be structurally strengthened by groove-ridges in a general way (Ref-24 Orr et al. 2007). This reinforcement hypothesis is supported by examples of many non-venomous eutherians with grooved canines and incisors (Ref-24 Orr et al. 2007; Ref-105 Folinsbee et al. 2007). This hypothesis was also reviewed and supported by Furió et al. (2010) (Ref-103).

The envenomation interpretation of the groove in canines and incisors in extinct mammals, both for *M. sungei* and for the above-mentioned eutherians, can be ambiguous for two reasons. First, canine and incisor groove and ridges are present in many non-venomous mammals, which do not support the structure-function association of the envenomation interpretation. Such non-venomous mammals with grooved canines or incisors include many (although not all) anthropoid primates. Some non-venomous primates show a certain expression of the longitudinal groove, others have a more fully developed groove on the incisors and/or canines (Ref-24 Orr et al. 2007). Other such examples include hippopotamids, many suids, and many pteropodid fruit bats (Ref-104 Folinsbee et al. 2007; Ref-24 Orr et al. 2007). South American procyonid carnivores, *Nasua narica* and *Nasuella olivacea* (also known as coatis), have grooved canines but both species are not venomous (Ref-24 Orr et al. 2007).

Second, a majority of venomous extant mammals do not have a groove on the incisors or canines for venom delivery. Instead, the prey are infected by saliva toxins through laceration or wound by biting in general, without relying on some specialized injection of venom through sharp teeth with delivery groove or canal, as in squamates (Ref-24 Orr et al. 2007; Ref-103 Furió et al. 2010; Ref-104 Folinsbee et al. 2007).

The incisors and canines are not grooved in the several eulipotyphlans known to be venomous by saliva toxin. Two semi-aquatic shrew species, *Neomys fodiens* (European water shrew) and *Neomys anomalus* (Mediterranean water shrew) are venomous by saliva (Ref-107 Dufton 1992); but these semiaquatic shrews have no groove on canines or incisors (Ref-24 Orr et al. 2007; Ref-104 Folinsbee et al. 2007). Other venomous eulipotyphlans without grooved canines and incisors include *Blarina brevicauda* (short-tailed shrew), *Sorex araneus* (common Eurasian shrew) and *Crociodura canariensis* (Canarian shrew) (Ref-107 Dufton 1992; Ref-114 Ligabue-Braun et al. 2012; Ref-115 Kowalski et al. 2022).

Outside eulipotyphlans, envenomous mammalian species are not common (Ref-24 Orr et al. 2007; Ref-103 Furió et al. 2010; Ref-104 Folinsbee et al. 2007). Two rare examples are the pygmy loris (*Nycticebus pygmaeus*) - a venomous primate (Ref-116 Nekaris et al. 2013) and the vampire bat (*Desmodus rotundus*), which has anticoagulant in the saliva that is delivered in a similar way as saliva toxin is delivered by venomous predators (Ref-24 Orr et al. 2007). The incisors or canines of loris and vampire bat all lack the groove-like structures. Overall, the grooved canines (or incisors) are developed most probably as reinforcement structure of the canines or incisors, and un-related to envenomation.

The three-rooted upper canine is a highly unique and an autapomorphic feature for *M. sungei*. For comparison, other docodontans known to have two roots of the upper canines are *Docofossor* (Ref-12 Luo et al. 2015), *Docodon* (Ref-25 Schultz et al. 2017), *Krusatodon* (adult specimen) (Ref-16 Panciroli et al. 2024). But *Agilodocodon* has a single root (Ref-10 Meng et al. 2015). Unfortunately the upper canine roots are unknown for *Castorocauda* and *Borealestes* (Ref-65 Panciroli et al. 2019). One docodontan upper canine in an isolated maxilla from the same site of *Khorotherium* and *Ergetiis* (Ref-18 Averianov et al. 2024) also shows two fully divided roots, but this maxilla specimen could not be designated to a species (Docodonta indet.) (Ref-18 Averianov et al. 2024: fig. 9). Among non-docodontan mammaliaforms, only *Hadrocodium* shows two fully divided roots for upper canine (Ref-88 Luo et al. 2022). No other early-diverging mammaliaform of the Mesozoic has the three-rooted upper canine.

The three roots of the left and right upper canines are identical. Thus the three-rooted pattern is not a variable feature for *Megacauda*. In extant therian mammals, the vast majority of species with canines are single-rooted. Among mammal species with single-rooted upper canine, only *Homo sapiens* has been examined for variability of canine root(s): only 1%-2% of humans have two-rooted upper canines among many case studies (Ref-117 Marin et al. 2020), and the variation to three roots of upper canine is exceedingly rare (Ref-118 Kanadasamy et al. 2019).

Occlusal Relationship of Upper and Lower Postcanines (Extended Data Fig. 5)– *Megacauda sungei* gen. et sp. nov. is distinct in upper and lower postcanine morphologies from all known Mesozoic mammaliaforms (although similar in the posterior lower premolars and m1 to *Castorocauda lurasimilis*). In *M. sungei*, the lower postcanines from premolar p2 to m1 have bilaterally compressed crowns and each possesses a tall primary cusp a that is recurved with a convex anterior crest and a posterior crest that is straight to slightly concave. The main cusp is in alignment with cusp c and cingulid cusp d; cusps a-c-d form a serrate structure. The anterior part of m2 has no cusp g and is also bilaterally compressed. The p3 through the anterior half of m2 are sectorialized.

The upper premolars and molars have corresponding occlusal features to the sectorialized lower postcanines. In labial view, the penultimate (P3) and ultimate (P4) upper premolars show a recurved cusp A, matching the recurved cusp a on the lower premolars. In occlusal view, the upper P3, P4 and M1 form a prominent series of prevallum shearing surfaces, which occlude with the serrated cusps a-c-d during phase 2 of occlusion when the lower postcanines move postero-lingually, before sliding out ventrally.

Functional Interpretation of Carnassial-like Occlusion – During occlusion of docodontans, the occlusal movement of the lower molars has a posterior trajectory, earlier recognized by Gingerich (Ref-119 Gingerich 1973; Ref-20 Butler 1988) and later confirmed by functional studies (Ref-25 Schultz et al. 2017; Ref-26 Grossnickle et al. 2022; Ref-63 Brinkkötter 2018). This posterior movement has been corroborated quantitatively for the Late Jurassic *Docodon* (Ref-25 Schultz et al. 2017) and also for *Haldanodon* (Ref-63 Brinkkötter 2018), using Occlusal Fingerprint Analyser (OFA) methods. Based on the topographical matching of the upper and lower molar crowns (**Extended Data Fig. 5**), we interpret that the movement of the lower molars in *Megacauda* had a similar posterior trajectory, as demonstrated for *Docodon*:

- Phase 1 occlusion (**Extended Data Fig. 5-c**) (*sensu* Ref-25 Schultz et al. 2017): the occlusion of lower and upper molars starts with the labial side of cusps b and a and the b-a crest (forming the V-shaped notch between b and a) of the lower molars shearing past cusps A and C and the connecting crest between these cusps of the corresponding upper molar; and the overall movement trajectory is postero-dorsal, and this movement continues until the tallest cusp a of the lower molar reaches the deepest point of the embrasure between the corresponding upper molars, also known as the centric occlusion.

- Phase 2 occlusion (**Extended Data Fig. 5-d**). After the centric occlusion, the trajectory of the lower molar movement is shifted in postero-lingual direction, and this brings the oblique a-c crest of the lower postcanines to contact with the pre-cingulum of the succeeding upper molar. The postero-lingual movement enables the serrated posterior crests (or the postvallid crests) of p5 -m1- m2 to shear against the anterior (= prevallum) surfaces of the corresponding upper molars (P4-M2). The shearing of the lower postvallid crest against the upper prevallum is the main occlusal action for the recurved primary cusp a with its posterior serrated crest (a-c-d) for chewing the animalivorous diet.

Pseudo-Carnassial Postcanine Occlusion – For the docodontan *Megacauda sungei* gen. et sp. nov. with bilaterally compressed sectorial postcanines, we interpret that the main occlusal shearing occurs between the postvallid crest of a preceding lower postcanine against the prevallum crest of a succeeding upper postcanine. By contrast, in carnivorous mammals of the crown therians, the primary shearing between the lower and upper postcanines occurs between the prevallid crest of the paracristid on the anterobuccal side of the trigonid of a succeeding lower molar against the postvallum crest on the posterior aspect of the preceding upper postcanine. This type of postvallum/prevallid carnassial teeth is exemplified by P4/m1 carnassial teeth for crown Carnivora, and multiple upper-lower pairs of P4/m1, M1/m2, M2/m3 for placental “creodonts” (hyaenodontids and oxyaenids). Or by P3/m1, M1/m2, M2/m3, M3/m4 in marsupial carnivores (Ref-120 Berkovitz and Shellis, 2018).

The postvallum/prevallid shearing teeth in placentals and marsupials are known as the carnassial teeth. By contrast, the postvallid/prevallum shearing teeth of *Megacauda* have their shearing surfaces located on the geometrically opposite side of the carnassial molars of extant therians. To highlight this contrasting pattern, here we call the shearing postcanines of *Megacauda* the pseudo-carnassial teeth (Extended Data Fig. 5).

Dietary Inference – The recurved main cusps on the bilaterally compressed crowns of *Megacauda sungei* gen. et sp. nov. and *Castorocauda lutrasimilis* are functionally analogous to the teeth of pinniped carnivores, but they are particularly similar to the cheek teeth of the leopard seal and crab-eating seal that are not only apex predators of other vertebrates in their ecological niches but can also filter-feed on aquatic invertebrates (Ref-29 Hocking et al. 2013; Ref-120 Berkovitz and Shellis 2018). Among mammaliaforms, the Mesozoic eutriconodontans – a crown mammalian clade – are also well-known for strongly recurved cusps on compressed postcanines: *Argentoconodon* (Ref-121 Rougier et al. 2007; Ref-122 Gaetano and Rougier 2012; also see Ref-123 Gao et al. 2009), *Volaticotherium* (Ref-84 Meng et al. 2006), *Dystriiconodon* and *Ichthyconodon* that are interpreted to be semiaquatic by their association with fossil fishes in marine sediments (Ref-124 Signogneau-Russell 1995) in the crown Mammalia. Their recurved triconodont-like teeth are specialized for a faunivorous diet, and have been interpreted to be for aquatic diet of fish and invertebrates (Ref-124 Signogneau-Russell 1995; Ref-13 Ji et al. 2006). The molar pattern of *Megacauda* is convergent also to several groups of

Cenozoic eutherians. For example to molars of carnivorous mesonychians (land-living eutherians) and the amphibious to fully aquatic “archaeocete” whales of the Eocene (Ref-28 Rose 2006). These recurved cusps in alignment on bilaterally compressed postcanines are widely regarded to be associated with aquatic animalivorous feeding in early whales. The best-known extant examples of the recurved teeth of *Megacauda* and *Castorocauda* are the postcanine teeth of the leopard seal (*Hydrurga leptonyx*) and by some extent also to the crabeater seal (*Lobodon carcinophaga*) that are capable of filter-feeding of krills. The likely prey could be small salamanders for *Megacauda*, or the abundant conchostracans for *Castorocauda*.

(6) Hyoid Apparatus and Palato-pharyngeal Anatomical Reconstruction

In this section of Supplementary Information, we provide a preliminary description of the osteology of the hyoid and palato-pharyngeal vault structures of *Megacauda sungei* gen. et sp. nov., and offer a novel musculoskeletal reconstruction of the pharyngeal soft tissue anatomy. Mammals are unique among major vertebrate groups in development of a saddle-shaped hyoid apparatus with a segmented greater hyoid horn (Ref-8 Zhou et al. 2019; Ref-32 Evans and de Lahunta 2013; Ref-33 Li et al. 2022; Ref-125 Sprague 1943, Ref-126 Sprague 1944; Ref-127 Gasc 1967). This highly mobile hyoid apparatus works together with a sophisticated palate-pharyngeal musculoskeletal system (Ref-39 Smith 1992) for the function of neonatal suckling (Ref-128 Edmonds et al, 2020; Ref-37 Mayerl and German, 2023), swallowing bolus of chewed food and liquid (Ref-36 Li et al 2025). The hyolaryngeal structure is integrated into the pharynx for respiration and phonation. The integrated system of the structures revolutionized the feeding function of mammals, in synergy with their derived dental occlusion for mastication and novel jaw structure and mandibular muscles for feeding and chewing function.

The *Megacauda sungei* holotype specimen is very rare in preserving both the hyoid structure (**Extended Data Fig. 4**) and the palato-pharyngeal vault (**Extended Data Fig. 7**). Furthermore, both mandibular middle ears are still closely attached to the mandibles. Thus we can clearly distinguish the hyoid segments from the middle ear in this fossil specimen (see the discussion by Ref-8 Zhou et al. 2019). This is very informative for interpreting the entire system of palato-pharyngeal and hyoid structure for a mammaliaform in an intermediate, and transitional position in the cynodont-mammal phylogeny.

Hyoid Apparatus

Hyoid Elements of the *Megacauda* holotype (PMOL-AM00026A, B) (Fig. 2, Extended Data Figs 4 and 7) – The relatively well preserved hyoid elements are the basihyal, the left and right ceratohyals, the left and right epihyals, and the left and right thyrohyals. The basihyal (6 mm long) is slender and rod-shaped. Its two ends are slightly enlarged, although its contact surface for the left thyrohyal appears to be cut off during fossilization. The left ceratohyal (4.5 mm long) is rod-shaped with two enlarged ends, and is better preserved than the right ceratohyal that is more flattened by fossilization. The left epihyal (6 mm long) is slightly curved, and its end toward the left ceratohyal is more robust than the other end. The right epihyal appears to have lost some bone material at both ends. The thyrohyal (9 mm long) is rod-like near the basihyal and thyrohyal joint, but widened to be paddle-shaped in the posterodorsal end. The thyrohyal is the longest among the preserved hyoid elements. Its length is 150% of the length of the basihyal, and 180-190% of the ceratohyal length.

The hyoid elements of the *Megacauda* specimen, although slightly detached, are associated in a post mortem layout that is the same as the associated hyoids of *Microdocodon* (Ref-8 Zhou et al. 2019: fig. s2-4). The ventral hyoid elements can be interpreted to have a saddle shaped ()—() configuration as in extant mammals (Ref-32 Evans and de Lahunta 2013; also see Ref-33 Li et al. 2022: fig. 2). This saddle shaped configuration ()—() is structured with the basihyal as the horizontal bar in the middle, and one pair of the ceratohyal and thyrohyal on either end of the basihyal. In live posture of the hyoids, the ceratohyal would be oriented anterodorsally from the basihyal-ceratohyal joint to link with the epihyal (also preserved in the specimen) and the thyrohyal would be oriented posterodorsally from the basihyal and thyrohyal joint, as seen in extant therian mammals (Ref-32 Evans and de Lahunta 2013; Ref-33 Li et al. 2022; Ref-127 Gasc 1967; Ref-129 Weissengruber et al 2002).

The new fossil of *Megacauda* adds three anatomical details for mammaliaform hyoids previously unavailable from *Microdocodon*: (1) the ceratohyal-basihyal joint and the ceratohyal-epihyal joint were likely synovial joints, as evident from the morphology of the ends of the ceratohyal and the epihyal; (2) the epihyal is slightly curved; and (3) the thyrohyal is the longest hyoid element and the thyrohyal and its contact end for the thyroid cartilage are widened, although the thyroid cartilage itself is not calcified thus absent from the fossil specimen.

Megacauda has actual cranial and hyoid skeletal elements preserved for accurate visualization, compared to the *Microdocodon* specimen in which much of the skull and hyoid morphologies are represented by molds and impressions. The CT visualizations of the actual bones are more reliable for anatomical interpretation of the delicate structures of the hyoids and the middle ear. Foremost, CT scans of *Megacauda* have now shown that the saddle-shaped configuration ()—() of the ventral hyoid elements is a shared feature of *Megacauda* and *Microdocodon*, as seen in extant mammals.

The stylohyal is not present in the new specimen (PMOL-AM00026) of *Megacauda*. However, we lack sufficient evidence to determine if this hyoid element was not preserved because it was cartilaginous and not ossified, or if it is absent in this fossil because it was not developed at all. Our assessment that the stylohyal is absent is based on the fact that the preserved hyoid elements are not scattered too far away from one another, nor are they separated far from the basicranium (Supplementary Video S1). Both the mandibles and their respective attached middle ears are still associated with each other, near the cranium. From the evidence of relatively well preserved skull and hyoids, it is less likely that the stylohyal alone got lost in fossilization. Therefore, we interpret that *Megacauda* lacked the stylohyal.

Extant mammals show two different configurations of the greater (anterior) cornu of the hyoids (Ref-8 Zhou et al. 2019; Ref-33 Li et al. 2022; Ref-35 Li et al. 2023; Ref-125 Sprague 1943, Ref-126 Sprague 1944; Ref-127 Gasc 1967): (1) The integro-cornuate configuration in which the anterior cornu is a complete chain of hyoid elements to connect the basihyal to the paroccipital process of the petrosal and/or other basicranial bones (basihyal– ceratohyal – epihyal – stylohyal – tympanohyal are all represented by bone or cartilage). Or (2) The discreto-cornuate configuration in which one or more elements can be absent such that the basihyal is not fully linked by bones or cartilaginous elements to the petrosal or other basicranial parts (Ref-33 Li et al. 2022; Ref-125 Sprague 1943). The phylogenetic distribution of these two character states varies among extant mammals. The discretocornuate pattern can also be classified according to which element of the anterior cornu is absent from the bony-chain

of these hyoid elements (Ref-33 Li et al. 2022). We interpret that *Megacauda* and *Microdocodon* both have the discreto-stylohyal configuration, following the discreto-cornuate hyoid types defined by Li et al. (2022: fig. 2) (Ref-33) and by comparison to extant mammals with discretocornuate hyoid configuration.

Our survey of the Mesozoic mammal clades known to have preserved at least some hyoid elements has revealed the following systematic variation across major clades – the spalacotherioid *Origolestes* most likely had a discreto-stylohyal chain - missing the stylohyal (Ref-8 Zhou et al. 2019: fig. s8; Ref-43 Luo et al. 2025). Multituberculates have variable pattern of the known hyoid elements. Among the djadochtatherioid multituberculates from the Upper Cretaceous of Mongolia, *Kryptobaatar* and *Chulsanbaatar* preserved an elongate stylohyal (Ref-45 Wible and Rougier 2000; Ref-54 Kielan-Jaworowska and Gambaryan 1994). This element can be identified as the stylohyal in *Kryptobaatar* because its proximal end appears still connected to the paroccipital process of the petrosal – an original anatomical connection of the hyoid cornu (Wible and Rougier 2000: fig. 14). But the epihyal, ceratohyal, basihyal and thyrohyal of *Kryptobaatar* are unknown (Ref-45 Wible and Rougier, 2000). Incomplete hyoids are also known from two sinobaatarid multituberculates. A specimen of *Sinobaatar* sp. (SDUST-V0001A) appears to have the basihyal, two thyrohyals and one ceratohyal and one epihyal, but this fossil is missing the stylohyal (Ref-8 Zhou et al. 2019: fig. s7). Another sinobaatarid, *Sinobaatar pani* (Ref-130 Mao et al. 2020) has a well preserved basihyal and thyrohyal, and a paired ceratohyal (Ref-130 Mao et al. 2020: shown in their supplementary movie S1-R1), plus two long stylohyals. The latter elongate elements are very similar to the stylohyals preserved in close proximity to the petrosal in *Kryptobaatar* (Ref-45 Wible and Rougier 2000: fig. 14). The evidence accumulated so far suggests that multituberculates are more likely to have a discreto-cornuate chain in their last common ancestor. However, there is not enough evidence to determine if this putative discreto-cornuate pattern would be discreto-epihyal, or discreto-stylohyal (*sensu* Ref-33 Li et al. 2022).

In monotremes, both *Ornithorhynchus* and *Tachyglossus* (short-beaked echidna) have an integrocornuate hyoid although the proximal part of stylohyal is known to co-ossify with the petrosal (Ref-8 Zhou et al. 2019; Ref-131 Kuhn 1971). After the stylohyal is transformed by this co-ossification, the rest of hyoid elements can be secondarily disconnected from the basicranium in the adult (Ref-8 Zhou et al. 2019: fig. S5). Furthermore, in adult long-beaked echidna (*Zaglossus*), the discretocornuate hyoids, disconnected from the basicranium, can descend along the cervical vertebral column (Ref-132 Wheelhouse et al. 2022: fig. 4). The x-ray radiography suggest that *Ornithorhynchus* may also have hyoid apparatus shifted to below cervical vertebrae C1-C2 (Ref-133 Vogelnest and Graeme 2015). The ancestral condition of the hyoid cornu for marsupials as a clade is clearly discreto-stylohyal. In summary the crown Mammalia is more likely to have the discreto-stylohyal type of hyoids.

Because an ossified stylohyal is missing in both docodontans with overall decent preservation of the hyoid apparatus (*Microdocodon* and *Megacauda*), it would not be unreasonable to argue that a cartilaginous, or fully missing stylohyal is common in mammaliaforms. This favors the likelihood that an overall discreto-cornuate pattern of the greater cornu chain is the prevailing ancestral condition for fossil mammaliaforms before the rise of extant Mammalia. This ancestral condition will be the new baseline for the evolutionary interpretation of hyoids for mammaliaforms as a whole.

Revised Interpretation of Hyoid in *Microdocodon* (Ref-8 Zhou et al. 2019) – The new scans of actual bones of *Megacauda* also revealed an error in our previous interpretation of hyoids of *Microdocodon* (Ref-8 Zhou et al. 2019: figs s3-s4) – we mis-interpreted the orientation of the ceratohyal and the thyrohyal of *Microdocodon*. The thyrohyal was misidentified as a “ceratohyal,” and the ceratohyal was misidentified as a “thyrohyal” in our previous illustrations. We made this error because we incorrectly flipped the orientation of these two elements relative to the basihyal (Ref-8 Zhou et al. 2019: figs s3-s4).

Palato-Pharyngeal Vault Structure

Megacauda sungei gen. et sp. nov. holotype (PMOL-AM00026) is the only docodontan specimen, so far, with the ventral mesocranium preserved well enough to show most characteristics of the palato-pharyngeal vault (the bony roof of the naso-oro-pharyngeal passage) and its associated palatine bone and pterygoid bone (including pterygoid hamulus), much of which can be visualized from CT scans (**Fig 2; Extended Data Fig. 7; Supplementary Video S1**).

The cranial parts of the docodontan *Haldanodon* have been described by Lillegraven and Krusat (1991) (Ref 40) and Ruf et al. (2013) (Ref-134). But the skull specimens of *Haldanodon* were fractured by a considerably compression in fossilization. The palate-pharyngeal structure in these flattened skulls is obscured by extensive fractures and covered up by displaced bone fragments (Ref-11 Martin 2005; Ref-40 Lillegraven and Krusat 1991; Ref-134 Ruf et al. 2013: fig. 1). It is extremely difficult, if not impossible to reconstruct the palato-pharyngeal vault for *Haldanodon*. The previous composite reconstruction of the palate-pharyngeal structure of *Haldanodon* is conjectural (Ref-40 Lillegraven and Krusat 1991: fig. 2), and lacks detailed information on the pharyngeal vault. Of the skull materials of other docodontans, the *Microdocodon* type specimen (Ref-8 Zhou et al. 2019) is preserved as molds and outline impressions, the skull of *Docofossor* is bilaterally (left-right) compressed (Ref 12 Luo et al. 2015), and the skull of *Agilodocodon* (Ref-10 Meng et al. 2015) is missing some bone material from the mesocranium. Although the skulls of these taxa are represented in their fossil materials to a varying degree, it would be extremely difficult to attempt a three-dimensional reconstruction of the palate-pharyngeal structures.

Based on the new specimen of *Megacauda*, it is now feasible to characterize the palatine, the palato-pharyngeal vault and the pterygoid for a representative docodontan. This has allowed us to map the evolution of these structures across the cynodont-mammal transition, by comparison to cynodonts and other mammaliaforms.

In cynodont outgroups, the palato-pharyngeal vault was well documented in probainognathian cynodonts (Ref-41 Martinelli and Rougier 2007) including tritylodontids (Ref-135 Sues 1986), ictidosauroids (including tritheledontids) (Ref-41 Martinelli and Rougier 2007), and brasilodontids (Ref-136 Bonaparte et al. 2005; Ref-6 Rawson et al. 2024). The palato-pharyngeal vault was also described for the mammaliaforms *Sinoconodon* (Ref-137 Crompton and Luo 1993), *Morganucodon* (Ref-138 Kermack et al. 1981; Ref-139 Hopson and Barghusen 1986; Ref-140 Hopson 1987; Ref-1 Kielan-Jaworowska et al. 2004). This structure was illustrated for *Hadrocodium* (Ref-141 Luo et al. 2001), haramiyidans (Ref-9 Meng et al. 2017; Ref-142 Huttenlocker et al. 2018). Although not yet fully described, the palato-pharyngeal vault structure is also known from Mesozoic stem therians such as eutriconodontans (Ref-143 Wang et al. 2001; Ref-144 Martin et al 2015; Ref-145 Li et al. 2003). The

palato-pharyngeal structure is fully described for multituberculates (Ref-1 Kielan-Jaworowska et al. 2004; Ref-45 Wible and Rougier 2000; Ref-146 Hahn 1987), spalacotherioids (Luo et al. 2025) and *Vincelestes* (Ref-147 Rougier et al. 1992; Ref-148 Rougier 1993; Ref-149 Rougier et al. 2021). Given the position of docodontans in mammaliaform phylogeny, and on the basis of the new anatomical information from *Megacauda* (**Fig. 2 and Extended Data Figs. 4 and 7**), we are proposing a novel reconstruction of the musculoskeletal anatomy of the palate and pharyngeal passage, for an evolutionary interpretation of the transformation of these structures across the cynodont-mammal transition.

Palato-Pharyngeal Vault of *Megacauda* (PMOL-AM00026) (Fig. 2; Extended Data Fig. 7) – The horizontal plate of the palatine is well preserved and forms a major part of the secondary bony palate. The anterior parts of the two palatines have an anteriorly convex suture with the horizontal palatal plates of the maxillas. The lateral suture between the palatine horizontal plate and the maxilla appears to be straight (**Fig 2; Extended Data Fig. 7. Supplementary Video S1**). The posterior margins of the palatine horizontal plates form the periphery of the choana, which is the posterior opening of the nasal cavity. Dorsal and posterior to the choana opening, the bony roof of the naso-pharyngeal passage, herein called the naso-pharyngeal vault (*sensu* Ref-46 Barghusen 1986), is constituted partly by the palatines (paired), partly by the vomer and the cultriform process of the basisphenoid (along midline), and partly by the pterygoids (also paired) (**Fig. 2, Extended Data Fig. 7**). The lateral margin of the pharyngeal passage is formed (in antero-posterior sequence) first by the saddle-shaped crest of the palatine and then by the pterygoid hamulus (Fig. 2: palatine saddle and pt-hamulus respectively). The hamulus is a vertical, plate-like structure (**Supplementary Video S1**). Posterior to the choana and medial to the lateral margins of the pharynx, the naso-oro-pharyngeal vault (= “bony roof of pharynx”) has two prominent pterygopalatine ridges (**Fig. 2: pt-pa ridge**) (*sensu* Ref-46 Barghusen 1986), which are longitudinally oriented and continue from the nasopharynx and posteriorly to near the poles of the petrosal promontoria. These ridges subdivide the naso-oro-pharyngeal vault into three parallel channels. Below we describe the noteworthy osteological landmarks of the secondary palate and pharynx individually.

The Palatine Bone – By CT scans and visualization, the greater palatine foramen can be clearly recognized, and this foramen is located in the anterior part of the palatine horizontal plate near the junction of the palatine and maxilla. The lesser palatine foramen is located in the posterolateral part of the palatine horizontal plate. The palatine forms a prominent pyramidal process at the posterolateral corner of the bone, and this process overhangs a recessed area of the palatine (**Fig 2 and Extended Data Fig. 7**: palatine recessed; or palatine saddle). In ventrolateral view this pyramidal process protrudes out from the ventral aspect of the orbital margin. Adjacent to the pyramidal process the lateral (orbital) surface of the palatine is concave, and this concave area is here interpreted to be for the medial pterygoideus muscle attachment. Medial to this recessed area of the palatine, the lateral side of the naso-pharyngeal vault is saddle-shaped (Fig. 2 and **Extended Data Fig. 7**: palatine saddle). This palatine saddle is interpreted to be the passage of the tensor veli palatini (TVP) (to be further explained below).

The Pterygoid Hamulus (Fig. 2) – The hamulus is a plate-like structure on the side margin of the pharyngeal passage. The anterior end of the base of pterygoid hamulus is located posterior to the palatine saddle. Posteriorly the hamulus forms a free-standing hook (**Supplementary Video S1**). The pterygoid hamulus as identified here, shows most of the common characteristics of the pterygoid

hamulus in extant therian skulls (**Fig. 2; Supplementary Video S1**). In *Sinoconodon*, morganucodontans and haramiyidans (Ref-1 Kielan-Jaworowska et al. 2004; Ref-9 Meng et al. 2017; Ref-96 Huttenlocker et al. 2018), the pterygoid hamulus (“transverse flange of the pterygoid”) forms a straight alignment with the lesser palatine foramen (**Extended Data Fig. 7**). By contrast, in *Megacauda* the pterygoid hamulus (= transverse flange) is medially off-set (or in-set) from the imaginary longitudinal line from the lesser palatine foramen, and its neighboring pyramidal process. The pterygoid hamulus is a landmark structure of the bony pharynx, for the tensor veli palatini and the pterygopharyngeus muscle in extant placentals (e.g., *Canis*, Ref-32 Evans and de Lahunta 2013) and marsupials, such as *Didelphis* (**Extended Data Fig. 7**; see “muscle reconstruction” below).

The Pterygopalatine Ridge and Trough (Fig. 2 and Extended Data Fig. 7: pt-pa ridge, pt-pa trough) – The pterygopalatine ridges (*sensu* Ref-46 Barghusen 1986) in *Megacauda* are formed mostly by the pterygoid bone although likely their anterior part on the naso-pharyngeal vault is formed by the palatine. The pterygopalatine ridges extend posteriorly onto the basipterygoid parts of the basisphenoid bone (*sensu* Ref-138 Kermack et al 1981). The two lateral pterygopalatine troughs (also called the lateral choanal channels by Ref-44 Kielan-Jaworowska 1971), one on each side, are located between the pterygopalatine ridge and the pterygoid hamulus on the lateral margin of the vault. In *Megacauda*, the roof of the pharyngeal passage consists of its midline trough and two lateral troughs subdivided by the two ridges. The naso-oro-pharyngeal vault of *Megacauda* is a tri-partite passageway (*sensu* Ref-46 Barghusen 1986), or a “tri-radiate structure” according to Ref-44 Kielan-Jaworowska (1971: p. 26).

The two pterygopalatine ridges are common features of the pharyngeal vault of many mammaliaforms, as seen in *Sinoconodon* and *Morganucodon* (Ref-1 Kielan-Jaworowska 2004; Ref-137 Crompton and Luo 1993) as well as the majority of Mesozoic multituberculates (Ref-44 Kielan-Jaworowska 1971; Ref-45 Wible and Rougier 2000; Ref-1 Kielan-Jaworowska et al. 2004). But the development of these ridges can be variable across the phylogeny of major clades - they are weakly developed in the mammaliaform *Hadrocodium* (Ref-141 Luo et al. 2001), the haramiyidan *Cifellidon* (Ref-96 Huttenlocker et al. 2018), and the gondwanatherian *Vintana* (Ref-150 Krause et al. 2014). The ridges are absent in eutriconodontans (Ref-143 Wang et al. 2001; Ref-144 Martin et al. 2015; Ref-145 Li et al. 2003), in spalacotherioids (Ref-43 Luo et al. 2025) and in crown therians. Although prominent in many multituberculates, these ridges are known to be absent in the Cretaceous *Sloanbaatar*, and in Paleocene *Taeniolabis* (Ref-151 Krause et al. 2021) and in the taeniolabid multituberculate *Lambdopsalis* (Ref-152 Miao 1988). This structure is likely also absent in *Catopsbaatar* (Ref-153 Kielan-Jaworowska et al. 2005).

In Mesozoic mammaliaforms in which these ridges are present, they divide the naso-oro-pharyngeal vault in three troughs: the median pharyngeal trough along the midline and between the two pterygopalatine ridges. The main midline trough is obviously an air passageway from the nasal cavity through the pharynx to the glottis (Ref-44 Kielan-Jaworowska 1971; Ref-46 Barghusen 1986; Ref-31 Allin and Hopson 1992, fig. 28.10: Eu2; Ref-45 Wible and Rougier 2000; Ref-42 Crompton et al. 2018). But there were competing interpretations concerning the soft tissue occupants of the lateral pterygopalatine troughs (to be further discussed below).

Palato-Pharyngeal Vault of Cynodont Outgroups – In comparison to non-mammaliaform cynodonts, *Megacauda sungei* gen. et sp. nov. is derived in several characters of the palato-pharyngeal

vault. In non-mammaliaform cynodonts from probainognathids to tritylodontids, tritheledontids and brasilodontids, the ventral mesocranium forms a narrow midline girder posterior to the transverse pterygoid flange and anterior to the basisphenoid (Ref-139 Hopson and Barghusen 1986; Ref-140 Hopson 1987; Ref-154 Hopson and Kitching 2001). The girder-shaped mesocranial region is also perforated by the interpterygoid vacuities near the junction of the pterygoid and the basisphenoid in some cynodonts. The shape and size of these vacuities can be variable (Ref-135 Sues 1986; Ref-41 Martinelli and Rougier 2007). In cynodont skulls with this mesocranial girder configuration, the pterygopalatine ridges on the naso-pharyngeal vault are short, limited to the ventral aspect of the pterygoid. These short ridges are present in brasilodontids (Ref-41 Martinelli and Rougier 2007; Ref-42 Crompton et al. 2018; Ref-6 Rawson et al. 2024). By contrast, in the derived condition of mammaliaforms, the pterygopalatine ridges extend more posteriorly in a much wider pharyngeal vault. These ridges reach and overlap the basiptyergoid wings of the basisphenoid in *Sinoconodon* and *Morganucodon* (Ref-138 Kermack et al. 1981). The pharyngeal vault is much wider at the level of the basisphenoid in *Hadrocodium* (Ref-141 Luo et al. 2001) and *Megacauda* than in *Morganucodon* (**Fig. 2** and **Extended Data Fig. 7**). In *Megacauda*, the pterygopalatine ridge reaches all the way to the anterior pole of the petrosal promontorium.

Palato-Pharyngeal Vault in Comparison to Other Mammaliaforms – Several landmark palato-pharyngeal structures show contrasting differences between *Megacauda* and other mammaliaforms (**Fig. 2** and **Extended Data Fig. 7**): presence of the palatine pyramidal process and the adjacent, recessed surface of the palatine, which is dorsal to the pyramidal process in *Megacauda* (**Extended Data Fig. 7**: palatine-recessed and pyramidal process), versus the absence of these features in *Sinoconodon* and *Morganucodon* (**Extended Data Fig. 7**); presence of a saddle-shaped side margin of the vault, anterior to the hamulus (**Extended Data Fig. 7**: palatine saddle), versus the absence of this shape in *Sinoconodon* and *Morganucodon* (Ref-137 Crompton and Luo 1993; Ref-138 Kermack et al. 1981). In *Megacauda*, the pterygoid hamulus is medially shifted, and in-set relative the palatine pyramidal process and to the lesser palatine foramen. This is contrasting to a longitudinal, straight alignment of the hamulus to the lesser palatine foramen in *Morganucodon* (**Fig. 2**; **Extended Data Fig. 7**), and also in *Sinoconodon* and *Maiopatagium*.

In these features, *Megacauda* (**Extended Data Fig. 7**) is more similar to Mesozoic and extant therians, than to other mammaliaforms. The orbital process of the palatine has a distinct pyramidal process near the lesser palatine foramen in *Megacauda*. These major landmarks are also present in paulchoffatiid multituberculates (Ref-146 Hahn 1987), eutriconodontans (Wang et al. 2001; Gao et al. 2009; Ref-144 Martin et al. 2015), and in spalacotherioids (Ref-43 Luo et al. 2025). By contrast, this pyramidal process is absent in nonmammaliaform cynodonts, *Sinoconodon*, morganucodontans, haramiyidans (Ref-9 Meng et al. 2017; Ref-142 Huttenlocker et al. 2018) and the gondwanatherian *Vintana* (Ref-150 Krause et al. 2014). The orbital process of the palatine in *Megacauda* is recessed from the pyramidal process and its associated lesser palatine foramen, in contrast to the absence of a pyramidal process and lack of the recessed curvature in this location of the palatine in *Morganucodon* (**Extended Data Fig. 7**). In *Megacauda* (**Supplementary Video S1**), the hamulus is more in-set and spaced apart from the mandible, in contrast to the transverse pterygoid flange in alignment with the lesser palatine foramen (**Extended Data Fig. 7**), and the hamulus is positioned next to the mandible, as in *Morganucodon* and *Sinoconodon*. The condition of *Sinoconodon* and *Morganucodon* is essentially the same plesiomorphic pattern as seen in cynodont outgroups (Ref-135 Sues 1986; Ref-6 Rawson et al. 2024). In sum, *Megacauda* is more therian-like in the configuration of these landmark palato-

pharyngeal structures (lesser palatine foramen, palatine pyramidal process, palatine saddle, and in-set of the pterygoid hamulus spaced away from the mandible), than *Sinoconodon*, *Morganucodon*, and haramiyidans (**Fig. 2; Extended Data Fig. 7**).

Muscle Reconstruction of Palate and Pharynx

Based on this new comparative evidence of fossils and the mesocranial osteological pattern of extant therians, we offer a new muscular reconstruction for the palate-pharyngeal structure of *Megacauda sungei* gen. et sp. nov. (**Fig. 2, Extended Data Fig. 7**):

(1) Medial Pterygoideus Muscle – The concave area on the lateral orbital wall (of the palatine and the alisphenoid) recessed next to the pyramidal process is for the attachment of the medial pterygoideus muscle (SI-movie: medial pterygoid depression). This is the same area as the attachment site of the medial pterygoideus muscle in placental mammals (e.g. *Canis*, Ref-32 Evans and de Lahunta 2013) and in the marsupial *Didelphis virginiana* from our diceCT visualization (**Extended Data Fig. 7d-7f**). A comparable cave area on the alisphenoid (or alisphenoid/maxilla) in multituberculates was similarly interpreted to be for the origination of the medial pterygoid (Ref-44 Kielan-Jaworowska 1971; Ref-155 Gambaryan and Kielan-Jaworowska 1995: fig. 8b, Ref-45 Wible and Rougier 2000: p. 34).

(2) Tensor Veli Palatini Muscle (Fig. 2 and Extended Data Fig. 7: yellow arrow from orbital wall crossing over the hamulus) – The saddle on the side margin of the pharyngeal vault and anterior to the hamulus (**Fig 2**: palatine saddle) is the “notch” for the tensor veli palatini to cross over the hamulus to the velum of the secondary palate. In extant therians (Ref-32 Evans and de Lahunta 2013: fig. 6.16), the tensor veli palatini is a slender muscle that originates from the pharyngo-tympanal (eustachian) tube, and continues anteriorly to the lateral side of the hamulus, before crossing over the hamular hook (a functional trochlea for the muscle) to join the tendinous soft secondary palate between the two hamuli. In our *Didelphis* diceCT reconstruction, the tensor veli palatini muscle originates from the posteromedial border of the tympanic process of the alisphenoid, in close proximity to the passage of the eustachian tube as well. In mammaliaforms with postdentary attached middle ear, the therian mammal-like eustachian tube was probably not developed. Instead we interpret that the tensor veli palatini originated from the petrosal lateral flange (which is lateral to the petrosal trough), and also from the adjacent posterior process of the alisphenoid overlapping the petrosal lateral flange. This tensor muscle then continued anteriorly, lateral of the pterygoid hamulus, and it further crossed over the hamulus to insert on the tendinous soft secondary palate (the velum). By this reconstruction, we hypothesize that *Megacauda* already developed a therian-like tensor veli palatini to stretch and provide tension of the soft secondary palate.

(3) Pterygopharyngeus muscle (Fig. 2 and Extended Data Fig. 7: yellow arrow in lateral trough) – We propose that the lateral trough between the pterygoid hamulus and the pterygopalatine ridge was the origination site of the pterygopharyngeus muscle for *Megacauda*. In extant therians, the pterygopharyngeus is variably classified as a distinct portion of the superior constrictor muscle complex (e.g., Ref-156 Harrington, 1945; Ref-157 Tsumori et al., 2007; Ref-158 Sumida et al., 2017) or homologized as the entirety of the superior constrictor itself (e.g., Ref-39 Smith, 1992; Ref-159 Reiss, 1997; Ref-160 Yoshida et al., 2002). In most extant therians, the pterygopharyngeus has generally been described as a long and slender muscle that arises from the pterygoid hamulus (*Canis*:

Ref-32 Evans and de Lahunta 2013: figs: 6.17-6.17), from both the hamulus and the posterior margin of the medial pterygoid plate (humans: Ref-157 Tsumori et al., 2007; Ref-158 Sumida et al., 2017), from the caudal end of the pterygoid bone (*Cyclopes*: Ref-159 Reiss, 1997; *Suncus*: Ref-160 Yoshida et al., 2002), or from the base of the hamulus and the wall of the pharyngeal vault (*Didelphis*; **Extended Data Fig. 7d-7f**). The muscle then passes posteriorly and dorsally over the pharynx to insert on the dorso-midline raphe, for drawing the pharynx toward the soft secondary palate and to constrict the pharynx (Ref-32 Evans and de Lahunta 2013). The location and passage of the pterygopharyngeus in extant therians correspond to exactly the same locations as the two lateral pterygopalatine troughs. The pterygopharyngeus in extant therians is also closely associated with the base of the pterygoid hamulus, corresponding to the pattern in *Megacauda*. Thus we propose a new anatomical interpretation that the lateral pterygopalatine trough is for the pterygopharyngeus of mammaliaforms. The comparative merit of this novel reconstruction, relative to other competing interpretation of the soft tissue occupants of the pterygopalatine troughs, will be detailed below.

(4) Levator veli palatini (Extended Data Fig. 7c: yellow arrow from the flange of petrosal lateral trough to soft secondary palate) – We tentatively reconstructed the levator veli palatini here for *Megacauda*. In extant therians (e.g., *Canis* – Ref-32 Evans and de Lahunta 2013: fig. 6.16), the levator veli palatini is a slender muscle that originates from the pharyngo-tympanal (eustachian) tube, and continues posteriorly and ventrally on the wall of the pharynx. It passes between the pterygopharyngeus and the palatopharyngeus, with action to lift the soft palate (Ref-32 Evans and de Lahunta 2013; Ref-161 Tachimura et al. 2006). However, in mammaliaforms that have the postdentary-attached middle ear, the extant mammal-like eustachian tube was probably not developed. In lieu of the eustachian tube, we interpret for *Megacauda* that the levator veli palatini originated from the flange of the petrosal lateral trough, and probably also from the adjacent structure of the alisphenoid posterior process. In extant therians, the levator veli palatini inserts on the soft secondary palate. By comparison, in fossil mammaliaforms, the soft secondary palate was also a reconstructed structure, on which the reconstruction of the levator veli palatini would be based. Thus our restoration of the levator veli palatini for *Megacauda* is dependent on a prior conjectural reconstruction of the soft secondary palate. The reconstruction of this muscle is more conjectural than the reconstruction of other muscles.

Previous Hypothetical Reconstruction of Soft Secondary Palate and the Soft tissue Occupants of Lateral Pterygopalatine Troughs in Cynodonts and Mammaliaforms

In our reconstruction of the soft secondary palate for *Megacauda sungei* gen. et sp. nov., the postulated location of the tensor veli palatini is largely consistent with the palate-pharyngeal interpretation by Barghusen (1986) (Ref-46) Allin and Hopson (1992) (Ref-31), and Smith (1992) (Ref-39), although our reconstruction has a key difference in highlighting the pterygopharyngeal muscle (or the superior pharyngeal constrictor) which has not been considered by Barghusen (1986) (Ref-46), or in reconstructions by other workers.

Barghusen (1986) (Ref-46) reviewed the previous reconstructions of the soft secondary palate in cynodonts (Ref-162 Parrington and Westoll 1940) and soft tissue reconstructions of the palato-pharyngeal structure of Mesozoic mammals (Ref-44 Kielan-Jaworowska 1971; Ref-138 Kermack et al. 1981). Barghusen's (1986) (Ref-46) interpretation of the muscularized velum and the air passageways was endorsed by Allin and Hopson (1992) (Ref-31) and Smith (1992) (Ref-39). An

alternative reconstruction of a muscularized velum for cynodonts was proposed by Crompton (1995: fig. 4.5) (Ref-163). More recently, Crompton et al. (2018) proposed a more detailed reconstruction of the velum and its associated pharyngeal muscle for the cynodont *Brasilodon* and the mammaliaform *Morganucodon*. The Crompton et al. (2018) (Ref-42) reconstruction is similar to those of Parrington and Westoll (1940) (Ref-162), and Kielan-Jaworowska (1971) (Ref-44) in muscular interpretation of the lateral pterygopalatine troughs. Below we will analyze these contrasting reconstructions of the velum, its associated muscles, and the putative air passageways from historical studies:

Historical Hypothesis (1) – The Parrington and Westoll reconstruction (1940: p. 332, fig. 14) (Ref-162): In this interpretation, the attachment of the hypothetical velum would be on the pterygopalatine ridges inside the vaulted region of the nasopharynx in cynodonts (but mammaliaforms were not considered because mammaliaform skull fossils were unknown in the 1930s). This reconstruction for cynodonts was adopted by Fourie (1974) (Ref-164). Kielan-Jaworowska (1971) (Ref-44) partly agreed with Parrington and Westoll's (1940) (Ref-162) interpretation of the pharyngeal vault of cynodonts, and she went further to postulate, although “entirely tentatively,” that the posterior part of the lateral pterygopalatine trough would be for the attachment site of the tensor veli palatini in multituberculates (Kielan-Jaworowska 1971: p. 26 Ref-44). This was also adopted and further expanded by Crompton et al. (2018: fig. 7) (Ref-42), who interpreted that the soft tissue velum is attached to the pterygopalatine ridges, and from these ridges the velum would envelop the nasopharynx. This spatial arrangement of the velum would be consistent with the location of the pterygopalatine ridges on the vault roof and positioned medial to the side margins of the nasopharyngeal vault, and the lateral pterygopalatine troughs would be lateral (and external) to the velum (Ref-42 Crompton et al. 2018: fig. 7).

Historical Hypothesis (2) - The Barghusen-Allin-Hopson reconstruction was initially explained by Barghusen (1986) (Ref-46), and then augmented by Allin and Hopson (1992: fig. 28.10) (Ref-31). In cynodonts, attachment of the soft secondary palate (= velum) is interpreted to be attached on the lateral margins formed by the pterygoid and the ectopterygoid along the side walls of the nasopharyngeal vault (termed the choanal crests). These choanal crests continue medially with the posterior edge of the hard secondary palate that forms the periphery of the choana. In this reconstruction, the pterygopalatine ridges and the lateral pterygopalatine troughs are inside the nasopharyngeal space, and these lateral troughs are also enveloped by the velum forming the ventral floor of the nasopharynx. The lateral pterygopalatine troughs were interpreted to be occupied by air passageways connecting the nasopharynx to the middle ear cavity (Barghusen 1986 Ref-46; Allin and Hopson 1992 Ref-31), not by the tensor veli palatini as interpreted by Kielan-Jaworowska (1971) (Ref-44) or other muscle(s). Barghusen (1986) (Ref-46) also interpreted that the elevated posterior part of the pterygopalatine ridges could support the velum. Implicit in this configuration is that the pterygoid hamulus of extant therians is a transformed homolog of the larger transverse flange of the pterygoid in of non-mammalian cynodonts. Some variant versions of this reconstruction were further illustrated by Allin and Hopson (1992: fig. 28.10 Ref-31). The Barghusen (1986) (Ref-46) pharyngeal model was adopted by Smith (1992) (Ref-39), by Luo et al. (2002) (Ref-165), and by our current study.

Historical Hypothesis (3) – The Crompton et al. (2018: figs. 7 and 11) (Ref-42) reconstruction (see also Crompton 1995: fig. 4.5) incorporated elements of Barghusen (1986) (Ref-46) and Allin and Hopson (1992) (Ref-31), and also those by Parrington and Westoll (1940) (Ref-162) and Kielan-Jaworowska (1971) (Ref-44). In contrast to the Barghusen-Allin-Hopson reconstruction of a velum covering the entire extent of the pterygoid transverse flanges, Crompton (1995: fig. 4.5; 2018: fig. 7)

(Ref-163) reconstructed a smaller velum that stops short of the ectopterygoid and the pterygoid in cynodonts. This would leave the pterygo-palatine ridges on the pharyngeal vault exposed, allowing for these ridges to serve as attachment for the more posterior part of the velum, which is similar to the proposal by Parrington and Westoll (1940) (Ref-162). Crompton et al. (2018) (Ref-42) further suggest that in mammaliaforms (as seen in *Morganucodon*), the tensor veli palatini could originate from the space of the lateral pterygopalatine trough, in contrast to the Barghusen-Allin-Hopson reconstruction, in which the lateral trough was a space for air passage only, and would have no muscle attachment.

Discussion – When Parrington and Westoll (1940) (Ref-162) outlined their first hypothetical reconstruction of the soft tissue velum in therapsids and cynodonts, there was no comparative information on palato-pharyngeal structures from Mesozoic mammals. It was not until the 1970s when the pterygo-palatine ridges were first described in multituberculates (Ref-46 Kielan-Jaworowska 1971) and in *Morganucodon* (Ref-138 Kermack et al. 1981). The findings from multituberculates and *Morganucodon* provided the Mesozoic mammalian pharyngeal vault osteology that is intermediate between the plesiomorphic structure of cynodonts and the derived structure of extant mammals. The finding of pharyngeal vault structures in multituberculates (Ref-44 Kielan-Jaworowska 1971) also introduced new questions into the studies of palate-pharyngeal musculoskeletal evolution leading to the muscularized velum in extant therians.

The questions about the pharyngeal vault evolution from cynodonts to mammals are further complicated by the fact that in derived cynodonts, the ventral mesocranium forms a narrow girdle between the pterygoid part of the cranium and the basicranium (Ref-139 Hopson and Barghusen 1986; Ref-140 Hopson 1987). In many cynodonts the girdle also shows the unique feature of the interpterygoid vacuities (Ref-135 Sues 1986; Ref-41 Martinelli and Rougier 2007). In most cynodont skulls with this mesocranial girdle and interpterygoid vacuity configuration, the pterygopalatine ridges do not extend so far posteriorly like those seen in *Sinoconodon* and *Morganucodon* (Ref-1 Kielan-Jaworowska et al. 2004) and now also in docodontans (Fig. 2 and Extended Data Fig. 7). This adds to the uncertainty in interpretation of the pharyngeal soft tissue structure between cynodonts on the one hand, and mammaliaforms on the other. To resolve this homology question, we need first-hand anatomical information on the soft tissue occupants of the later pterygopalatine trough in stem mammaliaforms.

The three main historical hypotheses (1-3) differ from one another in one key anatomical interpretation: whether the pterygoid hamulus of extant therians is a homolog to the pterygoid transverse flange, or homologous to the pterygopalatine ridges of cynodonts (Ref-162 Parrington and Westoll 1940; Ref-46 Barghusen 1986; Ref-31 Allin and Hopson 1992; Ref-39 Smith 1992; Ref-42 Crompton et al. 2018). Each of these alternatives also proposed a soft tissue occupant in the lateral pterygopalatine trough. Each reconstruction has been criticized by further studies (Ref-42 Kielan-Jaworowska 1971; Ref-155 Gambaryan and Kielan-Jaworowska 1995; Ref-45 Wible and Rougier 2000). Here we are summarizing their respective weaknesses and inconsistencies and place this in comparative context (see also a review by Ref-45 Wible and Rougier 2000).

(1) Lateral Pterygopalatine Trough as a Nasopharyngeal-Middle Ear Air Passageway in Cynodonts (Barghusen-Allin-Hopson reconstruction) – The lateral pterygopalatine trough was an air passage from the nasal cavity in cynodonts. In multituberculates, the posterior extension of this passageway would connect with the eustachian tube of the middle ear cavity (Ref-46 Barghusen 1986;

Ref-31 Allin and Hopson 1992). The posterior part of the pterygopalatine trough in multituberculates is for an air passageway similar to the therian eustachian tube (Ref-46 Barghusen 1986), but not for attachment of the tensor veli palatini as reconstructed by Kielan-Jaworowska (1971). Wible and Rougier (2000) (Ref-45) discussed that the posterior part of the lateral pterygopalatine trough could be for an air passageway in multituberculates. However, as also argued by Wible and Rougier (2000) (Ref-45), it would be unlikely for cynodonts to have possessed a therian-like eustachian tube, as postulated (Ref-46 Barghusen 1986: fig. 6; Ref-31 Allin and Hopson 1992: fig. 28.10: Eu1). In therians (Ref-45 Wible and Rougier 2000: p. 83), the entrance of the eustachian tube into the pharynx is more posteriorly positioned, but it is not located so anteriorly at the anterior part of the pterygopalatine ridges, deeply inside the nasal cavity as required by Barghusen (1986) (Ref-46). We agree with Wible and Rougier (2000 Ref-45) on this observation, and further add that, with the large middle ear fully attached to the mandible in cynodonts, cynodonts likely lacked a crown mammal-like middle ear cavity that more fully separated from the mandible, and probably lacked a therian-like eustachian tube.

It is entirely reasonable to reconstruct the eustachian tube into the posterior region of the pharyngeal vault in those Mesozoic mammals (e.g. multituberculates) with disconnected middle ear from the mandible, based on comparison to *Canis* (Ref-32 Evans and de Lahunta 2013; Ref-46 Barghusen 1986: fig 6C), or as interpreted by Allin and Hopson (1992: fig. 28.10: Eu2) (Ref-31). However, reconstruction of a channel for the eustachian tube to extend to the anterior end of the pterygopalatine ridges in cynodonts (Ref-46 Barghusen 1986: fig. 6a) is not supported by the pattern of the eustachian tube in therians (Ref-45 Wible and Rougier 2000).

(2) Lateral Pterygopalatine Trough as a Groove for Tensor Veli Palatini (Reconstruction according to Ref-42 Crompton et al. 2018; and partly according to Ref-44 Kielan-Jaworowska 1971) – Crompton and coauthors (2018: figs. 7 & 11) (Ref-42) postulated that the lateral trough held the tensor veli palatini for the mammaliaform *Morganucodon*. This is comparable to an earlier (although “very tentative”) reconstruction for multituberculates by Kielan-Jaworowska (1971) (Ref-44); in this reconstruction the tensor veli palatini is placed in the posterior part of the lateral pterygopalatine trough. For the cynodont *Thrinaxodon*, Crompton et al. (2018: fig. 7) (Ref-42) postulated that the short lateral pterygopalatine trough on the pharyngeal vault was the attachment site for the soft tissue velum as proposed by Parrington and Westoll (1940) (Ref-162). But Crompton et al. (2018: fig. 11) (Ref-42) went further in reconstructing a medial slip of the pterygoideus muscle to muscularize the posterior half of the velum for the cynodont *Brasilodon*. This hypothetical medial slip of pterygoideus muscle would be a precursor to the tensor veli palatini of therian mammals.

The location of the velum postulated by Crompton et al. (2018) (Ref-42) is different from the anatomical observations by others (Ref-46 Barghusen 1986; Ref-31 Allin and Hopson 1992; Ref-39 Smith 1992). The latter studies interpret the velum to be attached to the pharyngeal vault margins (Ref-46 Barghusen 1986; Ref-39 Smith 1992), not to the pterygopalatine ridges. More importantly and as pointed out by Wible and Rougier (2000) (Ref-45), the lateral pterygopalatine trough would not be a suitable location for attachment of the tensor veli palatini as this muscle in extant therians is positioned posterior to the pterygoid hamulus, instead of being positioned anterior (and also medial) to the hamulus, as postulated for this muscle in multituberculates by Kielan-Jaworowska (1971) (Ref-44). Another observation by Wible and Rougier (2000: p. 83) (Ref-45) regarding this reconstruction was that the pharyngeal vault space would become too narrow as in the posterior parts two

pterygopalatine ridges are converging to each other, in location of the velum as hypothesized by Kielan-Jaworowska (1971) (Ref-44). Wible and Rougier (2000: p. 83) (Ref-45) further argued the shape of the lateral pterygopalatine trough of multituberculates is not like the morphology of a “muscle-fossa” in extant therians. Lastly, Kielan-Jaworowska (1971) (Ref-44) herself also explicitly stated that the pterygopalatine ridges of multituberculates are not homologous to the pterygoid hamulus of extant therians. This critique of the Kielan-Jaworowska (1971) (Ref-44) reconstruction by Wible and Rougier (2000) is similarly applicable to the reconstruction of the medial slip of the pterygoideus (= tensor veli palatini) for *Brasilodon* and *Morganucodon* by Crompton et al. (2018: fig. 11) (Ref-42).

(3) Lateral Pterygopalatine Trough as a Groove for the Medial Pterygoideus Muscle

(Gambaryan-Kielan-Jaworowska 1995 Reconstruction) – Kielan-Jaworowska (1971) (Ref-44) proposed a variant model of muscle reconstruction by suggesting that the medial pterygoideus muscle could be attached to the posterior part of the lateral trough. This was reiterated by Gambaryan and Kielan-Jaworowska (1995) (Ref-155). Hahn (1987: Abb. 8) (Ref-146) followed this interpretation, and illustrated this part of the lateral pterygopalatine trough of a paulchoffatiid multituberculate as the “fossa scaphoidea,” assuming the posterior part of the lateral pterygopalatine trough to be homologous to the scaphoid fossa on the lateral side of the human pterygoid bone for the medial pterygoideus muscles (Ref-44 Kielan-Jaworowska 1971). This reconstruction of the medial pterygoid muscle in the lateral pterygopalatine trough (Ref-155 Gambaryan and Kielan-Jaworowska 1995: p. 60) has a weakness in that the medial pterygoid muscles would be positioned too far posteriorly for the medial pterygoid muscle to function. Further, this reconstructed location of the medial pterygoid muscle is too deep in the trough. The lateral crest of this trough would obstruct the medial pterygoid for it to pass toward an insertion on the pterygoid fossa of the dentary, not an ideal interpretation for the medial pterygoid muscle (Ref-45 Wible and Rougier 2000: p. 83). The concave area on the lateral side of the palatine as identified by most studies on multituberculates (Ref-45 Wible and Rougier 2000; Ref-1 Kielan-Jaworowska et al. 2004) is a more suitable location for the medial pterygoideus, than the lateral pterygopalatine trough. We also prefer for the medial pterygoideus to be attached to the orbital aspect of the palatine (Supplementary Video S1).

New Reconstruction of the Pterygopharyngeal Muscle in Lateral Pharyngeal Trough (Fig. 2; Extended Data Fig. 7; Supplementary Video S1).

The pterygoid hamulus of *Megacauda sungei* gen. et sp. nov. shows compelling similarity to that of therian mammals (**Extended Data Fig. 7**). As preserved, both left and right pterygoid hamules have retained the anatomical relationship to the pterygo-palatine ridges, to the lateral pterygo-palatal troughs, and to the opening of the choana, as seen in extant therians (**Extended Data Fig. 7**) and as preserved in similar pattern in the stem trechnotherian *Origolestes* (Ref-43 Luo et al. 2025). This lends support to the scenario where the mammalian hamulus is homologous with the transverse pterygoid flange of non-mammalian cynodonts (Ref-46 Barghusen 1986). Because the pterygoid hamulus with its diagnostic hook-like morphology, and the pterygo-palatal ridge that lacks the hook-like morphology are both present in the *Megacauda* specimen, this new fossil evidence does not support the hypothesis that the therian hamulus could have derived from the pterygo-palatine ridge of cynodonts (Ref-42 Crompton et al. 2018). Our new proposal is that the lateral pharyngeal trough was the origination site of the pterygopharyngeus muscle in *Megacauda*. This is based on the compelling similarity in the shape and location of the pterygopharyngeus of extant therians, and on the close

association of this muscle with the base of the pterygoid hamulus of therians, just as the pterygoid hamulus is now recognized in the pharyngeal vault region of *Megacauda*. In *Canis* (Ref-32 Evans and de Lahunta 2013), the pterygopharyngeus is a long and slender muscle that arises from the base of the pterygoid hamulus, medial to the lateral wall of the pharyngeal vault. This muscle passes posteriorly and dorsally over the pharynx to insert on the raphe along the dorsal midline of the pharynx. Its action is to pull the pharynx toward the soft secondary palate and to constrict the pharynx for swallowing (Ref-32 Evans and de Lahunta 2013). As seen in *Canis* (Ref-32 Evans and de Lahunta 2013), the muscle starts at the base of the hamulus and the passage of this slender muscle along the medial surface of the side wall of the pharyngeal vault. This corresponds to exactly the same location and shape pattern as the lateral pterygopalatine trough and the base of the pterygoid hamulus in *Megacauda*. We now visualized the pterygopharyngeus muscle in a similar association with the pharyngeal vault, in the opossum *Didelphis virginiana* by diceCT visualization (**Extended Data Fig. 7e-f**). This muscle has been previously identified by Diogo and Powell (2012) (Ref-166).

The presence of the pterygopharyngeus, as a distinct (long and slender) muscle situated with the lateral wall of the pharyngeal vault, is a distinctive feature of therian mammals (Ref-166 Diogo and Powell 2012). The pterygopharyngeus muscle is contiguous with and often merged into the super pharyngeal constrictor muscle group. Thus, the muscle is called the superior constrictor in most human anatomy textbooks (Ref-167 Standring 2008). Nonetheless the muscle is still identified as “the pterygopharyngeal part of the superior constrictor” in some textbooks (Ref-168 Tillmann 2012: p. 127). In other (non-human) placental mammals, the pterygopharyngeus has been identified in *Hylobates* (Ref-166 Diogo and Powell 2012), both caniniform and feliform carnivores (Ref-169 McWhorter et al. 1999; Ref-170 Takada et al. 2009; Ref-171 Adachi et al. 1997; Ref-166 Diogo and Powell 2012), shrews (Ref-160 Yoshida et al, 2002), anteaters (Ref-159 Reiss, 1997), and euarchontans (Ref-172 Ziermann et al 2019). Most authors would agree that the pterygopharyngeus at minimum represents a distinct portion of the superior constrictor muscle complex that arises from the pterygoid hamulus and the medial surface of the pharyngeal vault border wall formed by the pterygoid. In crown therian mammals examined so far by this study, there is a strong link between the presence of the pterygoid hamulus and the presence of the pterygopharyngeus. An additional structure of attachment of the superior constrictor complex is the pterygomandibular raphe, which also takes origin from the pterygoid hamulus and the pharyngeal vault margin formed by the pterygoid bone.

As such, the first appearance of the hamulus associated with the lateral pterygopalatine trough in *Megacauda* is strong evidence that a differentiated pterygopharyngeus muscle, or a distinct superior constrictor muscle complex was already present in mammaliaforms (**Fig. 2** and **Extended Data Fig. 7**). *Megacauda* has preserved a combination of palatopharyngeal musculoskeletal features with a hyoid apparatus that shares the same saddle-shaped configuration as in modern mammals. This fossil further constrains the timing of evolutionary assembly towards the modern mammalian oropharyngeal complex (Ref-39 Smith, 1992). Rather than a gradual, piecemeal transition, the evolution of the novel mammalian pharynx is characterized by co-evolution of multiple anatomical structures spanning the mesocranium to the hyoid, thereby facilitating a fundamental reorganization in the form and function of the oropharyngeal space, and heralding the origin of unique mammalian feeding behaviors including suckling, mastication and powered swallowing.

The pterygoid hamulus (**Fig. 2** and **Extended Data Fig. 7**) is also related to other pharyngeal muscles, in addition to the tensor veli palatine and the M. pterygopharyngeus. Chief among these are

the *M. palatoglossus* (anterior pillar of the faucet) and *M. palatopharyngeus* (posterior pillar of the faucet). Presence of pterygoid hamulus provides an osteological proxy for the approximate location for the origination of these muscles related to the pharyngeal faucet (Ref-168 Tillman 2012; Ref-32 Evans and de Lahunta 2013; Ref-36 Li et al 2025; Ref-37 Mayerl and German 2023; Ref-173 Mayerl et al. 2021). Furthermore, to facilitate the fluid transport and suckling, tongue and its muscles must also be involved, as discussed by Mayerl and German (2023) (Ref-37). The presence of ventral saddle and segmented great cornus in *Megacauda* suggests that some hyolingual muscles (the styloglossus, the hyoglossus) could be present. These would function with the palatoglossus and the extrinsic tongue muscles for formation of the seals (Ref-37 Mayerl and German 2023; Ref-36 Li et al. 2025). Although the tongue itself is not fossilized in the *Megacauda* fossil, it is logical to argue that evolution of the pterygoid hamulus alongside the pterygopalatine trough could be accompanied by other neomorphic muscles of the faucet and the tongue in one integrated musculoskeletal complex.

(7) Preliminary Description of Postcranial Skeleton

Forelimb and Manus

Humerus – The humerus is preserved on the main-slab and the counter-slab of the *Megacauda* specimen. About 80% of the right bone can be reconstituted from the right humerus in (PMOL-00026A), and lateral silhouette of the right humerus in PMOL-00026B. The outlines of the preserved features are very similar to the humerus of *Haldanodon* (Martin 2005), which is represented by multiple specimens and the best-preserved humerus among docodontans. The humeral head is lost above its base, but the preserved part between the humeral head and the main shaft in both humeri indicates that the humeral head is inflected posteriorly, as seen in the humerus of *Haldanodon* (Martin 2005: fig. 8 Ref-11). We interpret that a large greater tubercle is partially preserved in three-dimension on the main slab, and located in the proximo-lateral corner of the left humerus. In the left humerus, the greater tubercle is continuous ventrally with a hypertrophied and flaring deltopectoral crest. This crest is completely preserved in the right humerus on the counter-slab (in compressed condition). The characteristics of the greater tubercle and the deltopectoral crest are identical to those of *Haldanodon*. The lesser tubercle is incomplete, and the vertical crest below the lesser tubercle is complete, but plastically deformed. The teres tuberosity is located at the end of the lesser tubercle crest, and this tuberosity is positioned approximately mid-length of the humeral shaft, comparable to the location of this feature in *Haldanodon* (Ref-11 Martin 2005).

The distal part of the humerus shows an enlarged ball-shaped radial condyle, and a spindle-shape ulnar condyle. The ulnar condyle and the intercondylar groove separating it from the radial condyle are slightly oblique such that the ulnar condyle, the intercondylar groove and radial condyle are shaped like a “spiral screw” pattern. The entepicondyle is not completely preserved in *Megacauda*, but based on the preserved part, it would be an enlarged structure, as seen in *Castorocauda* (Ref-13 Ji et al. 2006). The ectepicondyle is a large and plate-like structure and it shows a distinct supinator process (Ref-11 Martin 2005) projecting dorsally from the main part of ectepicondyle. The shape of this supinator process and the ectepicondyle are identical in *Megacauda* here, and in *Castorocauda* (Ref-13 Ji et al. 2006; Ref-10 Meng et al. 2015). But the supinator process and the ectepicondyle in *Megacauda* are less massive than those of *Haldanodon* (Ref-11 Martin 2005). The distal humerus shows a large entepicondylar foramen (for the median nerve in extant mammals). In the better-preserved humeri of *Haldanodon* and *Agilodocodon*, the anterior opening of this foramen is on the

anterior aspect of the distal humerus and located dorsolateral to the ulnar condyle. The posterolateral opening of the entepicondyle foramen is on the lateral edge of entepicondyle. The bone above the entepicondyle is fractured, such that the posterolateral opening cannot be determined, but the anterior opening of the entepicondylar foramen is very large (subequal to the size of ulnar condyle). The large size of this foramen is a derived feature of all docodontans including *Megacauda*, *Castorocauda*, *Haldanodon*, *Agilodocodon*, *Borealestes* and *Krusatodon* (Ref-11 Martin 2005; Ref-10 Meng et al. 2015; Ref-16 Panciroli et al. 2024; Ref-174 Panciroli et al. 2022). It is much larger than the entepicondylar foramen of *Morganucodon*, haramiyidans, and extant monotremes (Ref-175 Gambaryan et al 2013; Ref-176 Regnault et al. 2020; Ref-56 Hand et al. 2025).

We can partially reconstruct the missing humeral head (after the humeral head of *Haldanodon* – Ref-11 Martin 2005) and restore the missing part of the entepicondyle of *Megacauda*, after the more complete humeri of *Castorocauda* and *Haldanodon*). The estimated width would be 15 mm and the length would be 27.2 mm after the restoration. The humeral length/width ratio (sensu Ref-177 Hildebrand 1985) would fall into the range of the humeral length/width ratio of fossorial mammals. We interpret that the humerus of *Megacauda* has the shape characteristics of the humeri of fossorial mammals, and this inference is also applicable to *Castorocauda*, as previously noted by Ji et al. (2006) (Ref-13).

For the size of the whole animal, the humerus is relatively short. The humeral length at 27.2 mm is only 34% of the skull length of the *Megacauda* specimen. A relatively short humerus compared to the skull length is also known in the monotreme *Ornithorhynchus* at 36%. By contrast, the docodontans with arboreal specialization tend to have longer humeri relative to the skull, as seen in *Agilodocodon* with humerus/skull length ratio at 48%, and *Microdocodon* with this ratio at 41-43%.

Ulna – The posterior part of the ulna is characterized by a large olecranon process, a shallow and concave semilunar notch for articulating with the ulnar condyle of the humerus, and a shallow radial facet for articulating with the head of the radius. The diaphysis of the ulna is a simple shaft with a distal end in truncated and rectangular outline. In dorsal view the enlarged olecranon process is asymmetrical relative to the long axis of the ulna and strongly skewed medially. In lateral and medial views the olecranon process is bending in proximo-dorsal direction, with most of the olecranon bent far more dorsally above the semilunar concavity. This bending of the olecranon is also accentuated by the prominently convex curvature of the ventral ulnar margin leading to the end of the olecranon, and this convex curvature starts anterior to the level of the semilunar (trochlear) notch of the ulna, in contrast to this convex curvature starting posterior to the semilunar notch in all other mammaliaforms and cynodonts, also in a majority of extant mammals (Ref-178 Martin 2013; Ref-174 Panciroli et al 2022: fig. 12). This is a derived docodontan feature, but is much exaggerated and more prominent in *Megacauda*, *Castorocauda*, *Docofossor*, and *Haldanodon*, than in other docodontans (Ref-10 Meng et al. 2015; Ref-8 Zhou et al. 2019; Ref-174 Panciroli et al. 2022). This feature of the ulnar curvature in *Megacauda* is very similar to that of *Ornithorhynchus*.

The semilunar (trochlear) notch of the ulna is a shallow concavity with a long oval-shaped outline. The semilunar fossa is posteriorly bound by the anconeal process. The radial fossa is a shallow concave area demarcated anterolaterally from the semilunar fossa with a low crest homologous to the coronoid process the defines the anterior boundary of the semilunar fossa. This low crest also the common condition of docodontans as a whole (Ref-8 Zhou et al. 2019; Ref-178 Martin 2013; Ref-

174 Panciroli et al. 2022). This is in contrast to most cynodonts and mammaliaforms that typically have a well-defined coronoid process that separates the articulation of the humeral ulnar condyle from the articulation of the radius head on the ulna.

Comparative Discussion on Ulna – More specialized fossorial mammals tend to develop a larger triceps brachii muscle and a longer olecranon process for more powerful extension of the elbow joint for digging (Ref-177 Hildebrand 1985). By comparison, the more generalized terrestrial mammals or arborealist mammals would tend to have a shorter olecranon process (Ref-179 Samuels and Van Valkenburgh 2008; Ref-180 Chen and Wilson 2015; Ref-9 Meng et al. 2017; Ref-7 Grossnickle et al. 2020). This could be informative for interpretation of the forearm lever function of *Megacauda*.

The whole ulnar length is 36 mm in the *Megacauda* specimen. There are two alternative measurements of the olecranon length. If measured from the anconeal process or the posterior end of the semilunar fossa (*sensu* Ref-180 Chen and Wilson 2015), the length of olecranon is 8 mm. And the remaining ulnar would be 28 mm. Alternatively, if measured from the coronoid process or the anterior end of the semilunar fossa according to Hildebrand (1985 table 6-2) (Ref-177) the olecranon length is 10.5 mm, and the remaining ulnar length would be 25.5 mm. Assuming the latter scheme of measurement (Ref-177 Hildebrand 1985), the olecranon/ulna index (OUI) (*sensu* Hildebrand 1985) would be 41%. This index value (Hildebrand 1985) for the olecranon/ulna leverage is comparable to the values of 40% for the echidna (a superbly capable fossorialist) and about around 38% for the platypus (both fossorial and swimming). This value is 47% for the fossil docodontans *Docofossor* and 35% for *Haldanodon*, which were inferred to be fossorial and subterranean. Additionally, *Haldanodon* was also suggested to be both fossorial and semiaquatic (Ref-181 Martin 2006). By comparison, this ratio is 22% in *Agilodocodon* and 20% in *Microdocodon* (Ref-8 Zhou et al. 2019), both of which are interpreted to be arborealist mammaliaforms (Meng et al. 2015; Zhou et al. 2019). For a comparison to small extant mammals, 41% of OUI of *Megacauda* would be more specialized for digging, than the small fossorial mammals in the comparative dataset by Meng et al. (2017) (Ref-9).

Radius – The head at the proximal end of the radius is cup-shaped and it shows a thick circular margin around a concavity that fits to the ball-shaped radial condyle on the humerus. The radius head is wider than the shaft of the radius. Distally the radius has a wide and robust distal end, which corresponds to the relatively massive proximal carpals, and has a massive appearance due to its greater ratio of width to length. The wide distal radius corresponds, in robustness and in size, to massive proximal carpals, especially the hamate. These features of the radius are reinforcing the strength of the wrist joint.

Carpals, Metacarpals and Phalanges – The proximal row of carpals includes a relatively massive scaphoid, which also appears to be fused to the lunate. The triquetrum is the smaller bone. A displaced bone on the lateral side of the proximal carpal row shows a peg-like shape, we tentatively identify as the pisiform that is commonly attached to the lateral side in the carpals. In the distal carpals, the hamate is likely the element on the lateral side. In the middle of the distal carpals is a larger element that appears to be fused from two bones (or two bones that are compressed together in fossilization), which we tentatively identify as the capitate and the trapezoid. One carpal bone was displaced to between the metatarsals 3 and 4. We tentatively identify it to be the trapezium. The metacarpals and phalanges from digit-ray 1 to 5 have a phalangeal formula of 2-3-3-3-3, the typical

plesiomorphic pattern of cynodonts (Ref-182 Hopson 1995) and a plesiomorphic feature of mammaliaforms (Ref-79 Zhou et al 2013; Ref-12 Luo et al 2015; Ref-91 Luo et al. 2017; Ref-183 Bi et al. 2014) and crown Mammalia. The longest digit-rays are 3 and 4.

Comparative Discussion – The metacarpals and proximal phalanges of digit-rays 2-5 of *Megacauda* are not some slender bones as seen in *Agilodocodon* and *Microdocodon*. The terminal phalanx for each of digits 2-5 shows the typical distal phalangeal morphology. A proximal surface has a dorsal lip and ventral lip for a concave surface for the pulley-shaped end of the intermediate phalanx. The terminal phalanx also has a small protuberance for insertion of the digital flexor muscle. The “claw” part of the terminal phalanx has a generalized morphology, closest to the shapes of generalized terrestrial mammals, neither bilaterally broad (as in *Docofossor*), nor bilaterally compressed with a tall profile in side-view as in *Agilodocodon* (Ref-10 Meng et al. 2015) and many other arboreal mammaliaforms (Ref-91 Luo et al. 2017) or crown mammals (Ref-184 MacLeod and Rose 1993; Ref-185 Maiolino et al. 2023).

The digit-ray 3 intrinsic phalangeal index (length proportion of [proximal phalanx + intermediate phalanx]/metacarpal) for the left hand of *Megacauda* is above the phalangeal index value of the terrestrial-semifossorial mammals (above the 75% quantile) and below the phalangeal index value of the extant arboreal mammals (below the 25% quantile), on a dataset by Meng et al. (2017 Ref-9) and also Grossnickle et al. (2020) (Ref 8).

Vertebrae, Ribs and Ribcage

Vertebrae and Dorsal Ribs (Extended Data Figs 1, 2) – The bone materials of the postcranial skeleton are mostly preserved on the main-slab (PMOL-AM00026A – Extended Data Fig. 1), while some bones are also preserved on the counter-slab (PMOL-AM00026B – Extended Data Fig. 2). A majority of postcranial features are also imprinted in outlines that can be reasonably well matched between the slab and the counter-slab.

The vertebrae, as exposed, show their features in lateral, or ventrolateral aspect. A full set of 18 ribs of the animal on the right side of the main part are accounted for. Individual ribs can be broken, with parts thereof split between the main part and the counter-slab. Or the ribs are represented by outlines matched between the two slabs. This series of 18 ribs is fully recognizable. We can identify from the first right rib (rib-r1) that would mark the thoracic inlet or the anterior opening of thoracic ribcage in life. The 18th right rib can also be identified, and this is the posterior-most rib recognizable.

The counter-slab (Extended Data Fig. 2) has preserved segmental outlines of the two posterior cervicals, which we identify as C6 (?) and C7 (?). We further identify the anterior (“thoracic”) vertebrae (T1-T3) that are preserved and reasonably well exposed upon the slit of the two slabs. On the main-slab, the cervical-thoracic transition is not fully exposed because it is covered up by the dislocated right scapula. Furthermore, the skull is exposed on its dorsal aspect, in contrast to the thorax that is mostly exposed on the right ventro-lateral aspect. From this we can infer the anterior cervical series got twisted in fossilization and damaged, which is further obscured by the coverage of the right scapula on the cervicals. Given this preservation, our identification of C6? and C7? are tentative, but we can at least identify these posterior cervicals. The cervicals lack fusion of cervical ribs. The identification of T1-T3 is more reliable as these are associated with thoracic ribs. *Megacauda* has a

total of 21 dorsal vertebrae. Dorsal vertebrae D1 through D18 have ribs. But dorsal vertebrae 19-21 lack ribs.

Our CT scans show two sacral vertebrae in articulation with the pelvis of PMOL-AM00026A, the same as in the un-named docodontan SDUST-V0007 and *Microdocodon* (Ref-8 Zhou et al. 2019). The sacrals have rectangular transverse processes (transversely expanded) for the ilio-sacral articulation. The two sacrals have fully developed zygapophyses, which are un-fused between Sacral 1 and Sacral 2. The articulation of Sacral 1 prezygapophysis to the D21 postzygapophysis is fully mobile. The articulation of the Sacral 2 postzygapophysis to the prezygapophysis of caudal 1 is also fully mobile. The sacral vertebral centra show oval outlines on their anterior and posterior ends.

Our rendering of CT scans confirms that the anterior (proximal) four caudal vertebrae (Ca1-Ca4) are pelvic caudals. Ca1-Ca3 are well inside the pelvic space; Ca4 is preserved in such a way it overlaps the ischial blade in the compressed fossil slab. But the Ca4 can be interpreted to be overhanging in the space above the ischial blade in life.

The region of proximal caudals (Ca1-Ca10) is defined as the caudals with zygapophyseal articulation (*sensu* Ref-186 Organ 2010; Ref-187 Russo 2015; Ref-188 Hofmann et al. 2021). The anterior ten caudal vertebral neural arches have recognizable zygapophyses – the most distal caudal vertebra on which we can identify bone traces of the anterior zygapophysis is Ca10 (on the counter slab). Based on this, we interpret Ca1 – Ca10 have zygapophyseal articulation, thus are defined as the proximal caudals according to categories of caudals by other studies on mammalian vertebral columns (Ref-186 Organ 2010; Ref-187 Russo 2015; Ref-188 Hofmann et al. 2021). Ca11-Ca15 are transitional caudals, ending in Ca15 which is the longest vertebra (*sensu* Ref-186 Organ 2010; Ref-188 Hofmann et al. 2021). Ca15 happens to be preserved with lateral view exposed, and its lateral silhouette clearly indicates the presence of a weakly developed neural arch-zygapophyseal structure. Ca16 is identified here as the last vertebra with some metapophyseal feature (*sensu* Ref-188 Hofmann et al. 2021). In the transitional Ca11 - Ca14, the neural arch structure is recognizable although only preserved as traces (not in 3D structure). From the Ca6 to more posterior positions through caudal 15, the dorso-ventral dimension of each caudal vertebra becomes more compressed.

The transverse process(es) are prominent features in the proximal and transitional regions of the caudal vertebral column. These show an antero-posterior gradient of variation. The first four caudals (Ca1-Ca4) have a single transverse process that is wing-like, elongate and long relative to the antero-posterior length of the centrum. The transverse processes on Ca1-Ca4 are represented either by bone, or impression outlines. The lateral end of this process has a rectangular outline. In Ca1-Ca4, the single transverse process is positioned near mid-length of the vertebra.

By contrast to the preceding caudals, Ca5 has two pairs of transverse processes, of which the anterior transverse processes are long and shifted to the anterior end of the vertebra. This pair of anterior transverse processes is in juxtaposition with the paired posterior transverse processes positioned in the posterior part of the Ca5 vertebra. The posterior processes are shorter than the anterior pair of processes, and less well expressed. As a result of this size difference between the anterior pair and the posterior pair of transverse processes, the Ca5 vertebra has a “butterfly-shape” in dorsal view (*sensu* Ref-13 Ji et al. 2006).

More specifically for *Megacauda* (although *Castorocauda* is slightly different) the vertebrae from Ca6 through Ca10 have the two pairs of transverse processes in approximately equal size, such that the vertebrae resemble an “H”-shape if the tail is oriented horizontally. This caudal vertebral pattern is also known as double (or “bifurcated”) transverse processes. Then the transverse processes of the caudals in successively more posterior positions are reduced in size and become hourglass (or dumbbell) shaped in Ca13-Ca14. More posteriorly from around Ca14, these transverse processes decrease in size, successively, from Ca16 to further caudals in more posterior positions, the vertebrae show a simple oblong outline.

From Ca16 to the tail end, the vertebrae are interpreted to be cylindrical in life but are preserved as oblong shape. The last four caudal vertebrae become even smaller posteriorly to diminishing small size in the last two segments. This is a typical pattern of the tail end of mammals. The last several caudals are surrounded posteriorly by soft tissue halo and the preserved pelage outline of the tail end. These features show that the entire tail of *Megacauda* is preserved.

Haemal Arches (Chevron bones) in Caudal Vertebral Column – The chevron bone or haemal arch is present in the caudal vertebral column of most mammals. Most of the haemal elements (chevron) that can be identified in the *Megacauda* holotype are small bones lodged between Ca5 (the first fully post-pelvic caudal) and Ca6. This determination is consistent with the pattern of many extant mammals in which the proximal-most haemal element is present at the first full post-pelvic vertebra (Ref-32 Evans de Lahunta 2013; Ref-189 Warburton et al. 2015; Ref-190 Zavodszky and Russo 2020). The last (distal-most) identifiable chevron is located between Ca18 and Ca19. The chevron located between Ca14 and Ca15, and another between Ca16 and Ca17 are V-shaped or open V-shaped, a common chevron bone feature. The anterior chevron bones are not exposed in *Megacauda*. Elsewhere in docodontans, a well-preserved forked chevron bone (in side view) and V or Y-shaped in cross section (*sensu* Ref-190 Zavodszky and Russo 2020) has been found in *Borealestes* (Ref-174 Panciroli et al. 2022). We interpret that the haemal arches in anterior caudal vertebrae of *Megacauda* would be similar.

The presence of the haemal arch element can be identified at the junction of Ca18 and Ca19, which we interpret to be the terminus of the haemal elements. The anterior-most “starting” chevron at the Ca5-Ca6 junction in *Megacauda* is consistent with the pattern in the well-preserved caudal vertebral column of *Microdocodon* (Ref-8 Zhou et al. 2019), in which the anterior-most chevron element is also located at the Ca5-Ca6 junction. The last (posterior-most) haemal element of *Microdocodon* is located at the Ca12-13 junction, in a caudal vertebral series that ends at Ca22 (Ref-8 Zhou et al. 2019: fig. 1). Thus, the total number of caudal vertebrae (a proxy to the length), and the posterior extent of the haemal arch elements (relative to the total tail vertebral count) are lower in *Microdocodon*, than in *Megacauda*. Shapes and sizes of the successive chevrons along the tail, and their posterior extent are proxies to the development of ventral caudal flexor muscles, which are relevant for prehensile capability and for function in body support and locomotion (Ref-186 Organ 2010; Ref-190 Zavodszky and Russo 2020; Ref-191 Dawson et al. 2014).

Several caudal vertebral characters have implications for the interpretation of the tail musculoskeletal functional morphology in mammals. These include (1) the antero-posterior gradient of vertebral morphologies (size, shape, relative positions in the series); (2) the elongate single transverse process of the proximal caudals; (3) the double transverse processes of middle caudals; and (4) the posterior

extent of the fully formed zygapophyseal articulation (Ref-48 Gambaryan et al. 2002; Ref-192 Argot 2003; Ref-186 Organ 2010; Ref-32 Evans and de Lahunta 2013; Ref-193 Ercoli et al. 2013; Ref-191 Dawson 2014; Ref-187 Russo 2015) would have implications for interpretation of the tail musculoskeletal functional morphology for mammals (Ref-192 Argot 2003). These are also key features in influencing tail shapes, which will be further explored in more details below.

Thoracic Ribcage Reconstruction – Three sternal segments (sternebrae) can be identified. These appear to correspond to the three sternebrae in the middle part of an intact sternal series preserved in *Microdocodon* (Ref-8 Zhou et al. 2019). But the paired sternal manubria and interclavicle, and the xiphoid process, as seen in *Microdocodon*, are missing in the *Megacauda* fossil. The interclavicle-sternal series in ventral aspect of the ribcage (**Extended Data Fig. 10**) is reconstructed from the well-preserved structure of *Microdocodon* (Ref-8 Zhou et al. 2019). The thoracic inlet (anterior opening) of the ribcage is conjectural. But the posterior opening of the ribcage can be reconstructed, more reliably, on the basis of very distinct costal plates of the posterior ribs that can be identified. These overlapping costal rib-plates are known to be positioned in the posterior part of the ribcage and are aligned around the posterior ribcage opening in extant monotremes (**Extended Data Fig. 10**), although we should note that these posterior costal rib plates and the reconstruction are putative.

Of the 18 rib-bearing dorsal vertebrae, D1-D7 bear the sternal ribs (or the “true” ribs) defined by each rib directly joining the sternebral series (*sensu* Ref-32 Evans and de Lahunta 2013). D8-D14 bear asternal ribs (also known as the false ribs), which are the ribs that are not directly connected to the sternal series, each individually. Rather they are characterized by plate-like costal cartilages overlapping each other; the adjoining costal plates join the sternal series as an assemblage. On the last dorsal vertebrae D15-D18, the ribs do not show costal cartilages. Each of these is successively shorter more posteriorly, and the rib on the last (D18) is only 3 mm long. We interpret that a costal cartilage is absent on D15-18 and these are floating ribs not connected to the sternal series. We interpret that the thoracic ribcage is at its widest in the D13-14 region because ribs 11-15 are relatively longer than the rest, and ribs 13-14 are the longest.

A noteworthy feature of the rib bones from the D6 to D14 positions is their plate-like morphology, in ventral (distal) half of the rib, in contrast to the dorsal (proximal) part of a rib, which is more rod-like (**Extended Data Fig. 10**: CT visualization of left ribs D6 and D7). The plate-like distal part is slightly twisted around the longitudinal axis of the rib, relative to the rib’s proximal section. The plate-like distal part appears to be also present in the more posterior ribs of D12-D14.

Imbricated Costal Rib Plates – The calcified costal ribs (as shown by XRF fluorescence photographs) are a strikingly distinct feature. Starting anteriorly at D7, the calcified cartilaginous costal ribs are plate-like. The calcified costal plates of D8-D12 are so wide and board-like that they are partially or extensively overlapping the previous costal plates and with each other; they collectively form a successively imbricated pattern of costal plates, through the costal cartilage of D13. The costal cartilages of D13 and 14 are thin-rods that are in side-by-side contact with each other and with the costal plate D12.

The imbricated costal rib plates are a distinct and highly derived pattern of *Megacauda*, in contrast to the thin and rod-like cartilaginous costal ribs of other docodontans fossilized with the ribcage (or parts thereof), as seen in *Agilodocodon*, *Docofossor* and *Microdocodon* (Ref-12 Luo et al. 2015; Ref-10

Meng et al. 2015; Ref-8 Zhou et al. 2019). *Borealestes* also has simple, rod-like primary ribs (Ref-174 Panciroli et al. 2022). Although its costal cartilaginous ribs are not preserved (Panciroli et al. 2022), we infer that *Borealestes* lacks the ventral widening of the primary ribs as seen in *Megacauda*. Likely *Borealestes* also has simple cartilaginous ribs. Plate-like and imbricated, (either cartilaginous or calcified) costal plates and the related widening of the distal parts of the primary ribs, are a highly derived feature of *Megacauda* and *Castorocauda*.

Re-interpretation of the Plated Ribs of *Castorocauda* – The better XRF photographs of the new *Megacauda* specimen can clearly differentiate the rib bones (proximal rib connected to each vertebra), and the imbricated bands of calcified costal plates. This has prompted us to re-examine the previous report on the “plated ribs” of *Castorocauda*. By better fossil evidence available now (**Extended Data Figs. 1, 2 and 10**), it becomes clear that the imbricated costal cartilage plates, as seen here in *Megacauda*, are also present in *Castorocauda*. But these were incorrectly interpreted to be “plated proximal ribs” (Ref-13 Ji et al. 2006: fig. 1 and p. 1126). We do not exclude the possibility that the proximal bony ribs can have a plate-like morphology in *Castorocauda*, by comparison to the plate-morphology of ribs 6 through 14 in *Megacauda* (**Extended Data Fig. 10**). But we re-interpret the area of wider overlaps in between “the proximal rib plates” as actually representing the calcified plates of costal cartilages. The statement on the similarity of these structures to the proximal rib plates of nonmammalian cynodonts (Ref-13 Ji et al. 2006: p. 1126) is no longer valid. This wrong interpretation was by Zhe-Xi Luo, one of the co-authors of both this paper and the Ji et al. (2006) paper (Ref-13).

Comparative Morphology of Ribcages of Monotremes (Extended Data Fig. 10) – This pattern of the imbricated costal plates of *Megacauda* (also re-interpreted to be present in *Castorocauda*) is shared by extant monotremes although slightly different. But these imbricated costal cartilage plates are absent in extant therians (“overlapping ventral ribs” of Ref-194 Gregory 1947, Ref-195 Gregory 1951; Ref-196 Lessertisseur and Saban 1967a).

In both *Ornithorhynchus* (**Extended Data Fig. 10**: FMNH16035, 16038) and *Tachyglossus* (FMNH42758, 60903, 60905), each costal rib has two segments: the ventral (sternal) segment also known as costal rib or costal plate (depending on rib position), and the intermediate segment between the rib and the ventral costal segment. The intermediate segment is a calcified cartilage rod in all dorsal rib positions (including both sternal and asternal ribs). By contrast, in the sternal ribs D1-D6, the ventral (sternal) segment is a rod-shaped bone (fully ossified) for ribs in these positions, and this ventral segment becomes a bone-plate at the D6 position. In the asternal rib positions (D7 and more posterior), the ventral segments are formed by broad plates oriented almost horizontally; each plate overlaps the preceding plate, in a successively imbricated pattern.

Tachyglossus and *Ornithorhynchus* show slightly different forms of this imbricated pattern: most specimens of *Tachyglossus* that we examined have six imbricated and calcified ventral costal plates. But one specimen of *Tachyglossus* (FMNH145467) has seven imbricated costal plates. In *Tachyglossus*, costal plates in more anterior rib positions of this series can become secondarily ossified into bone. By contrast, *Ornithorhynchus* has eight calcified costal plates in this imbricating series, and none of the calcified costal plates shows secondary ossification in the specimens that we have examined. Overall, *Megacauda* (**Extended Data Fig. 10**), likely also *Castorocauda* as re-interpreted here, have 6 calcified costal plates staggered into the imbricated series. By number of costal plates

staggered into the imbricated series these docodontans are more comparable to *Tachyglossus*, than to *Ornithorhynchus*.

There is a major morphological difference between extant monotremes and the Jurassic megacaudids. In monotremes, the sternal segment of the costal rib is fully ossified bone for thoracic ribs D1-D6, but the intermediate segment of these rib positions is calcified but not full ossified. By contrast, all costal ribs are calcified. Furthermore, the calcified costal ribs of D7 through D12 are also widened to be plate-like, forming the distinct pattern of imbricated costal-plates (**Extended Data Fig 10**).

Osteological Reconstruction of the Pelvis

Composite Pelvis Reconstruction (Extended Data Figs 1 and 2) – More bone material of the pelvic structure is preserved on the main slab (PMOL-AM00026A) than on the counter-slab (PMOL-AM00026B) of the *Megacauda* specimen. On the main-slab, it was feasible to visualize the preserved components of the pelvis on a local block of the main-slab from CT scans. But the counter-slab is not suitable for CT scans because only impressions are preserved. The sacral and proximal caudal vertebrae and the pelvis are compressed together and these compressed bones sustained damage. Nonetheless, our CT scans recovered some of the structures (**Fig. 4b**). In addition to CT visualization of the pelvis of the main-slab, XRF florescence photos of both the main-slab and counter-slab also revealed the matching outlines of bones, and this was helpful for identifying major features.

For this study, we were able to CT scan a well-preserved pelvis in intact articulation with sacral and associated proximal caudal vertebrae of an unnamed docodontan (SDUST-V0007) (**Fig. 4c**). The pelvis of SDUST-V0007 has yielded the bone morphology for a full restoration and three-dimensional model of the pelvis of *Megacauda*. The pelvis (**Fig. 4** and **Extended Data Fig. 8; Supplementary Video S2**) is a composite of the less complete and fractured bones of PMOL-AM00026 and the more complete pelvis of the unnamed docodontan SDUST-V0007.

The well-preserved pelvis of SDUST-V0007 is also informative for re-study of the CT scans of *Docofossor* (BMNH131735) by comparison. We can now identify major features preserved in the incomplete pelvic girdle of *Docofossor*. With search images newly available from this composite model of PMOL-AM00026A and SDUST-V0007, we have now also identified more of the previously un-identified features in the pelvis of *Microdocodon* (PMOL-AM00025). These newly identified features are now also consistent with those preserved in the *Agilodocodon* specimen, and with the features of the newly published pelvic elements of *Krusatodon kirtlingtonensis* (Pancirol et al. 2024: extended data fig. 6), although all pelvic elements are slenderer in *Krusatodon* (Pancirol et al. 2024), than in *Megacauda* and the specimen of SDUST-V0007. It is now possible to characterize the pelvic structure of docodontans as a whole.

Based on the composite anatomical reconstruction (**Fig. 4; Supplementary Video S1**), we can now fully interpret the three-dimensional configuration by both the left and the right halves of the pelvis for a docodontan. Each half pelvis consists of the ilium, the pubis and the ischium with all major structures of each bone. Previously, only the ilium was described for *Haldanodon* (Martin 2005). The pelvic anatomy of *Castorocauda* (Ref-13 Ji et al. 2006) has not been described because the pelvis and its associated vertebrae are compressed together into the slab and much of the pelvic anatomy is not exposed. Previously the separated ilium and ischium have been described for *Morganucodon* (Ref-

197 Jenkins and Parrington 1976). For comparative morphology of mammaliaform cynodonts, the ilia of the tritylodontids *Oligokyphus* and *Kayentatherium* were described (Ref-198 Kühne 1956; Ref-199 Sues and Jenkins 2006) followed by the study of a complete tritylodontid pelvis by Sullivan et al. (2013 Ref 200). A partial pelvis is also described for the mammaliaform *Brasilodon* (Ref-201 Guignard et al. 2019). However, the orientation of the iliosacral joint and the main features of the pubis - two key parts of the pelvic structure – are so far unknown for any mammaliaform cynodonts and for mammaliaforms.

Acetabulum, Obturator Foramen and Pelvic Symphysis (Fig. 4) – The acetabulum for the hip (acetabulofemoral) joint is on the lateral aspect of the pelvis. The joint structure is large relative to the overall size of the pelvis, and slightly larger than the obturator foramen. The acetabulum is a bowl-shaped depression and we tentatively interpret that the acetabular floor is formed more by the ischium and the pubis, than by the ilium, in a tripartite configuration, which is estimated from the faint suture pattern on the CT model. The acetabular depression has an oval shaped peripheral outline. The anterior to anteroventral circumference is defined by a curved crest, formed in part by the ilium anteriorly, and in part by the pubis anteroventrally. The posterior quarter of the acetabular circumference is a pronounced and curved crest, formed by the ischium, buttressing the acetabulum posteriorly. The acetabulum is emarginated on its dorsal part between the ilium and the ischium, and shows a concave contour in dorsal view of the pelvis. The emarginated part of the circumference crest is under-developed, and weaker than the circumference crests formed by the ilium and the ischium. The posteroventral part of the acetabulum has a well-developed acetabular notch and this notch is continuous with the acetabular fossa extending toward the center of the acetabular floor. The acetabular fossa has an oblong outline. The acetabular notch is a distinct feature and it segregates the ischial buttressing crest from the pubic crest around the acetabular margin.

The obturator foramen is best seen from the ventrolateral perspective of the pelvis. It has a pear-shaped outline, wider and more rounded along the periphery formed by the ischium, narrower in the periphery formed by the pubis, and shows a pubis notch. The pubic symphysis is formed by the left and right pubes in the anterior 1/3, and by the left and right ischia along the posterior two-thirds along ventral midline. In the ventral view of the symphyseal region of the pelvic girdle, the anterior border of fused pubes is nearly straight. The posterior border of the pubic symphysis is a wide “V”-shaped pubic notch (also known as ischiatic arch in veterinary anatomy, or pubic arch in human anatomy), formed between the left and right ischial plates (or blades). The entrance of the pelvic space (pelvic inlet in human anatomy) has a nearly rectangular shape.

Comparison on General Pelvic Features – The emarginated acetabulum is a common pattern for mammaliaforms (Ref-197 Jenkins and Parrington 1976; Ref-199 Sues and Jenkins 2006; Ref-201 Guignard et al. 2019; Ref-4 Bishop and Pierce 2023, Ref-216 Bishop and Pierce 2024a), and a phylogenetic plesiomorphic character (Ref-71 Rowe 1988; Ref-165 Luo et al. 2002). The relatively small obturator foramen (in proportion to overall pelvis size) is a common pattern of multituberculates (Ref-54 Kielan-Jaworowska and Gambaryan 1994) and spalacotherioid stem therians (Ref-202 Luo and Ji 2005; Ref-203 Li and Luo 2006), to some extent also of eutriconodontans (Ref-204 Hu 2006; Ref-205 Chen et al. 2017). Extant monotremes (Fig. 4) have small obturator foramen, and in the extreme case of *Tachyglossus*, the obturator foramen is even smaller than the acetabulum. However, in the crown therians and its near relatives (such as *Henkelotherium*) the obturator foramen is large (Ref-206 Jäger et al. 2019).

The slightly inflected head on a short (almost not developed) neck of the femur can fit into the emarginate acetabulum such that the femur can be held at a partly abducted angle from the sagittal plane (**Fig. 4**) in docodontans, as interpreted for other mammalianomorphs and *Morganucodon* that have similar morphologies of the acetabulum and the femur (Ref-197 Jenkins and Parrington 1976; Ref-199 Sues and Jenkins 2006; Ref-200 Sullivan et al. 2013; Ref-201 Guignard et al. 2019; Ref-4 Bishop and Pierce 2023). In this femur posture, the large lesser trochanter of the femur is aligned with the pubic saddle for the iliopsoas muscle tendon to insert on the lesser trochanter (more discussion on muscle reconstruction, below).

Ilium (Fig. 4; Supplementary Video S2) – The ilium consists of the acetabular region in posterior part, the wide and plate-like wing with flaring margin in the anterior part, and a robust shaft in the middle, and the shaft appears to be slightly constricted between the expanded acetabular part and the anterior wing. The medial side of the wing has the iliosacral surface for contact with the sacral vertebral transverse processes. The iliosacral surface is articulated with two sacral vertebrae (S1 and S2), although the anterolateral corner of the widened transverse process of the first caudal (Ca1) appears also to contact with the ilium. The posterior end of the iliosacral contact forms a protuberance on the dorsal margin, and this protuberance is called the posterior process of the ilium, which is a much larger structure in premammaliaform cynodonts (Ref-199 Sues and Jenkins 2006; Ref-200 Sullivan et al. 2013; Ref-201 Guignard et al. 2018). The concave margin posterior to the ilial posterior process is an equivalent to (albeit less developed than) the sciatic notch as seen in primates. The iliosacral contact has a rugose surface and an oblong outline from the CT model, and this contact surface provides the information on orientation of the ilium. In life, the anterior part of the ilium is pointed dorso-anteriorly and oriented obliquely to the plane of the iliosacral contact. The anterior plate of the wing is projecting well beyond the iliosacral contact, and this free-standing plate is bending (flaring) laterally. The lateral surface of the free-standing wing is divided into an elongate gluteus surface facing laterally, and a smaller iliac surface facing ventrolaterally; a part of this iliac surface is broken off. The former is for the origin of gluteus muscle group, and the latter is for the iliac muscle or a part of the iliopsoas muscle and concave and smooth. Just anterior to the ilial crest of the acetabulum, a faint depression may represent the origin area of the rectus femoris. The medial side of the free-standing part of the anterior wing is rugose.

Overall, the ilium of *Megacauda* is similar to the well-preserved ilium in *Krusatodon* (Ref-16 Panciroli et al. 2024: extended data Fig. 6) and to some extent to the ilium of *Haldanodon* (Martin 2005). The ilium of *Megacauda* is similar to that of *Ornithorhynchus*, although different in two features. First, *Megacauda* lacks the fully crested dorsal rim of the acetabulum of *Ornithorhynchus*. Second, in both *Ornithorhynchus* and *Tachyglossus*, the prezygapophyses of the sacral vertebra(e) are hypertrophied and are articulated, secondarily, with the blade of the ilium, in addition to the main iliosacral contact. The ilio-zygapophyseal articulation, which can become an extensive fusion in older adults, is developed between the ilium and sacral 1 in *Ornithorhynchus*, or between the ilium and sacra 1 and 2 in *Tachyglossus*. *Megacauda* and other docodontans lack this secondary ilio-zygapophyseal articulation, which is an autapomorphy unique to monotremes, and also developed convergently in a different manner in xenarthran placental mammals (Ref-207 Galliari and Carlini 2019).

Ischium (Fig. 4; Supplementary Video S2) – The anterior part of the ischium forms the ischial component of the acetabulum and an expanded acetabular rim. Next to the acetabular rim the ischium is slightly constricted. The posterior part of the ischium is the ischial blade, and this plate-like structure is uniformly concave on the medial surface. Its dorsal margin, often called the ischial spine, is also concave. Ventrally, the ischial blade forms the border of the obturator foramen. Horizontal part of the ischial blade is a thick plate that forms the main part of the pubic symphysis and the margin of the ischiatic notch. In life, the posterodorsal corner of the ischial blade forms the ischial tuberosity, but in the fossil specimen of *Megacauda* the ischial tuberosity is not fully preserved; it is also sheared off during fossilization in the pelvis of SDUST-V0007. The ischial tuberosity in the here restored pelvis (Fig. 4) is reconstructed from the preserved ischial tuberosity of *Agilodocodon* and *Microdocodon*.

Pubis (Fig. 4; Supplementary Video S2) – The pubis consists of two parts. The medioventral part – the pubis ramus that is partly rod-like, and partly widened to become the plate-like (pubic blade) floor of the pelvis, and to form the pubic symphysis. The dorsolateral part – the thicker body (sensu Ref-208 Hoffmann et al. 2020). The straight anterior (external) margin of the pubic ramus has a transverse, open groove, which we interpret to be the contact groove for a plate-like epipubis although the epipubis is not preserved in *Megacauda*. The posterior (internal) and slightly concave margin of the pubis ramus is the anterior border of the obturator foramen.

The body of pubis, which was also referred to as the pubic head (Ref-200 Sullivan et al. 2013) is developed dorsally into the acetabular component of the pubis, with a thick pubic acetabular margin. The body of the pubis has developed a laterally oriented pubic tubercle midway between the pubic symphysis and the acetabulum. This feature is equivalent to the pubic tubercle on the pubic of a tritylodontid described by Sullivan et al. (2013) (Ref-200), also known as the iliopectineal process of extant mammalian anatomy. An identical feature (pubic tuberosity) is also present in *Brasilodon* (Ref-201 Guignard et al. 2019: fig. 5).

The pubic tubercle is present in *Microdocodon* (PMOL-AM00025). It has been identified in the docodontan *Krusatodon* (Ref-16 Panciroli et al. 2024: extended data Fig. 6). By our observation, it is also present in the specimen of *Agilodocodon* (Ref-10 Meng et al. 2015). The pubic tubercle (or tuber) identified in *Krusatodon*, *Microdocodon* and *Agilodocodon* is a small structure, and far smaller than the pubic tubercle in *Megacauda*, in the SDUST-V0007 specimen, and in *Docofossor*. It is likely that in *Krusatodon* the pelvic girdle elements are slenderer, and the features of the pubis (including the pubic tubercle) are less robust in general. Among other mammaliaforms, the pubic tubercle (or tuber) is also present in the preserved pubic bone in haramiyidans. The pubic tubercle is not enlarged, but we can confirm its presence in *Maiopatagium* (Ref-9 Meng et al. 2017: BMNH2940) and *Vilevolodon* (Ref-91 Luo et al. 2017: BMNH2942) and the additional specimens that are referred to these two taxa. Furthermore we can also confirm its presence in two other haramiyidan taxa (Ref-90 Bi et al. 2014).

Based on these new comparative data, we postulate that the pubic tubercle character has two character states among docodontans: presence of a small pubic tubercle (*Krusatodon*, *Agilodocodon* and *Microdocodon*) is a plesiomorphic character state shared by haramiyidans, tritylodontid (Ref-200 Sullivan et al. 2013), most probably also *Brasilodon* (Ref-201 Guignard et al. 2019). By comparison, the enlarged and laterally pointed pubic tuber (or tubercle) in *Megacauda*, in the SDUST-V00007 specimen and *Docofossor* (BMNH131735) is an apomorphic character state.

We would clarify a semantic issue that the pubic tubercle identified here for cynodonts and mammaliaforms is not homologous to the different features that have been also labeled as the “pubic tubercle” in some text books of human anatomy or mammalian skeletal anatomy. In humans, the inguinal ligament attaches dorsolaterally to the antero-superior iliac spine, and ventromedially to an elevated structure near the pubic symphysis. The latter attachment point is also called the pubic tubercle in some human anatomy textbooks (e.g., Ref-209 Spence 1990; Ref-168 Tillmann 2012). In the osteology of the cat, the anterior point of pubic symphysis can be enlarged. This latter feature can be variable, but when present, it was also identified as the pubic tubercle (e.g., Ref-210 Crouch 1969). These latter structures are not the same as the pubic tubercle identified here for cynodonts and mammaliaforms.

Dorsal to the hypertrophied and robust pubic tubercle (iliopectineal process) is a saddle shaped area, which is located between the pubic tubercle, and the ventral margin of the acetabulum formed by the pubis. This saddle is very pronounced in *Megacauda* and the SDUST-V0007 specimen. We interpret that this saddle on the pubis of *Megacauda* and SDUST-V0007 is for the passage of the iliopsoas muscle, by comparison to the pelvic musculoskeletal pattern of the extant monotremes (Ref-48 Gambaryan et al. 2002).

Comparative Discussion – The enlarged and everted pubic tubercle and the saddle of the pubis are very similar to those on the pubes of *Ornithorhynchus* and the adults of *Tachyglossus*. But *Megacauda* lacks the enlarged psoas minor tuberosity on the anterior pubic margin of *Ornithorhynchus* and the full adults of *Tachyglossus* (Ref-48 Gambaryan et al. 2002; Ref-203 Li and Luo 2006). The size of the psoas minor tuberosity in *Tachyglossus* varies with age; it is smaller in juveniles (e.g., Fig. 4f), but enlarged significantly in older adults and is similar in proportion to this tuberosity in *Ornithorhynchus*. In overall shape of the pubis (except for the psoas minor tuberosity), *Megacauda* is also similar to monotremes (**Fig. 4**). *Megacauda* also bears notable resemblance to pinniped carnivores (Phocidae and Otariidae) (Ref-49 Howell 1930; Ref-50 Koretsky et al. 2016) and to the semiaquatic tenrec *Potamogale* that also developed strong features for muscle attachment in the anterior margin of the pubis.

The psoas minor muscle is a common muscle that attaches to the anterior aspect of the pubic. This muscle is variable across therian phylogeny and in populations of some species (e.g., it is known to be indistinct in some humans). Its attachment area on the pubis can be identified, but it is not distinctive enough to form its own tubercle in a majority of therian mammals with generalized pelvis (Ref-211 Lessertisseur and Saban 1967b; Ref-212 Hargaden and Singer 2012; Ref-32 Evans and de Lahunta 2013; Ref-193 Ercoli et al. 2013). Although relatively uncommon in extant therians, an enlarged iliopectineal (= pectineal) process developed in many bats (Ref-211 Lessertisseur and Saban 1967b; Ref-213 Walton and Walton 1970). A pubic tubercle is well developed in many bipedal hopping macropodid marsupials (Ref-211 Lessertisseur and Saban 1967b; Ref-191 Dawson et al. 2014). Some lagomorphs can also develop a small pubic tubercle (Ref-211 Lessertisseur and Saban 1967b).

Among semiaquatic mammals, a well-developed tubercle of psoas minor in the anterior aspect of the pubis is a diagnostic character of marine pinniped mammals (Ref-49 Howell 1930; Ref-50 Koretsky et al. 2016). The anterior part of the pubis has a psoas minor tubercle in close proximity to the iliopectineal crest in seals (*Phoca*) and in variant forms in sea lions (*Zalophus*). A pubic tuber is also

present in the semiaquatic giant otter shrew *Potamogale* (Afrotheria: Tenrecomorpha). These prominent muscle attachment features are structurally equivalent to the pubic tubercle of monotremes, for the psoas minor and pectineus muscles (Ref-50 Koretsky et al. 2016: fig. 6). These are specialized features of the transformed pelvic-hindlimb for swimming in semiaquatic marine mammals (Ref-49 Howell 1930; Ref-50 Koretsky et al. 2016). We interpret that the hypertrophied pubic tubercle of *Megacauda* is convergent to the combined psoas minor and pectineal crest of the pinnipeds. The minor difference is that the tubercle is relative much larger in *Megacauda* than in pinniped carnivores.

Epipubis – The anterior margin of the pubic ramus has a transverse groove, which we interpret to be for receiving the epipubis. In the incomplete pelvis of *Docofossor* (Ref-12 Luo et al. 2015), a plate-like bone can be interpreted to be an incomplete epipubis that can fit with the restored partial pelvis. This reinforces the inference of the epipubis by its corresponding groove on the pubis for most docodontans.

Pelvic Musculoskeletal Reconstruction (Fig. 4, Extended Data Fig. 8)

The deep iliopsoas muscle saddle and the prominent and everted iliopectineal process on the pubis of *Megacauda* show the same pattern as those in the pubis of the extant *Ornithorhynchus* (Fig. 4). The overall pelvic configuration is similar in many characters between *Megacauda* and extant monotremes but especially *Ornithorhynchus*. The muscle attachments of the pelvis and associated skeletal structure have been characterized for monotremes by Gambaryan et al. (2002: figs. 9-13) (Ref-48). The comparative pattern of pelvic muscle attachments of mammaliaforms and cynodonts have also been interpreted by Guignard et al. (2019) (Ref-200) and Guignard et al. (2018) (Ref-214). This is now further reconstructed extensively by Bishop and Pierce (Ref-4 2023; Ref-216 2024a). Based on the interpretation of these previous anatomical studies, we offer a reconstruction of several pelvic skeletal muscles that were likely associated with the iliopsoas muscle saddle and the prominent, everted iliopectineal process:

(1) Iliopsoas muscle (Fig. 4) – The iliopsoas is fused from the psoas major muscle and the iliac muscle. In extant mammals, the psoas major part of the iliopsoas takes its origin partly from the transverse processes (if present) of the anterior lumbar vertebrae, and the aponeurosis on the ventral and lateral surfaces of the posterior lumbar. The iliac part of the iliopsoas takes origin from the iliac surface of the ilium blade. The fused muscle of the psoas major part and iliac part passes posteriorly along the ventral margin of the ilium blade and below the pubic rim of the acetabulum, and its common tendon insert on the lesser trochanter of the femur (**Fig 4; Extended Data Fig 8**). The relatively small iliopsoas of therian mammals generally inserts on the top of the small lesser trochanter of the femur (Ref-32 Evans and de Lahunta 2013). By contrast, the large iliopsoas muscle of monotremes has a very large insertion area from the tip of the large lesser trochanter along the anterolateral aspect of femoral shaft, for more than half the length of the femur (Ref-48 Gambaryan et al. 2002: fig. 13). In *Ornithorhynchus*, the saddle-shaped passage dorsal to the large pubic tubercle is a major bony landmark associated with the large iliopsoas muscle (**Fig. 4e: ilps saddle**). This saddle is also well-developed in adult specimens of *Tachyglossus*. Based on the similarity to *Ornithorhynchus* and *Tachyglossus*, we propose that the saddle dorsal to the pubic tubercle of *Megacauda* is also for a similarly large iliopsoas muscle (**Fig. 4b**).

Comparative Discussion on Iliopsoas— This muscle is part of the puboischiofemoralis internus (PIFI) group according to the muscle classification of Bishop and Pierce (2023 Ref-4). It is a larger muscle in extant monotremes (Ref-48 Gambaryan et al. 2002) than in therians. In the sprawling hindlimb posture of *Ornithorhynchus* the femur is held nearly horizontally and inclined at a large angle to the sagittal plane of the torso. In this orientation of the femur, the action of the iliopsoas muscle is to rotate and pronate the femur (Ref-48 Gambaryan et al 2002). In contrast, for quadruped mammals (e.g., dog), the function of this muscle is to maintain the hindlimb posture and maintain limb stability. Additionally, its action helps to flex the hip joint and to rotate the thigh outward at the hip (Ref-48 Gambaryan et al. 2002; Ref-32 Evans and de Lahunta 2013). Jenkins (1971) (Ref-215) interpreted that the iliopsoas muscle was already present in Mesozoic stem mammals (mammaliaforms) and played a role in mammaliaforms hindlimb function. Guignard et al. (2018 Ref-214) further argued that by the presence of this muscle's osteological proxies in the derived cynodont *Prozostrodon*, an iliopsoas muscle already evolved in probainognathian cynodonts (Ref-214 Guignard et al. 2018; Ref-4 Bishop and Pierce 2023). Our new inference of this muscle by the presence of an iliopsoas saddle in the pubis in docodontans is consistent with the conclusion of these previous studies (Ref-215 Jenkins 1971; Ref-214 Guignard et al. 2018; Ref-4 Bishop and Pierce 2023).

(2) Psoas minor – The psoas minor muscle inserts on the anterior aspect of the pubis and it aids in the ventral flexion of the lumbar vertebral column and pelvis (Ref-32 Evans and de Lahunta 2013; Ref-193 Ercoli et al. 2013). This muscle is much larger in monotremes (Ref-48 Gambaryan et al. 2002) than in therians. In *Megacauda*, the entire anterior aspect of the pubis is dominated by the hypertrophied pubic tubercle, and its associated folding groove plus the pubic saddle for the iliopsoas muscle. There is not a suitable topographic feature that could be interpreted as the psoas minor tuberosity as seen in monotremes. But we offer an alternative interpretation that, if the psoas minor was present, it would also attach to the massive pubic tubercle in *Megacauda*.

(3) Pectineus muscle (Extended Data Fig. 8) – The main osteological proxy for the pectineus muscle is the pubic tubercle (Ref-200 Sullivan et al. 2013), also known as the iliopectineal or pectineal eminence in extant mammal anatomy including fissiped carnivores. In most therian mammals, it is a small muscle (small muscle belly with long tendon for insertion) and it arises from the anterior border of the pubis and inserts on a narrow and long area on the posterolateral aspect of the femur in extant therian mammals, and the extent of its insertion can be variable among therians. In most mammals, this relatively small muscle attaches to a pectineal line with a small “eminence” (iliopectineal eminence) on the pubis of rodents (Ref-212 Hargaden and Singer 2012) and of peramelid marsupials (Ref-213 Warburton et al. 2015), or no distinct topographical feature as in some carnivores (Ref-193 Ercoli et al. 2013). By comparison, the pectineus is a larger muscle in monotremes (Ref-48 Gambaryan et al. 2002: fig. 12) and its large size corresponds to the large and laterally everted pubic tubercle (larger and more prominent in *Ornithorhynchus* than in *Tachyglossus*) that provides a larger area for the muscle's origin (Fig. 4e, 4f.; *Ornithorhynchus* and *Tachyglossus*), and which has an insertion in the medial side about mid-length of the femur (Ref-48 Gambaryan et al. 2002: fig. 13).

We propose that the large and laterally pointed pubic tubercle in *Megacauda* (**Fig. 4b, 4c**) is more similar to the pattern of *Ornithorhynchus* and adult *Tachyglossus*, in which this large osteological structure of muscle attachment is for a large pectineus. This is in contrast to the small tubercle or iliopectineal eminence (if present at all) in most therians, except the semiaquatic pinnipeds, which evolved this larger tubercle, separately among carnivores.

Comparative Discussion of the Pectineus: – *Docofossor* also has an enlarged pubic tubercle from our segmentation of its CT scans. The pubic tubercle is also present in *Microdocodon*, although in a much smaller size. It is possible that the large pubic tubercle is a shared derived character of *Megacauda*, SDUST-V0007 and *Docofossor*. This is a hypothesis that can be tested when more complete pelvises of docodontans are discovered. The pubic tubercle is also reported for tritylodontids (Ref-200 Sullivan et al. 2013) and for *Brasilodon* (Ref-201 Guignard et al. 2019). It is possible that the presence of a pubic tubercle is a shared derived character of mammalian cynodonts, but the hypertrophied and laterally pointed pubic tubercle is a derived character of a small number of docodontans, and also for *Ornithorhynchus*.

The pubic tubercle is an osteological proxy to the pectineus muscle by their musculoskeletal association in monotremes, and we hypothesize that the *M. pectineus* was present in mammalian cynodonts. Our assessment here is consistent with the hypothetical reconstruction of the pectineus in mammaliaforms by Bishop and Pierce (2023) (Ref 4). In extant therian mammals, the action of the small pectineus muscle is for aiding adduction of the femur, facilitating for the hindlimb to be brought closer to the parasagittal pose.

But being phylogenetically plesiomorphic does not preclude its muscular features to have significant function - The well-developed pubic tubercle in *Megacauda* shows distinct resemblance to the muscle attachment sites on the anterior part of the pubis in pinniped mammals. Likely the pectineal muscle in *Megacauda*, despite its plesiomorphic resemblance to mammalian cynodonts and monotremes, is also convergent to the pectineal structure in the pubis of pinnipeds (Ref-49 Howell 1930). We will further discuss the functional implications of this, for swimming by *Megacauda* as a semiaquatic mammaliaform.

(4) Ambiens muscle (Extended Data Fig. 8) – The ambiens (sensu Ref-4 Bishop and Pierce 2023 = “*M. gracilis anterior*” of Ref-48 Gambaryan et al. 2002) is a muscle that arises from the anterolateral aspect of the pubic ramus and its origin is near the psoas minor tubercle and more dorsal to the origin of the pectineus in monotremes (Ref 48 Gambaryan et al. 2002). Its insertion is in the anterior tuberosity and crest (cnemial crest) of the tibia. The muscle is for multiple functions of flexing the hip joint and adducts the hindlimb. Because the enlarged and laterally pointed pubic tubercle is associated with the ambiens muscle, we infer that an ambiens muscle (or “*gracilis anterior*”) would be also present in *Megacauda* (**Extended Data Fig. 8a**). The ambiens muscle would be capable of flexing the hip joint and maintaining the tension of the hindlimb when it is protracted, functionally similar to the posterior part of the sartorius muscle of therians.

Comparative Discussion of the Ambiens Muscle – the ambiens muscle is present in monotremes. Previously, Bishop and Pierce (2024a) (Ref-216) inferred that this muscle was present in some cynodonts. Our inference of this muscle, according to the osteological features of the pubis in *Megacauda*, would have a wider distribution in cynodont-mammal phylogeny.

Reconstruction of Soft Tissue and Muscular Features of the Tail

Megacauda (**Fig. 1**) like its sister-taxon *Castorocauda* (Ref-13 Ji et al. 2006), has a broad and flattened tail with a shape outline intermediate between the tapered tail (sensu Ref-51 Fish et al. 2021)

that is common in most mammals, and the highly derived paddle tails (Ref-51 Fish et al. 2021) of the monotreme *Ornithorhynchus*, the beaver species of *Castor*, and the giant otter *Pteronura*.

The preserved outline of the pelage of both *Megacauda* slabs (**Extended Data Figs 1 and 2**) shows a noticeable indentation on one side of the tail base (**Extended Data Figs. 1-2**: the large triangle near the Ca6 position) but this feature on the other side of the tail is obscured by the right hindlimb. We interpret that this is similar to the tail base constriction on both sides of the tail in *Castorocauda* (Fig. 1. See also Ref-13 Ji et al. 2006: fig. 1). The widest part of caudal pelage outline is from Ca7 through Ca12, ranging from 32 mm to 30 mm wide (Supplementary Table 1). In this section of the tail, the tail is about 40% - 45% wider than the maximum width of the pelvic width (estimated to be about 24 mm at the level of Sacral 1-Sacral 2 transverse processes and the attached ilia). This is slightly less than (although still comparable to) the relative tail width in *Castorocauda*, in which the tail width near the Ca8 position is 50% wider than the maximum width of the pelvis (Ref-13 Ji et al. 2006).

The widest part of the tail (near Ca7-Ca12) at 30-32 mm starts to transition posteriorly into the slightly narrower width in the section of Ca14-16 (of which Ca15 is the longest caudal, a standard landmark) at 22-24 mm. Starting from Ca15-16, the outline of pelage is tapering relatively uniformly towards the posterior end at Ca28. The gradient of segmental size and morphology of the last five to six vertebrae, and that the last vertebrae are encircled by soft tissue pelage are strong indication that the entire tail is intact in the *Megacauda* specimen.

Interpretation of Soft Tissue Features of the Tail - Much of the tail constitutes soft tissues, because the vertebral bones are relatively small part of the total tail width. The width of Ca9 (measured between the two ends of the left and right anterior transverse processes) represents only 39% of the total width of the tail at the same position. The maximum width of Ca15 (the longest caudal) estimated at the ends of the centrum represents only 30% of tail width in this position.

Rybczynski et al. (2005) (Ref-217) described that, in the modern beaver, most of the tail volume lateral to the vertebral bone is an adipose matrix embedded with collagen fibers, in the paddle tail with scaly coverage. The fiber structures provide strong links between the vertebrae and the skin of the tail. By analogy, we interpret that the tail of *Megacauda* likely had similar soft tissue structure.

The preserved tail also shows clusters of patches of denser integumentary structures near Ca9 and Ca10, which we interpreted as dermal scales. The scale-like structures of *Megacauda* are similar to the scales interpreted for *Castorocauda* (Ref-13 Ji et al. 2006), although these are more sparse and limited in scope than those of *Castorocauda* (**Fig. 1**). A comparable example of sparse scales embedded in furs is known from the Cretaceous eutriconodontan *Spinolestes* (Ref-144 Martin et al. 2015). The integumentary structures of *Spinolestes* are preserved by phosphatization of soft tissues at the Cretaceous Los Hoyas lagerstätte in Spain, a distinctly different mode of fossilization from the carbonized and compressed furs in the Jurassic Yanliao Fossil Biota of the Haifanggou Formation (or Tiaojishan Formation). The sparse scales in *Spinolestes*, with finer structural preservation of phosphatization, suggest it is possible to fossilize the scales in patchy patterns, as seen in *Megacauda* and *Castorocauda*. The fossilized soft tissue features suggest that *Megacauda* and *Castorocauda* do not have the full scaly coverage tails of the extant beavers of the rodent group.

Tail Shape - The broad tails of *Megacauda* and *Castorocauda* are much wider in the proximal half (to about Ca14) than those of the majority of mammals (Ref-218 Grassé 1955, Ref-219 Grassé 1956; Ref-220 Hickman 1979). This wider, proximal part of the tail is demarcated from the rump by a slight constriction. The widened tail with a restriction at its base is a derived feature. But the wider proximal tail part of *Megacauda* and *Castorocauda* are not fully developed paddle-shaped tails, as seen in the monotreme *Ornithorhynchus*, the giant otter (*Pteronura*) of the lutrine subfamily, and the beaver species of rodents (all with paddle tails sensu Ref-51 Fish et al. 2021). The distal part of the tail (posterior to the longest “transitional” caudal vertebra 15) is tapering, which is a plesiomorphic feature. The reconstruction of a fully paddle-shaped tail for *Castorocauda* (Ref-13 Ji et al. 2006: fig. 1) over-represented the posterior breadth of the tail. The posterior half of the *Castorocauda* tail should be tapering (**Fig. 1**).

The widening of the proximal part of the tail corresponds to the widening of vertebrae by their laterally elongate transverse processes. The most proximal (immediately post-pelvic) caudal vertebrae have laterally elongate anterior transverse processes (more so than the posterior transverse processes), such that the vertebra(e) are butterfly-shaped. There is a single butterfly-shaped proximal cauda (Ca5) in *Megacauda*, in contrast to two butterfly-shaped vertebrae (Ca5 and Ca6) in *Castorocauda* (**Fig. 1**). Posterior to Ca5 (for *Megacauda*) or to Ca5/Ca6 (for *Castorocauda*), the next five caudals (for *Megacauda*) or six caudals (for *Castorocauda*) have the two pairs of transverse processes in equal or subequal size, on either ends of the vertebral centra, in “H-shape” if in horizontal orientation. These vertebrae with double transverse processes in “H-shaped” pattern also correspond to the pronounced widening of proximal part of the tail. The double transverse processes in “H” pattern in the caudals of *Megacauda* and *Castorocauda* are also well developed in the middle one-third of the caudal vertebral series in river and sea otters of the Lutrinae (Ref-13 Ji et al. 2006), as exemplified in Ca10-14 of the giant otter *Pteronura* of the Amazon river basin (Ref-53 Sennikov 2023). The configuration of long-anterior paired with short-posterior transverse processes is present in the vertebrae in the distal one-third of the caudal series in the semiaquatic beavers (Ref-13 Ji et al. 2006; Ref-53 Sennikov 2023), and is especially distinctive in Ca11-Ca18 of *Castor canadensis* (Ref-13 Ji et al. 2006; Ref-53 Sennikov 2023). Below we will further discuss the functional morphology of these features.

Interpretation of Tail Muscle Attachments - In extant carnivores, much of the dorsal aspect of the transverse process serves as the insertion of the sacrocaudalis dorsalis lateralis (SDL), in the post-pelvic caudals. The dorso-lateral aspect of the transverse process in the post-pelvic caudal vertebrae is primarily the insertion site of the intertransversarius dorsalis caudalis (IDC) (Ref-32 Evans and de Lahunta 2013; Ref-193 Ercoli et al. 2013). The ventral aspect of the transverse process of the post-pelvic caudal vertebrae is the insertion site of the sacrocaudalis ventralis lateralis (SVL). The ventrolateral aspect of the lateral end of the transverse process is for insertion of the intertransversarius ventralis caudalis (IVC) (Ref-32 Evans and de Lahunta 2013; Ref-193 Ercoli et al. 2013).

In the dog (Ref-32 Evans and de Lahunta 2013) the sacrocaudalis dorsalis medialis (SDM) and the sacrocaudalis ventralis medialis (SVM) have a much shorter posterior extension than the SDL and SVL muscles. In the lesser grison (a mustelid of South America) (Ref-193 Ercoli et al. 2013), the SDM and SVM muscles do not extend posteriorly to the caudal vertebrae much further beyond the pelvis. In the rat, the sacrocaudalis dorsalis medialis (SDM) and the sacrocaudalis ventralis medialis (SVM) appear to be similar (Ref-221 Hori et al. 2011). This appears to be a plesiomorphic pattern in placental mammals.

From this comparison, we interpret that, in *Megacauda* and *Castorocauda*, the elongation of the anterior transverse process in Ca5 (or Ca5/Ca6) with butterfly configuration, and the development of transverse H-shaped double transverse processes in next five or so vertebrae (Ca6 to Ca10 in *Megacauda*, or Ca7 to Ca12 for *Castorocauda*) would increase the attachment areas for the caudal muscles. These include M. sacrocaudalis lateralis (both for the dorsal SDM and for the ventral SVM) in the posterior caudal vertebral positions. Furthermore, the transverse processes in these vertebrae (Ca6-Ca10 for *Megacauda*, Ca7-Ca12 for *Castorocauda*, or Ca6-Ca12 collectively for both megacaudid taxa) would also increase the attachment areas for the intertransversarius lateralis caudalis muscles (both for dorsal muscle IDC, and for the ventral muscle IVC). Everything else being equal, the distinct osteology of H-shape double transverse processes for each vertebra for caudals Ca6-Ca12, would likely increase the muscle capability to extend (dorsiflex) the wide tail especially in the proximal half of the tail anterior to the transitional (long) vertebra (caudal 15). These likely enhance the capability to flex the tail ventrally, and to laterally flex (to abduct) the tail sideways, for locomotor function of a wide tail in swimming. We also infer that *Castorocauda* had similar capability in tail function.

According to the hindlimb muscular pattern of monotremes by Gambaryan et al. (2002) (Ref-48), the neural spines and lateral ends of the wing-shaped transverse processes of the several anterior caudal vertebrae are attachment sites for the M. semitendinosus pars vertebralis that inserts on the mid-shaft of the tibia.

Prehensile Capability of Tail – Several musculoskeletal features of caudal vertebrae of *Megacauda* and *Castorocauda* can be interpreted to be related to prehensile capability of the tail. Several features of caudal vertebrae are osteological proxies to some extensive ventral caudal flexor muscles. The size of the chevrons, the successively posterior extent of their presence along the tail, and their posterior extent of development are relevant for prehensile capability as widely documented for other mammals (Ref-186 Organ 2010; Ref-191 Dawson et al. 2014; Ref-190 Zavodszky and Russo 2020). Female platypuses can curl their prehensile tails and carry nesting materials into their burrows (Ref-222 Thomas et al. 2018), for nesting of juveniles (Ref-223 Thomas et al. 2019). It is conceivable that the tails of *Megacauda* and *Castorocauda* would be capable of a range of prehensile function as seen in extant female platypuses (Ref-222 Thomas et al. 2018, Ref-223 Thomas et al. 2019).

Hindlimb and Pedal Osteology

Femur

Approximately 80% of the fossil bone is preserved of the left femur, although in a compressed condition, in the main slab. The right femoral head is broken off from the shaft but is still associated with the partially preserved right acetabulum. These fossil materials can be visualized from the CT scans. Of the right femur, the greater trochanter is preserved and exposed on the counter-slab, as is the femoral shaft through to the lateral condyle, also in compressed condition. The right femoral medial condyle is represented by impression outline. Although the right femur cannot be scanned, this provides complementary information unavailable from the CT rendering of the left femur, for the overall anatomical restoration of the femur.

The femoral head is spherical and very large relative to the girth of the shaft. On the left femur the head appears to be slightly bent antero-medially from the shaft. The femoral neck is not distinctive and discernible only because of a slight twist of the head relative to the shaft and the prominent notches from the greater and the lesser trochanters. The greater trochanter is plate-like and has an oblong outline but it is fractured and shifted as preserved. A piece of broken bone below the greater trochanter is also fractured and displaced. But this broken piece appears to be the ventral shelf connected the greater trochanter, according to the intact greater trochanter and its related ventral shelf of *Docofossor* (BMNH131735). The greater trochanter shelf in these docodontans corresponds to a feature in the femur of *Ornithorhynchus* – an area below the greater trochanter with a tiny protuberance identified to be a minimal third trochanter by Gambaryan et al. (2002) (Ref-48). The posterior aspect of the femur below the greater trochanter is for the insertion of a large caudofemoralis as well as a part of the gluteus muscle group (Ref-48 Gambaryan et al. 2002). Similarly, Bishop and Pierce (2024) (Ref-216) also interpreted this area on the posterior aspect of the femur to be for the attachment of the caudofemoralis. On this comparison, we infer that the posterior area of the greater trochanter shelf is for the attachment of the caudofemoralis.

The lesser trochanter of *Megacauda* is robust with a blunt end in a triangular outline in posterior view. It is subequal in size to the greater trochanter. The lesser trochanter is more medially pointed and the medial aspect of the shaft below the lesser trochanter is concave, such that the femur appears to be curved. On the posterior aspect of the femur and between the greater and lesser trochanters there is a large, pronounced trochanteric fossa. No feature of the shaft can be described because the left femoral shaft is fractured along its length and the right femoral shaft is flattened. In the distal part of the femur, the lateral condyle is much larger than the medial condyle as seen in the CT rendering of the left femur. In posterior aspect, the condyles are convex with an intercondylar groove (fossa), which is relatively narrow in comparison to the girth of the femur. Both condyles are skewed laterally in posterior view. Overall, the distal part of the femur is asymmetrical and skewed postero-laterally. On the anterior part of the distal femur there is a narrow and shallow patellar groove. There is no indication of an ossified patella on both hindlimbs in the specimen of *Megacauda*.

Tibia and Fibula

Distal halves of the right tibia and fibula and the proximal two-thirds of the left tibia can be scanned. This information is complemented by the well-preserved outline and preserved bone of the para-fibular process. Taken together, it is feasible to fully restore the morphology of both the tibia and the fibula.

The proximal part of the tibia is much enlarged relative to the girth of the shaft, and is robust. In proximal view, its outline is triangular with a large, and platform-like anterior tibial tuberosity for insertion of the ambiens muscle, and rectus femoris (sensu Ref-48 Gambaryan et al. 2002) or the iliotibial muscle group (Ref-216 Bishop and Pierce 2024a), and the vastus medialis and lateralis (sensu Ref-48 Gambaryan et al. 2002; or the femorotibial muscle group of Bishop and Pierce 2024a Ref-216), and a projecting lateral tibial process for articulation with the tibial facet of the fibula. The proximal part the tibia is laterally concave and also bearing a deep fossa for the tibialis anterior muscle. The overall shape of the tibia is sigmoid. The mid-shaft is medially concave. The tibia cross-section is triangular in profile in the proximal part and more rounded in profile in the distal shaft. The distal end has a prominent tibial malleolus for articulating with the concavity on the medial side of the astragalus (**Extended Data Figs 8, 9**).

The fibula is characterized by an articulating process to the tibia (in contact with the proximolateral process of the tibia) and a large, plate-like parafibular process that has an almost rectangular outline. The maximum width across the tibial contact to the posterior corner of the parafibula is about 18 mm, about four times wide as the shaft of the fibula. The main shaft and distal part of the fibula is cylindrical. The distal part of the fibula is slightly wider than the mid-shaft and its contacting end for the calcaneum is slightly concave.

The rectangular outline of the parafibula (also known as parafibular process) is a very distinctive feature of *Megacauda* (**Extended Data Fig. 8-b**). It is formed by the tibial contact point (a process), a dorsal corner and a posterior corner. The outline between the tibia contact point and dorsal corner is slightly concave, the outline between the dorsal corner and the posterior corner is slightly convex, but the transition from the posterior corner to the shaft is strongly concave. This rectangular outline shape of *Megacauda* is different from the rounded outline of parafibula of *Castorocauda* (**Extended Data Fig. 8-c**) that is uniformly convex, and has no distinct corners, and forms a straight posterior margin with the fibula shaft. The morphology of fibula is more similar to the plesiomorphic pattern of fibula of docodontans as exemplified by *Agilodocodon* (**Extended Data Fig. 8-d**). The parafibula is slightly enlarged in *Microdocodon* (Ref-8 Zhou et al. 2019: SOM fig. s10) and greatly enlarged in *Docofossor* (Ref-12 Luo et al. 2015). But no other docodontans with enlarged parafibula has the distinctly rectangular outline like in *Megacauda*.

The hypertrophied parafibula of *Megacauda* is very large for the size of the hindlimb bones – it is even larger than the already large parafibula of *Castorocauda* and *Docofossor* (Ref-8 Ji et al. 2006; Ref-12 Luo et al. 2015). Elsewhere in docodontans, *Microdocodon* has a noticeably enlarged parafibula (Ref-8 Zhou et al. 2019), but *Agilodocodon* (Meng et al. 2015) has a small proximal end of the fibula, typical of other docodontans. *Agilodocodon* represents the plesiomorphic state of this character, shared by other mammaliaform outgroups such as morganucodontans (Ref-197 Jenkins and Parrington 1976) and many haramiyidans (Ref-90 Bi et al. 2014; Ref-9 Meng et al. 2017; Ref-91 Luo et al. 2017), and cynodonts in general (Ref-199 Sues and Jenkins 2006). In the gondwanatherian *Adalatherium* (Ref-208 Hoffmann et al. 2020) an enlarged but separate parafibula is present, which is also the general pattern of the parafibula in multituberculates although this element shows a wide range of size variation among multituberculates (Ref-224 Krause and Jenkins 1983, Ref-54 Kielan-Jaworowska and Gambaryan 1994; Ref-89 Luo et al. 2016; Ref-225 Yuan et al. 2013). Aside from *Megacauda*, *Castorocauda* and *Docofossor*, an enlarged parafibula fully fused to the fibula is also known from the spalacotherioid stem therian *Akidolestes* but not in other spalacotherioids (Ref-203 Li and Luo 2006; Ref-226 Ji et al. 2009; Ref-227 Chen and Luo 2013).

Interpretation of Tibia and Fibula Muscle Attachment

The tibia and fibula are very similar in *Megacauda* and the monotreme platypus (Gambaryan et al. 2002). The two most prominent features of these two bones in *Megacauda* are the robust anterior tuberosity at the proximal end of the tibia, and the hypertrophied parafibular process. The proximoanterior tibial tuberosity is the site of insertion for the ambiens muscles (sensu Ref-216 Bishop and Pierce 2024a; equivalent to the gracilis anterior and semimembranosus anterior of Ref-48 Gambaryan et al. 2002), and for the insertion of the rectus femoris (The iliotibial muscle group of Ref-4 Bishop and Pierce 2023; Ref-216 Bishop and Pierce 2024a, Ref-228 Bishop and Pierce 2024b) and

the vastus medialis and lateralis, which are parts of the femorotibial muscle group (Ref-216 Bishop and Pierce 2024a, Ref-228 Bishop and Pierce 2024b). And the anterior tibial (cnemial) crest is for insertion of the semimembranosus, semitendinosus and gracilis muscles. The proximal part of the tibia is for sites of origination for the tibialis anterior and tibialis posterior muscles, respectively for the function of dorsiflexion and planar-flexion of the foot at the ankle joint.

In monotremes, the hypertrophied parafibular process above the fibular-tibial articulation and the projecting proximo-lateral tibial tuberosity are related to a very different arrangement of several large muscles, in contrast to those of therians (Ref-48 Gambaryan et al. 2002). The lateral head of the gastrocnemius muscle is attached to the parafibula in monotremes, making it feasible to extend the ankle while the knee is in flex position, unlike its attachment to the lateral femoral epicondyle in therians (Ref-48 Gambaryan et al. 2002). The popliteus muscle is originating from the parafibula in monotremes, not from the lateral epicondyle of the femur as in therians, making it feasible to rotate fibula and tibia relative to each other, while the knee is flexed (Ref-48 Gambaryan et al. 2002). The larger size of the tibialis posterior muscle, made feasible by the large parafibular process, and the large tibialis anterior muscle in an enlarged fossa for the tibialis anterior muscle in anterolateral aspect of the tibia, can provide much larger force to the massive entocuneiform and metatarsal 1, for controlling the inversion and eversion of the feet. The hypertrophied parafibula certainly would accommodate a larger and longer peroneus muscle, and a larger pedal digit flexor muscle of the posterior margin of the fibula would result in more capability to evert and rotate the feet laterally at the ankle joint. For outgroup comparison of the contrasting differences between extant therians and monotremes, the therian pattern is almost certainly more similar to those interpreted for cynodonts and mammaliaforms by Bishop and Pierce (2024a: fig. 8) (Ref-216). The therian pattern is plesiomorphic for cynodonts as a whole, while the monotreme pattern is more derived. All these osteological correlates to the more specialized lower hindlimb and pes in monotremes are present in *Megacauda*, and by inference also in *Castorocauda*.

Astragalus, Calcaneus and Upper Ankle Joint

The entire pedal structure is preserved for the right foot, minus just one incomplete metatarsal. Most bones of this foot can be visualized from CT scans of the main slab and supplemented from the remaining bones of the same foot on the counter-slab (**Fig. 4** and **Extended Data Fig. 9**). For *Megacauda*, all tarsal and extra-tarsal elements can be recognized: the calcaneus, the astragalus, the cuboid, the navicular, the entocuneiform, the mesocuneiform and the ectocuneiform (**Extended Data Fig. 9**). All digit rays of the right foot are complete.

Bones on left foot are also on the main slab and can be visualized, and be supplemented by sparse bones on the counter-slab. Four digit rays (1-4) can also be reconstructed with confidence. Overall, the right foot is more complete than the left.

Astragalus (Fig. 4 and Extended Data Fig. 9) – The tibio-astragalar joint is groove-like in dorsal aspect, and the groove is more excavated and curved to become pulley-like in the posterodorsal view of the astragalus. The curved trochlear groove is flanked by two crests. The lateral side of the curved trochlear groove is flanked by the fibuloastragalar crest (**Extended Data Fig. 9**). The medial side of the trochlear groove is flanked by the tibioastragalar crest. The better developed version of this crest in *Docofossor* was also called the tibial trochlear crest (Ref-12 Luo et al. 2015; Ref-8 Zhou et al. 2019).

Further medial to the tibioastragalar crest is a concave, vertical surface – the astragalar medial concavity that corresponds to the distal malleolus of the tibia, following the interpretation of previous studies (Ref-12 Luo et al. 2015; Ref-8 Zhou et al. 2019). In the posterior view of the astragalus, the bone has developed ventrally to become the posterior shelf of the astragalus, which is continuous with the tibioastragalar crest (**Extended Data Fig 8c, d and e**). This shelf also borders on the astragalar medial concavity. There is an incomplete astragalar foramen located in the posterior part of the pulley (“trochlear”) groove. The anterior end of the astragalus has the navicular facet, an antero-ventrally facing and slightly convex surface, for articulation with the navicular bone. The ventral aspect the astragalus has an astragalar sulcus – a longitudinal groove that separates the antero-medial sustentacular facet and the postero-lateral astragalar facet, both for contacting the calcaneum.

Comparative Discussion of the Astragalus – The trochleate morphology of the tibio-astragalar joint, its flanking crests, and the astragalar medial concavity, are more prominently developed in *Megacauda* and *Docofossor* (**Extended Data Fig. 9**) than in other docodontans such as *Microdocodon*, *Borealestes* and *Krusatodon* (Ref-8 Zhou et al. 2019; Ref-16 Panciroli et al. 2024; Ref-174 Panciroli et al. 2022). We interpret that the dorsal trochlea-like groove has a variation range, and can be developed to a varying degree across the docodontan phylogeny (Ref-10 Meng et al. 2015; Ref-8 Zhou et al. 2019; Ref-16 Panciroli et al. 2024; Ref-174 Panciroli et al. 2022). The shallower groove on the astragalar dorsal surface, as seen in *Borealestes* and *Krusatodon* (Ref-174 Panciroli et al. 2022: fig 16; Ref-16 Panciroli et al. 2024: extended data fig. 7) is more comparable to the tibio-astragalar contact morphology of morganucodontans (Ref-197 Jenkins and Parrington 1976; Ref-229 Szalay 1994), and is phylogenetically more plesiomorphic. By contrast, the pronounced trochlear morphology (including sharper flanking crests) and the enlarged posterior shelf of the astragalus, as seen in *Docofossor*, are most derived and phylogenetically apomorphic. The degree of development of these features in *Megacauda* is more similar to *Docofossor* (**Extended Data Fig. 9**), than to other docodontans (Ref-8 Zhou et al. 2019; Ref-16 Panciroli et al. 2024).

The morphological polarity of the changes from the more highly trochleate pattern of the astragali of *Docofossor* and *Megacauda* (**Extended Data Fig. 9**) and the lesser development of a similar pattern in other docodontans (Ref-8 Zhou et al. 2019; Ref-16 Panciroli et al. 2024; Ref-174 Panciroli et al. 2022) are parallel to the morphological polarity of these characters in monotremes (Ref-48 Gambaryan et al. 2002), from the highly trochleate astragalus morphology (or the “condyle surface” Ref-48 Gambaryan et al. 2002) of the semiaquatic *Ornithorhynchus* to the less extreme “spherical” morphology of the astragalus of the terrestrial *Tachyglossus* (Ref-48 Gambaryan et al. 2002: p. 25).

Calcaneus (Fig. 4 and Extended Data Fig. 9) – The anterolateral aspect of this bone is the location of the peroneal shelf. The peroneal shelf is incomplete and has a rugose surface, possibly because it was not fully ossified in life. By comparison of relatively well preserved peroneal shelves in other docodontans (Ref-8 Zhou et al. 2019; Ref-10- Meng et al. 2015; Ref-174 Panciroli et al. 2022) and in *Morganucodon* (**Extended Data Fig. 9**) (Ref-205 Chen et al. 2017; Ref-229 Szalay 1994), the margin of the peroneal region of *Megacauda* likely had a round outline in life. The anterior part of the shelf has a peroneal notch for the passage of the tendon of the peroneus longus muscle.

The cuboid facet is a slightly concave area on the anterior end of the calcaneus, and it is faced antero-ventrally, and side-by-side with the navicular contact surface of the astragalus. The sustentacular facet and the astragalar facet on the medial side of the calcaneus are aligned antero-posteriorly but these two

facets are separated by the calcaneal sulcus (**Extended Data Fig. 9**). The dorsal aspect of the main body of the calcaneus has a prominent and elevated platform, which is the calcaneo-fibular contact. The calcaneofibular contact and the fibuloastragalar contact are side-by-side as the calcaneus and astragalus are articulated in life. The slightly concave distal end of the fibula would articulate with the convex calcaneo-astragalar surface, allowing significant rotation of this joint. The dorsal aspect of the anterior part of calcaneus has a longitudinal ridge (**Extended Data Fig. 9**: dorsal ridge), which is for reinforcement of the calcaneo-cuboid contact.

The ventral aspect of the calcaneus is generally concave, from the cuboid facet in the anterior end to the calcaneal tuber in the posterior end. There are two well-developed crests on the ventral aspect of the calcaneus, both of which are unique to *Megacauda* (visualized by CT scans), and can also be seen on the exposed ventral aspect of the calcaneus of *Castorocauda*. These crests are not developed, or indistinctly expressed in other docodontans (Ref-16 Panciroli et al. 2024; Ref-174 Panciroli et al. 2022) or in *Morganucodon* (**Extended Data Fig. 9**). The first, and more anteriorly placed ventral ridge forms the border of the cuboid facet and concurrently also reinforcing the peroneal shelf (**Extended Data Fig. 9**: ventral ridge), this structure is not well developed in other mammaliaforms. The second, longitudinal ridge is posteriorly positioned and extending anteriorly from the calcaneal tuber, for about half of the calcaneal length. This ridge is strongly developed, and it increases the depth of the bone of the calcaneal tuber region. We interpret that the structure reinforces the calcaneal tuber that is the main insertion point of the Achilles tendon muscles for flexion of the pes at the ankle joint.

Comparative Discussion of Calcaneus – For comparison to the calcanei of mammalian cynodonts and other mammaliaforms (such as *Morganucodon* and Jurassic haramiyidans), we note that a distinct (although not elongate) calcaneal tuber is present in tritylodontids (Ref-229 Szalay 1994), prochilodontids (Ref-201 Guignard et al. 2019), and in *Morganucodon* (Ref-197 Jenkins and Parrington 1976; Ref-229 Szalay 1994). However, the vertically oriented calcaneal tuber ridge in *Megacauda* and *Castorocauda* is absent in ventral aspect of the calcanei of cynodonts and other mammaliaforms (Ref-10 Meng et al. 2015; Ref-12 Luo et al. 2016; Ref-205 Chen et al. 2017; Ref-229 Szalay 1994). *Megacauda* shows a posteriorly pointed calcaneal tuber; this differs from the Jurassic haramiyidans such as *Megaconus*, *Vilevolodon* and *Xianshou*, which lack this characteristic. The calcanei of the haramiyidans show a rectangular peroneal region (Ref-9 Meng et al. 2017: fig. s7), instead of the rounded peroneal shelf in the calcanei of docodontans (**Extended Data Fig. 9**).

We would clarify that the posteriorly pointed calcaneal tuber of mammalian cynodonts, *Morganucodon* and docodontans is a plesiomorphic feature that is different from the calcaneal tuber of extant monotremes. By contrast, in monotremes the calcaneal tuber is an obtuse tuberosity oriented postero-ventrally (Ref-229 Szalay 1994), not a straight and posteriorly oriented tuber as seen in *Morganucodon* and docodontans.

In monotremes, the more ventrally oriented calcaneal tuber is also smaller than the hypertrophied and curved peroneal process. The large and curved peroneal process of monotremes for more massive peroneal muscles and pedal flexor muscles originated from the parafibula (Ref-229 Szalay 1994; Ref-48 Gambaryan et al. 2002).

The calcaneus of docodontans (including *Megacauda*) does not show the extreme morphology of a hypertrophied and curved peroneal process of extant monotremes (Ref-12 Luo et al. 2015; Ref-48 Gambaryan et al. 2002; Ref-229 Szalay 1994). The calcanei show a rounded peroneal shelf in all docodontans so far (**Extended Data Fig. 9**) (Ref-8 Zhou et al. 2019; Ref-16 Panciroli et al. 2024).

Astragalus-Calcaneus Size and Position – Overall the astragalus is smaller than the calcaneus. The astragalus is only 67% of the calcaneus in length, about 60% of the calcaneus by maximum in dorsal view. This configuration of a much smaller astragalus associated with much larger calcaneus is also observed in other docodontans, such as *Krusatodon* (Ref-16 Panciroli et al. 2024), *Agilodocodon* (Ref-10 Meng et al. 2015), and *Microdocodon* (Ref-16 Zhou et al. 2019). As preserved in the *Megacauda* specimen, the astragalus and calcaneus are side-by-side. The orientation of the sustentacular surfaces and the astragalar facets on both bones clearly indicates that they are in juxtaposition (side-by-side). These features are related to pedal posture, to be discussed below.

Other Tarsal Bones and Os calcaris – The navicular bone has a concave posterior surface to articulate with the astragalar head, and a slightly convex anterior surface that support the entocuneiform, the mesocuneiform and the ectocuneiform. The entocuneiform is much larger than the mesocuneiform and ectocuneiform; and the entocuneiform has an expanded distal part, corresponding to thick and robust metatarsal 1. The cuboid bone is side-by-side with the navicular, but much larger than the navicular. The cuboid has an oblong outline in dorsal view, with a large concave notch – the cuboid notch – on the lateral side. This bone has a slightly enlarged proximal end to contact the cuboid facet of the calcaneus, and a slightly enlarged distal end to support metatarsals 4 and 5. The large cuboid notch is for the passage of a large tendon of the peroneus longus (Ref-229 Szalay 1994) to insert on the ventral side of the entocuneiform and metatarsal.

Comparative Discussion on Cuboid – The cuboid notch is an osteological correlate to the peroneus longus and its tendon. The action of this muscle is plantarflexion of digit ray 1 and the eversion (moving laterally) of the entire foot. This eversion of the foot could be conceivably facilitated by rotation of the convex proximal end of the cuboid, with regards to the calcaneal cuboid facet. These features of the cuboid would play a functional role for the strongly everted foot, both for terrestrial locomotion and for swimming.

Os calcaris – The Os calcaris is present. We interpret that a bone piece of approximately rhomboid shape is the Os calcaris, a supernumerary bony element (or an extra-tarsal bone) lodged posterior to the astragalus and also in contact with the medial side of the calcaneal tuber, as preserved in the main slab of *Megacauda*. In extant monotreme species, the Os calcaris is present in males, and also in females with intraspecific variation by age according to Hurum et al. (Ref-230 Hurum et al. 2006). Other studies reported that the Os calcaris is present in young females but regressed in older females (Ref-231 Griffiths 1978; Ref-232 Whittington and Belov 2014). This extra-tarsal bone bears the horny external spur with canal connected to the crural gland in the hindlimb. The horny spur is not visible in XRF photograph and we interpreted that it was not preserved in the specimen. Presence of an Os calcaris is a general (plesiomorphic) feature for Mesozoic mammals.

Metatarsals, Phalanges and Digit-Rays (Extended Data Fig. 8) – The metatarsals and phalanges of the five pedal digit-rays have a formula of: 2-3-3-3-3 from digit 1 (big toe) to digit 5 (lateral toe). This is a general feature of the vast majority of mammals, an evolutionary plesiomorphy traced to the

therapsid ancestry of mammals (Ref-12 Luo et al. 2015; Ref-182 Hopson 1995; Ref-233 Ji et al. 1999). But beyond the digit-ray formula, there are two outstanding and striking morphological features in the proportion of the pedal digital rays for *Megacaula* and *Castorocaula*:

(1) Digit ray 1 in *Megacaula*. This digit ray shows two interrelated features: a very large entocuneiform, and a massive thicker metatarsal 1 and proximal phalanx 1, than the slenderer homologous bones of digit-rays 2-5. The entocuneiform and its corresponding metatarsal 1 are so wide that the entocuneiform shaft width is equal to the combined width of the mesocuneiform and ectocuneiform. Moreover, the entocuneiform distal end is more enlarged than the shaft of the bone. Metatarsal 1 is comparable in width to the entocuneiform. This bone has also nearly twice the width of the other metatarsals. Overall, *Megacaula* has a more robust digit ray 1 that is much thicker than the remaining pedal digit rays. The preserved pes of *Castorocaula* shows a similar pattern. By comparison, the common pattern is that the metatarsal 1 has about the same girth and robustness, as the other digit-rays, across the majority of extant mammals.

(2) The metatarsal-phalangeal length (combination of metacarpal + proximal phalanx + intermediate phalanx) of digit-rays 4 and 5 are slightly longer than that of digit-ray 3 (the middle toe). The elongation of the lateral two digit-rays is a highly derived pattern for *Megacaula* and *Castorocaula* (**Extended Data Fig. 8**). This is a contrasting feature to the common mammalian pedal digit-ray pattern that the middle toe (digit 3) is the longest digital ray, while the medial and lateral side digit-rays (1 and 5 respectively) are relatively shorter. It is also common that the metatarsal 1 has about the same girth and robustness, as the other digit-rays. These common mammalian features are also phylogenetically plesiomorphic characters of docodontans as a whole (**Extended Data Fig. 8**), as evidenced by the intact pes of *Agilodocodon* and the reconstructed pes of *Krusatodon* (Ref-10 Meng et al. 2015; Ref-16 Panciroli et al. 2024). This primitive feature is also present in most cynodonts.

Comparative Discussion on Digit-Rays – The combination of characters of a more robust entocuneiform, and a wider and thicker metatarsal 1 (than other metatarsals) are derived features of *Megacaula* and *Castorocaula*. This is developed also in *Docofossor* (Ref-12 Luo et al. 2015) but otherwise absent in other docodontans (Ref-10 Meng et al. 2015; Ref-8 Zhou et al. 2019; Ref-16 Panciroli et al. 2024). This combination of features, although rare for docodontans and other mammaliaforms, is also present in extant monotremes. The entocuneiform is thicker in girth and enlarged in *Ornithorhynchus*, very much comparable to the characteristics of *Megacaula*. Likewise, *Tachyglossus* has a widened entocuneiform, metatarsal 1 and proximal phalanx 1. Metatarsal 2 is also widened. In most line drawing illustrations of the echidna in the typical dorsal view of the foot, metatarsal 1 is not shown to be wide. This is because the bone is rotated to the plantar aspect of the pes in life related to the peculiar contacting posture of the pes for the echidnas (Ref-237 Pridmore 1985; Ref-238 Gambaryan and Kuznetsov 2013). But the 3-dimensional anatomical structure of this bone has a wide girth. The widening of the digit-rays 1 and 2 appears also to be visually slightly distorted, by the proximo-distal shortening of digit-rays 1 and 2 in echidnas. We interpret that the wide and more robust entocuneiform and metatarsal 1 are ancestral characters of monotremes as a group. These robust and reinforced bones of both the platypus and echidna are likely functionally related, to the habitual substrate contact of the anteromedial side of the strongly abducted and inverted pes. The more robust elements of digit-ray 1 are related to this specialized foot contact of monotremes in walking locomotion (Ref-237 Pridmore 1985; Ref-238 Gambaryan and Kuznetsov 2013; Ref-239 Jenkins 1970).

In proportion to the entire pedal length, the robust entocuneiform and metatarsal 1 in *Megacaula* and *Castorocaula* are more comparable to those of the platypus, than to the strongly shortened pedal bones (except the terminal phalanges) of the echidna. *Megacaula* and *Castorocaula* can be interpreted to have a dual function of the pes, as seen in the platypus, related both to the medial contact of the abducted and inverted feet during terrestrial walk, and to the posture of the entire hindlimb (including inverted pes) abducted and held side-by-side to the pelvic girdle, for swimming. On the debit side, we note that the calcanei of *Megacaula* and *Castorocaula* have a typical docodontan peroneal shelf on the lateral side. This differs from the curved and elongate peroneal process of monotremes, enabling the extreme abduction of the pedes during locomotor movement of monotremes (Ref-12 Luo et al. 2015; Ref-48 Gambaryan et al. 2002; Ref-229 Szalay 1994; Ref-238 Gambaryan and Kuznetsov 2013). We interpret that although the pes of semiaquatic docodontans could abduct and evert, the extent of their pedal abduction is less than in the lateral pedal movement during terrestrial locomotion as seen in extant monotremes (Ref-48 Gambaryan et al. 2002; Ref-238 Gambaryan and Kuznetsov 2013).

Also relevant to this study is the elongation of the bone elements of lateral digit-rays 4 and 5 in *Megacaula*. This is a typical feature of semi-aquatic mammals, related to the swimming locomotion by the web-feet of most semiaquatic mammals, which are developed to the extreme in the fin-feet of the pinniped mammals. By comparison, the elongation of two lateral pedal digit-rays (4 and 5) is relatively uncommon in mammals, but is known in the pedes of some arboreal mammals (Ref-54 Kielan-Jaworowska and Gambaryan 1994: fig. 59; table 6), volant mammals with feet-up roosting behavioral adaptation (Ref-7 Grossnickle et al. 2020; Ref-9 Meng et al. 2017) and in peramelemorph and diprotodont marsupials with syndactyly in which the pedal digit 2 and 3 are reduced and bound by skin. Due to the reduction of digit-ray 2 and 3, digit-rays 4 and 5 are relatively longer in these marsupials (Ref-211 Lessertisseur and Saban 1967b; Ref-240 Weisbecker and Nilsson 2008).

Here we interpret that the elongation of lateral digit rays (4 and 5) is an osteological proxy to more extensive area for webbing in semiaquatic mammals for swimming. The elongation of lateral digit-rays is noticeable in semi-aquatic mammals of the river otters of the Lutrinae subfamily; but it is much more prominent in the giant otter *Pteronura* (FMNH70768) and the marine otter *Enhydra lutris* (FMNH78762) than the other river otters of the Lutrinae. In such pinnipeds as seals and sea lions, the lateral digit-rays 4 and 5 are the extreme cases of elongation. The semiaquatic platypus has longer metatarsal-phalangeal lengths of digit-rays 4 and 5, than the terrestrial echidnas that show no more elongation of metatarsal and phalanges of the lateral digits than the middle toe. This pattern is developed to the extreme in the fin-feet of pinniped marine mammals (seals and sea lions; Ref-49 Koretsky et al. 2016; Ref-234 Berta et al. 2015; Ref-235 Adam 2018; Ref-236 Würsig et al. 2018). The semiaquatic platypus has longer metatarsal-phalangeal lengths of digit-rays 4 and 5, than the terrestrial echidnas that show no more elongation of metatarsals and phalanges of the lateral digits than the middle toe.

Hindlimb Posture – We interpret that *Megacaula* had a sprawling hindlimb posture, in standing or for ambulatory walking on substrate, on the similarity in osteological features to *Ornithorhynchus* characterized by this posture. This interpretation of the hindlimb posture for *Megacaula* is based on several similarities to the platypus: (1) emarginated acetabulum and the absence of a medially inflect femoral neck; (2) a large lesser trochanter of the femur, which is related to the horizontal posture of

the femur in *Ornithorhynchus* (Ref-48 Gambaryan et al. 2002), both for standing pose, and in walking of the platypus. During walking, the femur of the platypus can pronate (rotate around the long axis of the femur) during the propulsive phase of locomotion (Ref-48 Gambaryan et al. 2002). The femur can move and retract posteriorly in a limited range in the dorsal view (Ref-237 Pridmore 1985; Ref-48 Gambaryan et al. 2002) while the pronation (rotation) of the femur generates the posterior movement of the crus (tibia and fibula) for the propulsive phase of the locomotion. While monotremes have an overall similar hindlimb posture, Gambaryan et al. (2002 Ref-48) interpreted that this sprawling posture is more strongly developed in the platypus than in the echidna.

For mammaliaforms in general, the emarginate acetabulum of the pelvis, the large size of the lesser trochanter on the femur, the lack of an inflected femoral head and the overall configuration of the proximal part of the femur (e.g., Ref-4 Bishop and Pierce 2023: fig. 32; 2024b) are usually associated with a sprawling posture for the femur (e.g., Ref-4 Bishop and Pierce 2023), with the femur oriented antero-laterally with a range of angle (Ref-228 Bishop and Pierce 2024b). We infer that the hindlimb posture of *Megacaula* was generally similar, and its capability of hindlimb movement for terrestrial locomotion would be within the ranges estimated for mammaliaforms by Bishop and Pierce (Ref-228 Bishop and Pierce 2024b).

Posture of Knee Joint – We interpret that the knee joint of *Megacaula* is habitually flexed, as in monotremes. In monotremes, the medial and lateral condyles of the femur are asymmetrical and the lateral condyle are larger and wider. More importantly, the hypertrophied and plate-like parafibular process of the fibula is projecting dorsally beyond the fibular articulation with the lateral distal condyle. With these platypus-like features, it is most probably that the knee joint is flexed as seen in extant monotremes, and it would be impossible for *Megacaula* to flex and extend in parasagittal plane like in most therians. The knee of this animal has to be flexed, in standing pose, or during walking on substrate. In standing pose, the lower hindlimb (tibia and fibula) would be approximately vertical under the flexed knee. During walking, the lower hindlimb would move posteriorly with the rotation of the largely horizontal femur, in the propulsive phase of locomotion.

The hypertrophied parafibula is the most striking hindlimb feature of *Megacaula*. Aside from the spalacotherioid *Akidolestes* (Ref-227 Chen and Luo 2013), which represents an independent evolution of this hypertrophied parafibula within the spalacotherioids, most of which lack this feature (Ref-13 Ji et al. 2006; Ref-203 Li and Luo 2006; Ref-226 Ji et al. 2009), the hypertrophied parafibula in *Megacaula*, *Castorocaula* and *Docofossor* are unique among mammaliaforms.

Based on the monotreme pattern of the muscles originating from the parafibula (Ref-48 Gambaryan et al. 2002) for lower hindlimb and pedal functions, we interpret that the musculoskeletal features of *Megacaula* were similar to those in monotremes. This docodontan was capable of large force for the movement of tibia and fibula relative to each other. *Megacaula* was also capable of a rotating movement of the ankle joint as seen in extant monotremes (Ref-12 Luo et al. 2015: fig. 3; Ref-48 Gambaryan et al. 2002), and capable of inversion (or pronation) and eversion of the feet. The hindlimb of *Megacaula*, with a horizontally held femur and a flexed knee joint, was oriented as seen in the platypus. The function of such a hindlimb with specialized ankle joint and pes for terrestrial locomotion, could be easily coopted for hindlimb propulsion in swimming. This will be discussed separately, below.

Pedal Posture – The orientation of the calcaneo-astragalar contact indicates that, in life, the astragalus and the calcaneus were in juxtaposition, horizontally and side-by-side, in *Megacauda*, as in *Agilodocodon* and *Microdocodon* (Ref-8 Zhou et al. 2019; Ref-12 Luo et al. 2015). This interpretation is based on the observation that the sustentacular facet and astragalar facet on the astragalus (ED Fig. 9-b) and the reciprocal facets on the calcaneus (ED Fig. 9-h) are oriented vertically when the astragalus and the calcaneus are in full articulation. The vertical contact between the astragalus and calcaneus suggests that these two tarsals lack superposition, which is a more derived ankle joint configuration in more derived therians (Ref-226 Luo et al. 2016; Ref-229 Szalay 1994; Ref-239 Jenkins 1970). Furthermore, the side-by-side juxtaposition of the calcaneus and astragalus also means that the ankle contact to the substrate is relatively wide (wider than the type of ankle with some degree of astragalus-calcaneus superposition). The “wide ankle” pedal morphology (mostly related much wider calcaneus at the peroneal shelf level) is correlated with plantigrade foot posture, which is ancestral for mammaliaforms, for mammalian locomotion on diverse substrates, but more common in terrestrial mammals (Ref-226 Luo et al. 2016).

Mobility of the Upper Ankle Joint – This joint is also known as the calcaneo-astragalo- tibiofibular joint. The medial aspect of the astragalus shows a distinctive concavity, for the contact of the distal tibial malleolus. This concavity can be identified for all docodontans preserved with astragalus, although with a varying degree of development. This feature is most prominently developed in *Docofossor*, and also here in *Megacauda*. This feature is not fully exposed but can be inferred for *Castorocauda*. With the contact of the astragalar medial concavity and the distal tibial malleolus, the upper ankle joint is capable of a wide range of pivotal rotation of the pes (Ref-12 Luo et al. 2015: fig 3). The fibular contact to the convex fibular facet on the calcaneus, and to the fibula-astragalar crest on the astragalus is also capable of significant rotation. The calcaneo-fibular contact and the fibuloastragalar contact are side-by-side as the calcaneus and astragalus are articulated in life. These two structures form a convex surface in oval outline in dorsal view. This fits to the slightly concave distal surface of the fibula. These ankle morphologies likely enabled a significant plantar flexion at the upper ankle joint, simultaneously also a significant capacity for eversion and/or abduction, as well as for inversion of the pes relative to the zeugopod part of the hindlimb.

In extant monotremes, the capacity for the pes to pivot at the medial astragalar concavity and the tibial malleolus (Ref-12-Luo et al. 2015: fig. 3; Ref-241 Griffiths 1988), and a concurrent pedal rotation around the pulley-like contact of the tibia and astragalus can facilitate plantar flexion, and abduction of the feet relative to the tibia and fibula. This mobility contributes not only to ambulatory terrestrial locomotion, but also to pedal digging in the vertical burrowing behavior of the short-beaked echidna (Ref-48 Gambaryan et al. 2002; Ref-242 Augee et al. 2006). In the platypus, the pulley morphology is so-well developed in the astragalus that the bone is almost shaped like a spool, which is even more effective for pivotal rotation. This is interpreted to be a feature more effective for swimming in the platypus (Ref-48 Gambaryan et al. 2002), in addition to walking.

By comparison to monotremes, we speculate that the hind feet of *Megacauda*, with its capacity for abduction at the ankle joint, are oriented with toes pointed antero-laterally in resting pose with its sprawling hindlimb posture, and with feet oriented anteriorly or antero-laterally in locomotor gaits. We speculate that the pes can be habitually abducted and everted during locomotion in water.

The feet of the specimens of *Megacauda* and *Castorocauda* are preserved with an abducted pose and

the plantar side (“bottom”) up. Both feet of the *Megacauda* specimen are fossilized in a strongly everted posture and an upward exposure of the plantar side of the foot. In *Castorocauda*, the left foot is preserved with the plantar side up in a strongly everted foot. Although the right femur through ankle is lost, the right foot is also preserved in plantar side up, in *Castorocauda* (Ref-13 Ji et al. 2006: fig. 1). We interpret that this is a habitual posture of the feet when the animals were active in swimming. This habitual orientation of the ankle and posture of the feet may have enhanced the possibility that the feet were fossilized in the same manner. By contrast, this pattern of preservation in strongly everted position relative to tibia and fibula is relatively rarely seen in Mesozoic mammal specimens embedded in rock slabs, as shown by a survey of the hindlimb posture of Mesozoic mammals (Ref-243 Kielan-Jaworowska and Hurum 2006).

(8) Functional Interpretation of Musculoskeletal Morphology for Swimming

Forelimb and Manus

The humerus and ulna of *Megacauda* suggest fossorial function, by several common fossorial musculoskeletal features. The olecranon elongation of the ulna indicates better leverage of a strong triceps brachii muscle to extend the elbow. The robust and wide humerus, with hypertrophied entepicondyle, indicates strong muscles for pronation of the forearm and for flexion of the wrist and the manual digits. The large ectepicondyle of the humerus suggests well developed muscles for supination of the manus and extension of the wrist. Because many quadrupedal semiaquatic mammals have also strong propensity for digging (Ref-55 Rose and von Koenigswald 2005), the above-mentioned forelimb features can be used, alternately, for fossorial adaptation and also for swimming, by observation in many mammalian functional morphology studies (Ref-177 Hildebrand 1985; Ref-55 Rose and von Koenigswald 2005; Ref-13 Ji et al. 2006; Ref-56 Hand et al. 2025). *Ornithorhynchus*, with its fossorial features of the forelimb, is known for alternate pectoral paddling in water (Ref-244 Fish 1993; Ref-245 Fish 2016). Presence of robust forelimbs in *Megacauda* and *Castorocauda*, by itself, may not be sufficient or exclusive to indicate swimming. But they are consistent with an inference for swimming capability because the musculoskeletal function for digging can be coopted for swimming, as shown by the behavioral pattern that many quadrupedal semiaquatic mammals are well adapted for digging (Ref-55 Rose and von Koenigswald 2005; Ref-13 Ji et al. 2006; Ref-56 Hand et al. 2025). It is probable that *Megacauda* and *Castorocauda* could do alternate pectoral paddling, but it is not possible to infer if these docodontans would be capable of pectoral paddling in surface swimming (*sensu* Ref-245 Fish 2016) or possibly even rowing in submerged swimming.

Tail Morphology

The horizontally wide and dorsoventrally flattened tail of *Megacauda* and *Castorocauda* is the foremost musculoskeletal structure that is indicative of swimming function. Extant semiaquatic mammals use tails for locomotor function such as propulsion in conjunction with pelvis and hindlimb, and for balancing and steering in water. Semiaquatic mammals show three tail morphotypes (Ref-49 Howell 1930; Ref-51 Fish et al. 2021; Ref-220 Hickman 1979; Ref-244 Fish 1993):

(1) Bilaterally compressed and narrow tails (=“Keeled Tail” of 51-Fish et al. 2021). Examples of this type include *Desmana* (Talpidae of Eulipotyphla), the watershrew *Neomys* (Soricidae), the otter shrew

Potamogale (and related tenrec species of afrotherians), the narrow-tailed muskrat *Ondatra* (a rodent), the crab-eating rat *Ichthyomys*, the Australian water rat *Hydromys* (or rakali), etc.

(2) Round tails (“Tapered Tail” of Ref-51 Fish et al. 2021). Examples of this type include the water opossum *Chironectes* (a marsupial), the Eurasian water shrew *Neosorex*, the nutria or *Myocastor* (a hystricomorph rodent), the European water vole *Avicola*, the round-tailed muskrat *Neofiber*. This type of tail is present in most of the diverse river otter species of the Lutrinae subfamily.

(3) Horizontally flattened and wide tails (= “Paddle Tail” of Ref-51 Fish et al. 2021): the monotreme *Ornithorhynchus*, beaver species of the Castoridae family (of Rodentia), the giant otter *Pteronura* (the Lutrinae subfamily), and the sea otter *Enhydra* with a wider (although shorter) tail than the round-tailed river otters (also of the Lutrinae of Mustelidae).

As evidenced by the preserved outline of the tail pelage, and by osteological characters of the caudal vertebral column, *Megacauda* and *Castorocauda* clearly have horizontally flattened and wide tails. Their tail outlines are very similar to the flattened wide tail type of extant swimming mammals in the semiaquatic ecomorphotype. However, the two semiaquatic docodontans are also different from each extant swimming mammal in some specific details of the flattened wide tails. In swimming docodontans, the tail shape starts to become gradually narrower posterior to Ca10, and is further tapering after the longest (transitional) caudal vertebra (Ca15) toward the tail end. These tail shape characteristics are more similar to that of *Pteronura* (although *Pteronura* is a much larger animal). Both semiaquatic docodontans lack the broad and rounded tail end of the beaver species and the platypus. Because the flexion of the body and tail can help generate propulsive traveling waves, which tend to be faster posteriorly, and increase its amplitude toward the end of the tail. The wider and round tail ends of flattened tails of extant semiaquatic swimmers can be effective in propulsion (if needed) (Ref-244 Fish 1993; Ref-245 Fish 2016). By comparison, the semiaquatic docodontans, with a tapering tail-end, likely lacked such a functional capacity to generate propulsive force with the distal part of their tails.

In extant semiaquatic swimming mammals, the post-pelvic region of the flattened wide tail is internally supported by two types of post-pelvic vertebrae: the proximal caudals with single wing-like anterior transverse process, within the pelvis; the butterfly-shaped caudals posterior to the pelvis; and by “middle” caudals with “H”-shaped, double transverse processes in the middle region of external tail. Similarly, both types of specialized post-pelvic caudal vertebrae are also developed in *Megacauda* and *Castorocauda*. But there are differences for each vertebra type along the series of caudal vertebrae, and also in relative positions in the caudal series for each type.

The two semiaquatic docodontans have fewer anterior vertebrae with single and elongate transverse process than those of extant mammals with paddle tails. *Megacauda* has a single post-pelvic proximal caudal (Ca5) with “butterfly-shaped” proportion of the anterior vs. posterior transverse process, and *Castorocauda* has two such “butterfly-shaped” post-pelvic vertebrae. This is in contrast to the five such post-pelvic vertebrae in *Pteronura* and seven such post-pelvic vertebrae for *Castor canadensis*. These super-elongate transverse processes are well developed in most proximal four caudals (Ca1-Ca4), although the size of these processes is decreasing further posteriorly, through Ca14-15.

In *Ornithorhynchus*, Ca6-Ca16 have especially prominent and super-elongate transverse processes, for the widening of the paddle contour. In *Castor* species, the Ca2-Ca5 have single transverse processes more elongate than the rest of caudals (Ref-53 Sennikov 2023). A similar pattern of relative elongation of some caudals compared to the rest is present, although weakly expressed, in the giant otter *Pteronura* (Ref-53 Sennikov 2023). By contrast, the semiaquatic docodontans lack these super-elongate transverse processes that correspond to the convex contour of the paddle-shaped tails of extant comparative taxa.

Development of the caudal vertebrae with H-shaped double transverse processes is highly comparable between the two semiaquatic docodontans and extant beaver species and with wide tails. They are also similar to semiaquatic mustelids with either flat wide tail or round tail, and to the water opossum *Chironectes*. But there are positional differences between the semiaquatic docodontans and extant semiaquatic comparative taxa. The dorso-ventrally compressed vertebrae with wide double transverse processes are well-developed in *Megacauda* and *Castorocauda*, and this type of vertebrae is located in caudal vertebrae Ca5 – Ca12. By contrast, the vertebrae with similar morphologies are far more distally positioned in Ca15 to Ca21 in the beaver species (e.g., *Castor canadensis*), and to the Ca10-Ca14 in the tail of the giant otter *Pteronura*.

Implications for Tail Functional Morphology – The positional differences of these specialized types of vertebrae, along the caudal series, indicate some differences in muscle size, by comparison to the extant semiaquatic mammals with (or without) a flat and wide tail. The size of muscle attachment features, and how far posteriorly these muscle attachment features would be present in the two docodontans in question can be informative for interpreting the tail functional morphology. With a longer series of post-pelvic caudal vertebrae with single elongate transverse process in extant giant otter and beavers, their sacrocaudalis dorsalis and ventralis muscles are much larger, and longer so as to extend farther posteriorly into the middle section of the tail. This is further than was possible for *Megacauda* and *Castorocauda*. The more posteriorly positioned double transverse processes in *Pteronura* and *Castor* species also indicate a more posterior extension of the latter muscles inserting on the double transverse processes, well into the middle region of the tail. This posterior extension of the intertransversarius muscle would be unlikely for *Megacauda* and *Castorocauda*, in which the double transverse processes are limited to the proximal region (before Ca10-Ca12). This suggests that, although *Megacauda* and *Castorocauda* have convergently developed a similar musculoskeletal pattern for the tail, the homologous muscles have smaller size and shorter contraction ranges than those in extant swimming mammals with similarly flattened tails.

The H-shaped caudals with double transverse processes are developed, in slightly different variant forms, in many extant mammals of different ecomorphotypes, but all with enhanced capability related to functions of the tail (Ref-220 Hickman 1979; Ref-186 Organ 2010; Ref-187 Russo 2015). The morphology of double transverse processes may not be an osteological proxy to a wide (especially paddle shaped) tail contour, by itself, because the platypus has a paddle tail with all single wing-like transverse processes on all caudals and none of its caudal vertebrae have H-shaped double processes. The majority of otter species of the Lutrinae subfamily have rounded tails and also the H-shaped caudals in the middle section of the tail. The characters combination of H-shape middle caudals with a round tail is also present in the water opossum *Chironectes*.

Double transverse processes on the caudal vertebrae are also present in pantolestid eutherian mammals of the Eocene, such as *Paleosinopa* from North America interpreted to be both fossorial and semiaquatic (Ref-55 Rose and von Koenigswald 2005) and *Buxolestes* (Eutheria) from the Eocene lake ecosystem of the Messel lagerstätte that is interpreted to be semiaquatic (Ref-246 von Koenigswald 1980; Ref-247 Pfretzschner, 1993, Ref-248 Pfretzschner 1999).

Mammals of other ecomorphotypes than the semiaquatic species can also have this type of H-shaped caudal vertebrae with round tail correlated with strong capability to maneuver the tail, or for terrestrial locomotor function. One such example is the grey kangaroo *Macropus fuliginosus* that has a strong musculoskeletal system of the tail for balancing the ricochet hopping on hindlimbs, and for support when standing (Ref-191 Dawson et al. 2014). The caudal vertebrae have well-developed double transverse processes, accompanied by enlarged mammary processes from the prezygapophyses; these structures together accommodate the well-developed sacrocaudalis dorsalis lateralis muscle, and the intertransversarius (both ventral and dorsal) muscles that extend far posterior along the caudal vertebral column, for locomotor and for supporting functions (Ref-191 Dawson et al. 2014).

But variant types of double transverse processes are also present in the eutherian *Leptictidium* that is evidently a bipedal hopping terrestrial mammal (Ref-249 von Koenigswald and Storch 1987). It is also known in terrestrial *Solenodon* (a eulipotyphlan placental) (Ref-55 Rose and von Koenigswald 2005). It is conservative to interpret that the double transverse processes indicate better development of muscle attachments foremost by intertransversarius muscles but also by sacrocaudalis dorsalis and ventralis muscles for a stronger and more maneuverable tail, that can be part of different ecomorphological specializations. It is consistent with and helps to reinforce the interpretation of semiaquatic adaptation of *Megacauda* and *Castorocauda*, although only with other corroborating evidence.

The better development of the postfemoral muscles of the tail and hindlimb can also aid the hindlimb function related to swimming for the platypus (Ref-48 Gambaryan et al. 2002): the caudal neural spines and the broad transverse processes along the caudal vertebral column are for extensive attachment of a larger semitendinosus pars vertebralis, which would insert on the lower hindlimb, to hold the hindlimb close to the pelvis for pelvic paddling. The large attachment site of the caudofemoralis in the femur of *Ornithorhynchus*, which is also inferred to be present in *Megacauda*, would also be consistent with the capability to hold the hindlimb to the pelvis, for swimming.

Pelvic Girdle Functional Interpretation

The new anatomical information on the hypertrophied pubic tubercle and pubic saddle for the iliopsoas muscle has now opened some possible functional interpretation for the lumbar and pelvic girdle for swimming. In the platypus, the hypertrophied psoas minor (with large psoas minor tuberosity for its insertion) is for flexing the lumbar vertebrae and the pelvis. This action is partly synergistic with the action of the iliopsoas, which inserts on the lesser trochanter of the femur, can flex lumbar and pelvis, and additionally also the femur. In pinniped swimmers, the psoas minor tuberosity is also a major feature on the pubis (Ref-49 Howell 1930, Ref-50 Koretsky et al. 2016), which presumably also enable some lumbar-pelvic flexion. It is a better supported comparative interpretation that the *Megacauda* had a similar function to flex the lumbar, the pelvis and the femur together, as in the platypus. However it is less certain if the synergistic action of the psoas minor and the iliopsoas, as seen in the platypus, would be developed to the same extent in *Megacauda*. It is

unlikely that *Megacaula* would have the flexing capability of the lumbar and pelvis as seen in pinnipeds that are specialized for pinniped-like propulsion with fin-feet.

Hindlimb and Pedal Function in Swimming

We interpret that the postcranial features of *Megacaula* and *Castorocaula* are capable of both fossorial and semiaquatic swimming behavior, similar to many extant semiaquatic placental mammals that have propensity for digging (Ref-250 Fish 1994; Ref-55 Rose and von Koenigswald 2005). These docodontans are ecomorphologically comparable to extant monotremes (especially the platypus), which are adapted to living in burrows (the platypus) and are also capable of powerful digging (the echidna). Both monotreme taxa are very capable of swimming. The platypus is well-known for swimming and foraging in water. Although the short-beaked echidna lives by foraging terrestrially, its swimming behavior is also well documented (Ref-242 Augee et al 2006).

The musculoskeletal features of the hindlimbs and pedes of *Megacaula* and *Castorocaula* can be interpreted to have dual function both for terrestrial locomotion and for swimming, as extant semiaquatic mammals must be capable of both (Ref-244 Fish 1993, Ref-250 Fish 1994; Ref-52 Thewissen and Fish 1997; Ref-55 Rose and von Koenigswald 2005). The musculoskeletal function of the hindlimb and pes for terrestrial locomotion of semiaquatic mammals are coopted into swimming (Ref-244 Fish 1993, Ref-251 Fish et al. 2016). In *Megacaula*, its sprawling hindlimb with flexed knee for standing pose or terrestrial locomotion could be coopted into holding limb to the pelvic girdle and tail for swimming as seen in the platypus. Thus, abduction of the femur in ambulatory gaits on land is an exaptation to holding the hindlimb to the pelvis and maintaining the flexed knee for lower hindlimb to be close to the tail (Ref-48 Gambaryan et al. 2002), for better functioning for the pelvic paddling behavior.

The enlarged parafibula of *Megacaula* would accommodate a larger gastrocnemius muscle for strong pedal rotation and abduction. The enlarged “para-fibular” muscles with such a large para-fibula that would be comparable to the homologous muscles as seen in the platypus that extend and evert the ankle. Functioning together with highly mobile ankle joint of *Megacaula*, these large peroneal muscles can further spread of lateral digit-rays (Ref-48 Gambaryan et al. 2002: p. 35). This larger peroneal digit muscles can abduct and facilitate a wider spreading of elongate lateral digit-rays, especially during swimming.

Megacaula and *Castorocaula* are similar to the platypus in the elongation of the lateral digit-ray and robust entocuneiform and metatarsal 1, both reinforcing a robust digit-ray 1. In pinniped marine mammals (seals and sea lions), the fin-formed feet are longer and much enlarged by significantly elongate lateral digit-rays and medial digit ray 1. The pinniped feet are the major locomotor structure for propulsions (Ref-236 Würsig et al. 2018), in a functional trade off with the short tails (Ref-49 Howell 1930; Ref-220 Hickman 1979; Ref-244 Fish 1993, Ref-252 Fish 2000; Ref-52 Thewissen and Fish 1997). A similar pattern is also developed in the phylogenetically un-related sea otter (*Enhydra*) that has longer feet than other river otters of the Lutrinae subfamily. The longer fin-feet of *Enhydra* for propulsion in swimming have been interpreted to be compensating for the sea otter’s shorter tail (Ref-253 Mori et al. 2015). We interpret the longer autopod (feet) relative to the zeugopod (tibia and fibular) and the stylopod (femur) of the hindlimb in *Megacaula* and *Castorocaula* are a phylogenetic apomorphy, which has evolved from the common ancestor of docodontans that would have a more

plesiomorphic proportion of the hindlimb and pes as exemplified by *Agilodocodon* (**Extended Data Fig. 8**). This evolutionary apomorphy is more effective for dual function of swimming as well as terrestrial locomotor gaits, for the semiaquatic ecomorphotype.

We interpret that during swimming of *Megacauda*, its entire hindlimb would be abducted and held side-by-side to pelvic girdle. During the active swimming, its feet were abducted and hyper-flexed so that its plantar side was facing up, made possible by the mobility of the upper ankle joint consisting of a pivot of the astragalar medial concavity and distal tibial malleolus, as well as the trochlea-like contact between astragalus and the tibia and fibula (Ref-12 Luo et al. 2015: fig 3).

This habitual orientation of the ankle and posture of the feet may have enhanced the possibility of the feet to be fossilized in the same manner: both feet of the *Megacauda* specimen are fossilized in strongly rotated posture and the plantar side of foot facing dorsally. We speculate this fossilized position of the pes was likely the swimming posture for this animal. In *Castorocauda*, the left foot is preserved with plantar side up in a strongly everted foot (Ref-13 Ji et al. 2006: fig. 1), but the right hindlimb is too incomplete to interpret.

Dual Fossorial–Semiaquatic Function of Docodontans

The behavior of swimming in many semiaquatic mammals has conserved the modified neuromotor pattern and gait characteristics of their phylogenetic relatives that are terrestrial (Ref-245 Fish 2016). As mammal evolution of secondary aquatic locomotion from the ancestrally terrestrial locomotion, it is expected that this evolution would go through a transition of semiaquatic locomotion (Fish 2020). Many placental mammals have propensity for digging (Ref-55- Rose and Koenigswald 2005). For mammals capable of efficient forelimb paddling in water, the musculoskeletal functional morphology of the forelimb is mostly similar to those of fossorialists (Ref-13 Ji et al. 2006). The most prominent of this kind of examples is the extant *Ornithorhynchus* that forages in water while sheltering in burrows near water (Ref-231 Griffiths 1978, Ref-241 Griffiths 1988); its forelimbs are well adapted to paddling during swimming but also effective in movement on land, and also capable of burrowing. The Cretaceous monotreme *Kryoryctes* on the stem to extant Monotremata has the dense bone in humerus that is typical for aquatic adaptation, while its humeral musculoskeletal feature is also similar to fossorial mammals (Ref-56 Hand et al. 2025). In a similar light, it has been postulated that the docodontan *Haldanodon* was a semiaquatic swimmer (Ref-181 Martin 2006). We interpret that the fossorial ecomorphotype and semiaquatic ecomorphotype for the forelimbs are adjacent and closely related ecomorphotypes.

Sánchez-Villagra and Asher (2002) (Ref-254) and Miyamae et al. (2025) (Ref-254) have noted that many extant semiaquatic mammals have significantly larger infraorbital foramina than their terrestrial counterparts of various groups (*Ornithorhynchus* and *Tachyglossus*, marsupials, sorcid and talpid lipotyphlans, murid rodents and afrotherian tenrecs). A further study by Crumpton and Thompson (2013) (Ref-256) of 22 extant talpid species shows that fossorial and semiaquatic talpid species have larger sized infraorbital foramina in semiaquatic forms (e.g., *Desmana moschata*) than in related terrestrial taxa (e.g., *Talpa europaea*). Pfretzschner (1993) (Ref-247) and Pfretzschner (1999) (Ref-248) has also showed that the semiaquatic carnivorans have larger infraorbital foramina (or canals) than terrestrial carnivores, a difference that is especially prominent for river otters (Ref-247 Pfretzschner 1993: fig. 14). The larger infraorbital canals are associated with a larger infraorbital nerve

from the trigeminal nerve system, which is a common pattern of the semiaquatic mammals (Ref-257 Dunstone 1998) because the infraorbital nerves from the Trigemini innervate the vibrissae of the head for detection for prey and general sensory function in the aquatic environment. This enhanced tactile sensory function compensates for the reduction or loss of olfaction and eyesight, in such semiaquatic forms as ichthyomyine rodent species that are carnivorous and semiaquatic (Ref-258 Voss 1988). The semiaquatic Pyrenean desman (*Galemys pyrenaicus*) is blind and depends entirely on tactile sensations (Ref-259 Richard 1985; Ref-260 Sendral and Santos 2025). In general, the enlargement of the infraorbital nerve is positively correlated with larger sizes of the infraorbital canal in mammals (Ref-261 Muchlinski 2008; Ref-262 Muchlinski et al. 2020), with an important caveat that in major groups of rodents, the infraorbital canal/foramen can be modified and enlarge to accommodate the elaborated masseter muscles.

The enlarged infraorbital canal is informative for functional morphology of *Megacauda* which is clearly a semiaquatic species, and of *Haldanodon* which we postulated to be a dual fossorial-semiaquatic ecomorphotype by forelimb features. The infraorbital foramen is larger than in these species that in other docodontans. We interpret that the moderate enlargement of the infraorbital foramen in *Megacauda* and very large infraorbital foramen of *Haldanodon* are evidence for a larger infraorbital nerve related to enhanced innervation of vibrissae tactile sensation, which could be consistent with an adaptation to fossorial, semiaquatic, or both (Ref-257 Dunstone 1998; Ref-254 Sanchez-Villagra and Asher 2002; Ref-255 Miyamae et al. 2024; Ref-256 Crumpton and Thompson 2013). We further note that the Late Jurassic *Docodon* from North America (Ref-25 Schultz et al. 2017), which is closely related to *Haldanodon* and *Docofossor* (Figure 5), also has much enlarged infraorbital foramen, but its postcranium is still unknown and the relevance to infraorbital sensory function can not be interpreted any further.

Megacauda and *Castorocauda* have two mental foramina connected to the mandibular canal in the lower jaws. These foramina are larger in *Megacauda* than in *Castorocauda* (Fig. 3). In the transverse sections of the mandible, the mandibular canal is not significantly enlarged as the large mandibular canal in the fossil monotreme *Teinolophus* (Ref-263 Rowe et al. 2008; Ref-56 Phillips et al. 2009; Ref-264 Rich et al 2016) and extant *Ornithorhynchus* (Ref-255 Miyamae et al. 2025). By inference, the inferior alveolar nerve is not as enlarged in *Megacauda*, as in monotremes. In monotremes, the enlarged infraorbital foramen and the enlarged mental foramen and the mandibular canal are related to electroreception, especially for the platypus in foraging in aquatic environment (Ref-263 Rowe et al. 2008; Ref-56 Phillips et al. 2009; Ref-255 Miyamae et al. 2025). By the small size of its mandibular canal, it is far less likely that *Megacauda* would be capable of such sensory function.

Summary

Megacauda is more similar to lutrine otters and to beavers in tail structure, than to the platypus. The similarities to the otters are mainly in the muscular features related to the double transverse processes of the caudal vertebrae, which are present in otters but absent in the platypus. The tail of *Megacauda* is dorso-ventrally flattened and wide in its proximal part. This is partly similar to the tails of the platypus and the giant otter (*Pteronura*) and the sea otter (*Enhydra*). The dorso-ventrally compressed caudals in the mid-part of the tail of *Megacauda* are also similar to those of *Pteronura* and *Enhydra*, but different from the vertebrae in the round tails of most river otters. In the pelvic paddling of extant otters, the hindlimb held to the pelvis and the proximal part of the tail can dorso-ventrally undulate,

together, for propulsion in water (Ref-250 Fish 1994). Likely *Megacauda* could undulate its hindlimb, pelvis and proximal part of the tail, in the same way as extant otters.

Megacauda is more similar to the monotreme *Ornithorhynchus* in the overall musculoskeletal features of the pelvic, hindlimb, and pes, than to otters. The proportion of stylopod, zeugopod, autopod ratio can be informative for inference of swimming adaptation (Ref-55 Rose and von Koenigswald 2005; Ref-251 Fish et al. 2016). The tibia and pes are significantly more elongate relative to the femur in *Megacauda* and *Castorocauda*, than in *Agilodocodon* and *Microdocodon*. In most osteological characteristics of the hip joint, the knee joint, and the ankle joint and their related muscles, *Megacauda* is similar to the monotreme *Ornithorhynchus*. On this comparative basis, we infer that *Megacauda* was functionally most similar to the platypus in hindlimb and pedal movement during swimming.

The pedal digit ray pattern of *Megacauda*, with its elongate lateral digit and robust first digit, is most similar to the web-feet of the platypus. But its feet also bear strong resemblance of the fin-feet of the sea otter (*Enhydra*) and pinnipeds in which the feet provide more propulsion than in the platypus. For relative functional importance of the feet for propulsion, *Megacauda* likely was intermediate between *Enhydra* and the platypus.

By the functional indices of limb morphometrics, the femoral length vs. pedal length ratio, the tibia/femoral length ratio or the crural index (Ref-55- Rose and von Koenigswald 2005), and the overall length pattern of femur-tibia-pedal segments (Ref-245 Fish 2016; Ref-253 Mori et al. 2015; Ref-265 Kilbourne 2021), we can separate the semiaquatic docodontans from the terrestrial-arboreal docodontans (Table 1; **Extended Data Fig 8**).

Our comparative musculoskeletal patterns strongly favor that *Megacauda* was primarily a pelvic paddling swimmer, and its swimming was dominated more by hindlimb and tail, than the forelimb. However, we also postulate that the forelimbs of *Megacauda* were capable of swimming, likely by alternate pectoral paddling, functionally coopted from fossorial and terrestrial locomotor features. Consistent with this interpretation are two other skeletal proportion indices: the intermembral index of the forelimb-hindlimb length ratio and the metacarpal/metatarsal length ratio (Ref-52 Thewissen and Fish 1997; Ref-55 Rose and von Koenigswald 2005). These two indices cannot rule out the swimming by quadrupedal padding for *Megacauda*.

Limitation of Inference

Semiaquatic ecomorphotypes of extant mammals evolved convergently from a wide range of land mammal clades long separated by deep histories from one another (Ref-48 Howell 1930; Ref-58 Hood 2020; Ref-234 Berta et al. 2015; Ref-252 Fish 2000). The swimming behavior of these convergent species may be enabled by disparate musculoskeletal features that are taxa-specific, different by species, and far from uniform. Different species of the semiaquatic ecomorphotypes may have exploited a narrower subset of a wider range of the musculoskeletal features known to be associated with swimming, across separate clades. Most species with this broad convergence to swimming have developed incomplete convergences to one another (Ref-7 Grossnickle et al. 2020), and have coopted a different subset of features for swimming. Such incomplete convergences tend to be challenging to untangle in a clear-cut way (Ref-266 Grossnickle et al. 2024).

The musculoskeletal features in *Megacauda* interpreted here to be for swimming function are also incomplete convergences to the swimming feature of the extant semiaquatic mammal species. *Megacauda* is not a perfect fossil analogue to any of extant semiaquatic mammal species, as much as no extant semiaquatic mammal species is exact analogue to one another. The musculoskeletal features for swimming function are known to be disparate among major mammalian groups with semiaquatic ecomorphotypes (e.g., lutrine otters vs. pinnipeds, water opossum vs. the platypus, beavers vs. tenrecs), although some general principles of biomechanics are applicable to all (Ref 51 Fish et al. 2021; Ref-244 Fish 1993; Ref-250 Fish 1994; Ref-251 Fish et al. 2016). The features of *Megacauda* related to swimming function are a combination of features that are not uniformly present or equally functional across all extant semiaquatic species, all of which are different in their own right. *Megacauda* only exploited some of the features known to be correlated to swimming in a subset of extant semiaquatic species. A further limitation to functional inference of fossil semiaquatic mammals is that the musculoskeletal features could have multiple functions, and a semiaquatic species can be capable of several modes of swimming behavior, which are not mutually exclusive (Ref-250 Fish 1994). All these add to the uncertainty in our inference of the swimming behavior of an extinct species phylogenetically distant from the semiaquatic species of the crown Mammalia.

We interpret that the instability of the Docodonta node of our phylogenetic tree topology is likely caused by the incompleteness of *Gondtherium*, a late Early Jurassic taxon from India represented by a single upper molar, and by the incompleteness of *Nujalikodon* from the Lower Jurassic of Greenland represented by a single anterior lower molar. *Gondtherium* was commonly assumed to be a sister taxon to the Docodonta in Luo and Martin 2007 (Ref-17) and some subsequent studies). *Gondtherium* has unstable positions in various consensus trees of our phylogenetic analyses. This is a prominent weakness of our phylogenies. *Gondtherium* is excluded from the Docodonta clade in the 50% majority consensus tree of the 23 EPTs (equally parsimonious trees) from PAUP search. But in our preferred Adam consensus tree, it forms an unresolved trichotomy with *Nujalikodon* and the rest of docodontans.

We suspect that instability of *Gondtherium* is likely caused by the fact that it is a single upper molar (therefore missing all characters of lower molars) and *Nujalikodon* is represented by a single lower molar (missing all characters of the upper molars). None of the lower molar characters scored for *Nujalikodon* can be scored for *Gondtherium*, and vice versa. The missing data problems for *Gondtherium* and *Nujalikodon* is the cause for the uncertainty of *Gondtherium* phylogenetic placement. This issue can only be resolved until better preserved fossils of a sister taxon to the Docodonta is discovered in the future.

(9) Phylogenetic Character List for Analysis of *Megacauda* among docodontans

Our main focus of this phylogenetic analysis is on the placement of the new taxon, *Megacauda sungei*, in the generic phylogeny of docodontans. For character state scorings on molars of docodontans, we are mostly following the two earlier studies of Luo and Martin (2007) (Ref-17) and Hu et al. (2007 Ref-73). Several scorings of these two studies were subsequently modified, and the character list was expanded, by Averianov et al. (2010) (Ref-64). These modifications by Averianov et al. (2010) are adopted here. The next studies that further expanded the characters sampling on more taxa are Zhou et al. (2019) (Ref-8) and Panciroli et al. (2019, 2021) (Ref-65, Ref-66). In the recent two years, a further expansion of the matrix to include newly discovered taxa, or new and better fossil specimens to augment the scorings of characters in the matrix are by Averianov et al. (2024) and Panciroli et al. (2024) (Ref-16). Patrocínio et al. (2025) (Ref-19) is the latest and highly relevant study on the earliest-known docodontan *Nujalikodon* from Greenland. Character scorings of *Nujalikodon* (Patrocínio et al. 2025 Ref-19) are also incorporated into our analysis of *Megacauda* here.

This systematic analysis is not designed to reassess all controversial taxonomic questions in the historical literature of all taxa. But nonetheless, here we wish to clarify how we treated several taxa. “*Peraiocynodon*” is excluded from this study because the type specimen of *Peraiocynodon serendipidus* is comprised of deciduous premolars (Ref-25 Schultz et al. 2017; Ref-267 Butler 1939; Ref-268 Averianov 2004). Also following Averianov (2004) (Ref-268), the species of “*Peraiocynodon major*” (Ref-269 Sigogneau-Russell 2003) has been regarded to be a junior synonym of *Krusatodon kirtlingtonensis*, as argued by Averianov (2004) (Ref-268). The latter taxonomic opinion is followed here. Martin et al. (2010) argued that “*Acuodulodon sunae*” (Ref-73 Hu et al. 2007) was a junior synonym of *Dsungarodon zuoi*. Although *Acuodulodon* is still regarded to be a separate taxon by some (Ref-65 Panciroli et al. 2019), here we follow Martin et al. (2010) (Ref-99) on this taxonomic opinion. *Tikitherium* (Ref-270 Datta 2005) was included in earlier analyses, starting with Luo and Martin (2007) (Ref-17), but it is now deleted in light of the reinterpretation of this fossil and correction by Averianov and Voyta (2024) (Ref-271).

Terminology of molar characters - The molar terminology of docodontans is illustrated by Luo and Martin (2007 Ref-17). This molar terminology system is based on a homology scheme of molar cusps first advocated by Butler (1997) (Ref-61). This nomenclature differs in some aspects from the molar cusp terminology of Sigogneau-Russell (2003) (Ref-269) under an alternative homology scheme, which was adopted with slight modification by Kielan-Jaworowska et al. (2004) (Ref-1). Additional molar cusp features have been recognized and illustrated by Hu et al. (2007) (Ref-73), as modified and updated by Averianov and colleagues (Ref-18 Averianov et al 2024; Ref-64 Averianov et al 2010). More recently Panciroli and colleagues (Ref-16 Panciroli et al. 2024; Ref-65 Panciroli et al. 2019, Ref-66 Panciroli et al 2021) have further updated this series of character lists and matrices. For possible synonymy of some of these dental characters, according to our own interpretation, please consult Luo and Martin (2007) (Ref-17) and Panciroli et al. (Ref-16 Panciroli et al. 2024; Ref-65 Panciroli et al. 2019, Ref-66 Panciroli et al 2021).

Character state scorings on docodontan molars are continuing to change in recent years, largely necessitated by discoveries of new fossils, or new specimens of existing taxa that revealed new features. The character scorings on taxa here are based on Zhou et al. (2019) (Ref-8), further expanded by Panciroli colleagues (Ref-16 Panciroli et al. 2024; Ref-64, Panciroli et al 2019,) by Averianov et al.

(2024 Ref-18), and most recently by Patrocínio et al. (2025) (Ref-19). In this study, we further revised the systematic scorings from our own re-assessment of docodontan dental morphology.

Mandibular Features -

1. Mandible – Shape of the angular region (character state revised from Meng et al. 2015):

(0) Pointed mandibular angle (two sides of the angular process forming an angle of 90 degrees and smaller): *Sinoconodon*, *Morganucodon*, *Hadrocodium*;

(1) Obtuse mandibular angle (two sides of the angular process forming an angle of greater than 90 degrees): *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon* (scored on *Acuodulodon* specimen by Hu et al. 2007 according to the taxonomic assignment of this fossil as a junior synonym of *Dsungarodon*, Martin et al. 2010), *Megacauda*, *Castorocauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*;

(2) Rounded angular region: *Dinnetherium*, *Megazostrodon*, *Kuehneotherium*;

(?) Unknown: *Delsatia*, *Woutersia*, *Gondtherium*, *Itatodon*, *Simpsonodon* (not preserved on *S. rossicum* according to AOA's specimen), *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Dobunnodon*, *Nujalikodon*, *Khorotherium*, *Ergetiis*.

Megacauda = 1

Castorocauda = 1

2. Angular process of the mandible: efflected ventral crest:

(0) Absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*;

(1) Present: *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon* (scored on *Acuodulodon* Hu et al. 2007), *Megacauda*, *Castorocauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*, *Ergetiis* (Averianov et al. 2024: fig 7C shows the base of the angle preserved, although incomplete. But it can be scored)

(?) Unknown: *Delsatia*, *Woutersia*, *Gondtherium*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Itatodon*, *Simpsonodon*, *Nujalikodon*, *Dobunnodon*, *Khorotherium*.

Megacauda = 1

Castorocauda = 1

3. Mandible angular region – receiving structure for ectotympanic:

(0) Medially facing concavity for ectotympanic: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*;

(1) Posteriorly facing groove for ectotympanic: *Haldanodon*, *Docodon*, *Docofossor*, *Megacauda*, *Castorocauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon* = 1 (revised from Zhou et al. 2019), *Ergetiis* = 1;

(?) Unknown: *Delsatia*, *Woutersia*, *Gondtherium*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Borealestes*, *Dsungarodon*, *Itatodon*, *Simpsonodon*, *Dobunnodon*, *Nujalikodon*, *Khorotherium*.

Megacauda = 1

Castorocauda = 1

4. Protuberance on the medial ridge over postdentary trough:

(0) Absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*;

(1) Present: *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon* (scored on “*Acuodulodon*” specimen, Hu et al. 2007, according to the taxonomic opinion of Martin et al. 2010), *Megacauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*;

(?) Unknown: *Castorocauda* (Medial side of the mandible not exposed), *Tashkumyrodon*, *Tegotherium*. *Hutegotherium* (the known specimen is incomplete on this part of mandible), *Sibirotherium* (the available specimen is incomplete on this part of mandible) *Itatodon*, *Simpsonodon*, *Dobunnodon*, *Nujalikodon*, *Khorotherium*, *Ergetiis*.

Megacauda = 1

Castorocauda = ?

5. Meckel’s groove to ventral margin of mandible:

(0) Convergent to the ventral margin: *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Borealestes*, *Krusatodon*, *Ergetiis* = 0 (below m2-m3), *Nujalikodon*,

(1) Parallel to ventral margin: *Sinoconodon*, *Haldanodon*, *Docodon*, *Docofossor*, *Itatodon*, *Megacauda*, *Agilodocodon*, *Microdocodon*, *Sibirotherium*, *Hutegotherium*, *Tegotherium*, *Simpsonodon*, *Khorotherium*;

(?) Unknown: *Delsatia*, *Itatodon*, *Tashkumyrodon*, *Castorocauda* (Medial side of the jaw not exposed), *Dobunnodon*.

Megacauda = 1

Castorocauda = ? (Medial side of the jaw not exposed).

6. Replacement dental lamina (Crompton’s groove; visible along the lingual alveolar margin of last molars):

(0) Present: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Kuehneotherium*, *Khorotherium*, *Ergetiis*;

(1) Absent: *Hadrocodium*, *Haldanodon*, *Docodon*, *Docofossor*, *Megacauda*, *Castorocauda* (visible on occlusal view of the fossil preparation), *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*, *Tegotherium*, *Sibirotherium*, *Hutegotherium*, *Simpsonodon*;

(?) Unknown: *Delsatia*, *Woutersia*, *Gondtherium*, *Dsungarodon* (not clear on *Acuodulodon*), *Borealestes*, *Tashkumyrodon*, *Itatodon*, *Dobunnodon*, *Nujalikodon*.

Megacauda = 1

Castorocauda = 1

7. Depth of anterior mandible (as measured in the canine region):

(0) Deep (mandibular depth/height near incisor 4- canine region $\geq 70\%$ of mandibular depth under middle lower molars m2-m3): *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Docodon*, *Docofossor*, *Megacauda*, *Castorocauda*.

(1) Shallow (mandibular depth/height near canine-p1 region $\geq 75\%$ of mandibular depth under m1): *Hadrocodium*, *Kuehneotherium* (following Gill et al's. 2014 reconstruction), *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*, *Sibirotherium* (Averianov et al. 2023: fig 2);
(?) Unknown: *Delsatia*, *Woutersia*, *Gondtherium*, *Dsungarodon*, *Tashkumyrodon*, *Itatodon*, *Simpsonodon*, *Dobunnodon*, *Nujalikodon*, *Khorotherium*, *Ergetiis*.

Megacauda = 0

Castorocauda = 0

Upper Molar Characteristics -

8. Transverse widening of upper molars (Sigogneau-Russell 2003: character 1; Luo and Martin 2007: character 1):

(0) Absent: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Hadrocodium*;

(1) Present: *Woutersia*, *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon* (based on Martin et al. 2010 interpretation), *Megacauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*, *Gondtherium*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Simpsonodon*, *Khorotherium*;

(?) Unknown: *Delsatia*, *Castorocauda* (upper dentition not exposed), *Tashkumyrodon*, *Itatodon*, *Dobunnodon*, *Nujalikodon*, *Ergetiis*.

Megacauda = 1

Castorocauda = ? (upper dentition not exposed)

9. Mesio-lingual cusp X of upper molars (Luo and Martin 2007: character 2):

(0) Absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Woutersia*;

(1) Cusp X present with wear facets present on the labial side of the cusp: *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon*, *Megacauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*, *Borealestes*, *Krusatodon*, *Khorotherium*, *Gondtherium*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Simpsonodon*.

(?) Unknown: *Delsatia*, *Castorocauda* (not exposed), *Tashkumyrodon*, *Itatodon*, *Dobunnodon*, *Nujalikodon*, *Ergetiis* = ? (upper molars not preserved).

Megacauda = 1

Castorocauda = ? (upper dentition not exposed)

10. Anterior upper molars: Transverse antero-lingual and antero-labial crests between cusp A and cusp X (Luo and Martin 2007: character 3):

(0) Absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Woutersia*, *Gondtherium*, *Megacauda*, *Khorotherium*;

(1) Present and complete: *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Simpsonodon*;

(?) Unknown: *Delsatia*, *Tashkumyrodon*, *Itatodon*; not exposed: *Castorocauda*, *Dobunnodon*, *Nujalikodon*, *Ergetiis* = ? (upper molars not preserved).

Megacauda = 0

Castorocauda = ? (not exposed)

11. Posterior upper molars: Transverse antero-lingual and antero-labial crests between cusp A and cusp X on (See graphic definition of Luo and Martin 2007; scored sensu Meng et al. 2015):

(0) Absent: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Woutersia*, *Agilodocodon*, *Krusatodon*, *Gondtherium*, *Krusatodon* (this crest is absent on the posterior M3-M4), *Khorotherium*;

(1) Present and complete: *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon*, *Megacauda*, *Borealestes*, *Microdocodon*, *Tegotherium*, *Sibirotherium*, *Simpsonodon*;

(?) Unknown: *Delsatia*, *Tashkumyrodon*, *Itatodon*, *Castorocauda* (not exposed), *Dobunnodon*, *Nujalikodon*, *Ergetiis* = ? (upper molars not preserved).

Megacauda = 1

Castorocauda = ? (not exposed)

12. Cusp Y (=upper disto-lingual cusp) (Luo and Martin 2007: character 4):

(0) Absent or indistinctive: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Woutersia*, *Gondtherium*;

(1) Present as a distinctive cusp: *Dsungarodon*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Simpsonodon*, *Khorotherium*;

(2) Present, as crest aligned in antero-posterior line: *Docodon*, *Haldanodon*, *Docofossor*, *Megacauda*;

(?) Not preserved: *Delsatia*, *Castorocauda* (Not exposed), *Tashkumyrodon*, *Itatodon*, *Dobunnodon*, *Nujalikodon*, *Ergetiis* = ? (upper molars not preserved).

Megacauda = 2

Castorocauda = ? (not exposed)

13. Upper Molar Cusp C (Luo and Martin 2007: character 5):

(0) Cusp C present and enlarged: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Gondtherium*, *Dsungarodon*, *Megacauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*, *Gondtherium*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Simpsonodon*, *Khorotherium* = 0 (Averianov et al. 2024);

(1) Reduced cusp C twinned with cusp A: *Woutersia*, *Haldanodon*, *Docodon*, *Docofossor*;

(?) Not preserved: *Delsatia*, *Tashkumyrodon*, *Castorocauda* (not exposed), *Itatodon*, *Dobunnodon*, *Nujalikodon*, *Ergetiis* = ? (upper molars not preserved).

Megacauda = 0

Castorocauda = ? (not exposed)

14. Posterior transverse crest extending from the disto-labial cusp (C) to the posterior cingulum (Luo and Martin 2007: character 6, systematic distribution modified according to comment by Averianov et al. 2010):

(0) Absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Woutersia*, *Gondtherium*;

(1) Present: *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon*, *Megacauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Simpsonodon*, *Khorotherium*;

(?) Unknown: *Delsatia*, *Tashkumyrodon*, *Itatodon*; *Castorocauda* (not exposed), *Dobunnodon*, *Nujalikodon*, *Ergetiis*.

Megacauda = 1

Castorocauda =? (not exposed)

15. Cusp E - separation from cusp B and alignment of Cusps E and B (best seen on posterior upper molars) (Luo & Martin 2007: character 7).

(0) Present: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*;

(1) Cusp E present and in an angled (labio-lingual) alignment with cusp B: *Woutersia*, *Megacauda*, *Agilodocodon*, *Krusatodon*, *Microdocodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Simpsonodon*, *Khorotherium*, *Gondtherium*, *Borealestes cuillinensis* (on several upper molars), *Borealestes serendipidus* (present on ultimate upper molar, broken crown on other molars);

(2) Absent: *Haldanodon*, *Docodon*, *Docofossor*;

(?) Unknown: *Delsatia*, *Dsungarodon* (only lingual half of the upper is known), *Castorocauda* (not exposed), *Tashkumyrodon*, *Itatodon*, *Dobunnodon*, *Nujalikodon*, *Ergetiis*.

Megacauda = 1 (present on M2-M4, but not on M1)

Castorocauda =? (not exposed)

16. Constricted waist between the labial part and the lingual part of upper molars (Luo and Martin 2007: character 8).

(0) Absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Woutersia*, *Gondtherium*, *Simpsonodon*;

(1) Present: *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon* (half tooth, but it shows the constriction well enough), *Megacauda*, *Agilodocodon*, *Borealestes* (0/1), *Krusatodon*, *Microdocodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Khorotherium*;

(?) Unknown: *Delsatia*, *Castorocauda* (not exposed), *Tashkumyrodon*, *Itatodon*, *Dobunnodon*, *Nujalikodon*, *Ergetiis*.

Megacauda = 1 (present on M2-M4), not applicable on M1

Castorocauda = ? (not exposed)

17. Upper Molars anterior fovea (Panciroli et al. 2019)

(0) Absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Woutersia*, *Haldanodon*, *Docofossor*, *Dsungarodon*, *Agilodocodon*, *Krusatodon*, *Microdocodon*, *Sibirotherium*, *Hutegotherium*, *Simpsonodon*, *Khorotherium*;

(1) Present: *Docodon*, *Megacauda* (Present on M3 and M4), *Borealestes*;

(?) Unknown: *Delsatia*, *Castorocauda* (not exposed), *Gondtherium*, *Tashkumyrodon*, *Tegotherium*, *Itatodon*, *Dobunnodon*, *Nujalikodon*, *Ergetiis* (upper molars not preserved).

Megacauda = 1

Castorocauda = ? (not exposed)

18 (= 53 of Zhou et al. 2019) Anteriorly protruding prestylar lobe in cusp B or cusps E-B region.

(0) Absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Woutersia*;

(1) Present: *Haldanodon*, *Docodon*, *Docofossor*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Megacauda*, *Microdocodon* = 1, *Hutegotherium*, *Simpsonodon* = 1, *Khorotherium* = 1

(?) Unknown: *Delsatia*, *Gondtherium*, *Tashkumyrodon*, *Castorocauda* (not exposed), *Tegotherium*, *Dsungarodon* (mesio-labial corner of the upper unknown), *Itatodon*, *Dobunnodon*, *Nujalikodon*, *Ergetiis* = ?.

Megacauda = 1

Castorocauda = ? (not exposed)

19 (= 48a of Zhou et al. 2019). Upper molar pre-stylar groove (bound by cusp A, E and anterior cingulum).

(0) Absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium* (following Gill et al 2014 reconstruction), *Woutersia*, *Haldanodon*, *Docodon*, *Docofossor*, *Megacauda*, *Borealestes*, *Krusatodon*, *Simpsonodon*;

(1) Present: *Agilodocodon* (scored on M1), *Hutegotherium*, *Sibirotherium* (on an upper molar, described by Averianov et al. 2010), *Microdocodon* = 1, *Khorotherium* = 1;

(?) Not preserved: *Dsungarodon* (preservation incomplete), *Delsatia* (not preserved), *Castorocauda* (not exposed), *Dobunnodon*, *Nujalikodon*, *Ergetiis* = ?.

Megacauda = 0

Castorocauda = ? (not exposed)

Lower Molar Characteristics -

20. Lower molar cusp c on lingual cingulid and in alignment with antero-lingual cusp g (mesio-lingual) (On Butler's cusps b-a-c scheme: Luo and Martin 2007: character 9; distribution is revised from Meng et al. 2015):

(0) Absent: *Morganucodon*, *Dinnetherium*, *Megazostrodon*;

(1) Present: *Delsatia*, *Woutersia*, *Haldanodon*, *Docodon*, *Docofossor*, *Megacauda*, *Castorocauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Itatodon*, *Simpsonodon*, *Khorotherium*, *Ergetiis*, *Dobunnodon*, *Nujalikodon*.

(?) Not applicable: *Sinoconodon*, *Hadrocodium*, *Kuehneotherium*, (?) Unknown: *Gondtherium*.

Megacauda = 1

Castorocauda = 1

21. Lower molar cusp c, morphology and relationship to cusp g in straight alignment on lingual side:

(0) Cusp c has a rounded anterior face, cusp g has a round posterior face, an open embayment present between cusps c and g: *Delsatia*, *Woutersia*, *Docofossor*, *Dsungarodon*, *Megacauda*, *Castorocauda*, *Tashkumyrodon*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*, *Tegotherium*,

Hutegotherium, *Sibirotherium*, *Itatodon*, *Simpsonodon*, *Dobunnodon*, *Nujalikodon*, *Khorotherium*, *Ergetiis*;

(1) Cusp c has anterior crest and cusp g has a posterior crest, and the two crests form a V-notch on lingual cingulid: *Haldanodon*, *Docodon*.

(?) Not applicable (because these taxa do not have their cusp c on the lingual side, and cusp c not in alignment with cusp g): *Morganucodon*, *Megazostrodon*, *Dinnetherium*,

(?) Not applicable because these taxa have no cusp g): *Sinoconodon*, *Hadrocodium*, *Kuehneotherium*;

(?) Unknown: *Gondtherium* (no lower molar known)

Megacauda = 0

Castorocauda = 0

22. The V-notch between cusp a – cusp c (postero-main crest of Sigogneau-Russell, 2003; Luo and Martin 2007: character 11; scorings revised as proposed by Averianov et al. 2010):

(0) Present: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Woutersia*, *Haldanodon*, *Dsungarodon*, *Megacauda*, *Castorocauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*, *Tashkumyrodon*, *Hutegotherium*, *Sibirotherium*, *Itatodon*, *Simpsonodon*, *Dobunnodon*, *Nujalikodon*, *Khorotherium*, *Ergetiis*;

(1) Absent: *Docodon*, *Docofossor*;

(?) Unknown: *Gondtherium*.

Megacauda = 0

Castorocauda = 0

23. Absence vs. presence of cusp g, shape and placement of cusp g (mesiolingual) (Sigogneau-Russell 2003; Martin and Averianov 2004; Luo and Martin 2007; Zhou et al. 2019 – Scorings of this character are extensively revised, as necessitated by Panciroli et al. 2019; 2021; 2024; Averianov et al. 2024a [*Sibirotherium*] and 2024b [*Khorotherium* and *Ergetiis*]):

(0) Absent: *Sinoconodon*, *Hadrocodium*, *Kuehneotherium*;

(1) Small and posterior (cusp g placed more posteriorly/distally to the transverse level of main cusp a): *Morganucodon*, *Dinnetherium*, *Megazostrodon*;

(2) Distinct cusp, opposite to primary cusp a: *Delsatia*, *Woutersia*;

(3) Distinct cusp, anteriorly positioned (cusp g placed more anteriorly/mesially to the transverse level of main cusp a): *Haldanodon*, *Docodon*, *Docofossor*, *Borealestes*, *Krusatodon*, *Microdocodon* = 3, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Tashkumyrodon* (cusp g base is preserved), *Sibirotherium* (Averianov et al. 2024: figs 2 and 3), *Khorotherium*, *Ergetiis*;

(4) Distinct and hypertrophied (more massive), and anteriorly placed: *Dsungarodon* (Pfretzschner et al. 2005: Fig. 2), *Megacauda*, *Castorocauda*, *Agilodocodon*, *Tegotherium*, *Hutegotherium*, *Itatodon*, *Simpsonodon*;

(?) Not preserved: *Gondtherium*.

Megacauda = 4

Castorocauda = 4

24. Cusp c to cusp g size ratio (Luo and Martin 2007: character 10) (scoring on posterior molars is available):

- (0) Cusp c much larger than cingular cusp g (if the latter is present): *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Docodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Khorotherium*, *Ergetiis*
- (1) Sub-equal to the mesio-lingual cusp g: *Delsatia*, *Woutersia*, *Docofossor*; *Megacauda*, *Castorocauda*, *Agilodocodon*, *Microdocodon*, *Sibirotherium*, *Tegotherium*, *Itatodon*, *Simpsonodon*, *Nujalikodon*
- (?) Not applicable: *Sinoconodon*, *Hadrocodium*, *Kuehneotherium*;
- (?) Unknown (incomplete preservation): *Gondtherium*, *Tashkumyrodon* (cusp g tip is not preserved).

Megacauda = 1 (scored on m3 and m4) but not on m1
Castorocauda = 1

25. Development of pseudo-talonid (Martin and Averianov 2004: character 2; Luo and Martin 2007: character 13; Hu et al. 2007: character 18):

- (0) Absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Woutersia*;
- (1) Present and its anterior border by b-g crest: *Dsungarodon*, *Megacauda*, *Castorocauda* (following Panciroli et al. 2019), *Borealestes*, *Krusatodon*, *Microdocodon* (revised), *Dobunnodon*, *Nujalikodon*;
- (2) Present and its anterior border by b-e crest: *Simpsonodon*, *Agilodocodon*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Itatodon*, *Khorotherium* = 2, *Ergetiis* = 2;
- (3) Present but cusp b is much taller than g so the pseudotalonid appears to be lingually open: *Docodon*, *Haldanodon*, *Docofossor*;
- (?) Unknown: *Gondtherium*.

Megacauda = 1
Castorocauda = 1

26. Raised a-g crest (Luo and Martin 2007: character 14; Hu et al. 2007: character 11):

- (0) Absent: *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Delsatia*, *Woutersia*, *Khorotherium* = 0 (pseudotalonid basin has no a-g crest or V-notch), *Ergetiis* = 0;
- (1) Present and showing a distinctive v-notch: *Dsungarodon*, *Megacauda*, *Castorocauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Microdocodon*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Itatodon*, *Simpsonodon*;
- (2) Present as low and sloping crest (without distinct V-notch): *Haldanodon*, *Docodon*, *Docofossor*;
- (?) Not preserved: *Gondtherium*;
- (?) Not applicable (no cusp g): *Sinoconodon*, *Hadrocodium*, *Kuehneotherium*.

Megacauda = 1 (on left m5 & right m4-m5, not preserved enough in anterior molars)
Castorocauda = 1

27. Crest b-g (Hu et al. 2007: character 12):

- (0) Absent, or weakly developed: *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Itatodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*; *Khorotherium* = 0 (smooth basin no a-g crest); *Ergetiis* = 0 (smooth basin no a-g crest);
- (1) Present: *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon*, *Megacauda*, *Castorocauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*, *Tashkumyrodon*, *Simpsonodon*, *Dobunnodon*, *Nujalikodon*;

(?) Not applicable: *Sinoconodon*, *Hadrocodium*, *Kuehneotherium*, *Woutersia*, *Delsatia*;
(?) unknown: *Gondtherium*.

Megacauda = 1 (better preserved on m3-5)

Castorocauda = 1

28. The c-d (or c-d-f) crest in the posterior basin – presence/absence and alignment (Luo and Martin 2007: character 15):

(0) Absent: *Dsungarodon*, *Megacauda*, *Castorocauda*, *Microdocodon* = 0 (cusp c and cusp d are very reduced), *Tegotherium*, *Hutegotherium*, *Sibirotherium*;

(1) Present, c-d crest or c-f-d crests straight: *Nujalikodon*, *Haldanodon*, *Docodon*, *Docofossor*, *Tashkumyrodon*, *Itatodon*;

(2) Present, c-d crest angled or curved: *Agilodocodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Simpsonodon*, *Khorotherium* (present as a curved crest), *Ergetiis* (curved);

(?) Not applicable: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Woutersia*, *Delsatia*;

(?) Not preserved: *Gondtherium*.

Megacauda = 0

Castorocauda = 0

29. Crest extending from cusp c to cusp df or the cusp df position (Hu et al. 2007: character 15):

(0) Absent: *Haldanodon*, *Docofossor*, *Dsungarodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*;

(1) Present: *Docodon*, *Megacauda*, *Castorocauda*, *Agilodocodon*, *Microdocodon*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Itatodon*, *Simpsonodon*, *Khorotherium*, *Ergetiis*;

(?) Not applicable: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Hadrocodium*, *Dinnetherium*, *Kuehneotherium*, *Delsatia*, *Woutersia*;

Not preserved: *Gondtherium*.

Megacauda = 1

Castorocauda = 1

30. Placement of cusp d (modified from Sigogneau-Russell 2003: character 7; Luo and Martin 2007: character 16; assuming homology of cusp d in morganucodontans and in docodontans):

(0) Labial position (in alignment with a-b crest, or nearly so): *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Woutersia*, *Haldanodon*, *Docodon*, *Docofossor*, *Megacauda*, *Castorocauda*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Tashkumyrodon*, *Sibirotherium*, *Itatodon* (revised from previous scoring), *Simpsonodon*;

(1) Median placement (nearly halfway along the transverse width of posterior crown): *Dsungarodon*, *Agilodocodon*, *Microdocodon*, *Tegotherium*, *Hutegotherium*, *Khorotherium*, *Ergetiis* (shows a crest in the cusp d position, crest oriented in postero-lingual direction but placed in the median position);

Note: *Itatodon* Lopatin and Averianov 2005 (holotype) and additional specimens (Averianov and Lopatin 2006; Averianov et al. 2010) all show cusp d on labial side of the lower crowns;

(?) Not preserved: *Gondtherium*.

Megacauda = 0
Castorocauda = 0

31. Molars distal Cusp d-f (=cusp dd of Hu et al. 2007: character 7; adopted by Averianov et al. 2024 Cretaceous Research paper):

(0) Absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Woutersia*;

(1) Present: *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon*, *Megacauda*, *Castorocauda* (represented by a crest connected to a reduced cusp d), *Agilodocodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Microdocodon*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Itatodon*, *Simpsonodon*, *Khorotherium* = 1 (d-f = dd of Averianov 2024), *Ergetiis*;

(?) Not preserved: *Gondtherium*.

Megacauda = 1
Castorocauda = 1

32. Ultimate and penultimate lower molars: shortening/reduction of crown posterior to primary cusp a (best viewed from lateral view):

(0) No reduction: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Woutersia*, *Haldanodon*, *Docodon*, *Docofossor*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Itatodon*, *Simpsonodon*, *Khorotherium*, *Egetiis*.

(1) Reduced/shortened: *Dsungarodon*, *Megacauda*, *Castorocauda*, *Microdocodon*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*;

(?) Not preserved: *Gondtherium*, *Dobunnodon* (not preserved), *Nujalikodon* = ? (not preserved)

Megacauda = 1
Castorocauda = 1

33. Folding enamel (on either upper or lower) (Sigogneau-Russell, 2003: character 5; Luo and Martin 2007: character 17, scored on the posterior face of lower cusp a or lingual face of upper cusps A-C):

(0) Absent or weakly developed: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Woutersia*, *Gondtherium*, *Docofossor*, *Dsungarodon*, *Megacauda*, *Castorocauda*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Microdocodon*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Itatodon*, *Khorotherium*, *Ergetiis*;

(1) Present: *Haldanodon*, *Docodon*, *Agilodocodon*, *Simpsonodon*.

Megacauda = 0
Castorocauda = 0

34. Upper molar: connecting structure of cusps a and d, best seen in middle molars (modified from Luo and Martin 2007: character 19; Hu et al. 2007: character 14):

(0) Not connected: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Woutersia*;

(1) Incomplete (crest present only on either d or a): *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Microdocodon*;

(2) Connected by a crest with v-notch: *Megacauda*, *Castorocauda*, *Agilodocodon*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Itatodon*, *Simpsonodon*, *Khorotherium*, *Ergetiis*;
(?) Not preserved: *Gondtherium*.

Megacauda = 2

Castorocauda = 2

35. Alignment/Angulation/shape of posterior crest of cusp a towards cusp d (postero-main crest of Sigogneau-Russell 2003; as defined in Luo & Martin 2007: character 18):

(0) Present and straight: *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon*, *Megacauda*, *Castorocauda*, *Borealestes*, *Microdocodon*, *Tegotherium*, *Sibirotherium*, *Itatodon*, *Simpsonodon*, *Tashkumyrodon*;

(1) Present and angled: *Agilodocodon*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Khorotherium*, *Ergetiis*;

(?) Not applicable: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Woutersia*;

(?) Not preserved: *Gondtherium*.

Megacauda = 0

Castorocauda = 0

36. The b-g crest - Crest between the mesio-labial cusp and mesio-lingual cusps (Sigogneau-Russell 2003: character 8; Martin and Averianov 2004: character 7; Luo and Martin 2007: character 20):

(0) Absent: *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Delsatia*, *Woutersia*, *Microdocodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Khorotherium*, *Ergetiis*,

(1) Present as a v-shaped valley: *Megacauda*, *Castorocauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Itatodon*, *Simpsonodon*;

(2) Present and continuous: *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon*;

(?) Incomplete: *Tashkumyrodon*, (?) Not preserved: *Gondtherium*;

(?) Not applicable: *Sinoconodon*, *Hadrocodium*, *Kuehneotherium*.

Megacauda = 1

Castorocauda = 1

37. Size of cusp e (equivalent to cusp “bb” of Averianov et al. 2010; Martin and Averianov 2004: character 3; Luo and Martin 2007: character 21):

(0) Present and distinctive: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Woutersia*, *Nujalikodon*, *Dobunnodon*, *Agilodocodon*, *Microdocodon*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Khorotherium*, *Ergetiis*;

(1) Reduced: *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon*, *Megacauda*, *Castorocauda*, *Borealestes*, *Krusatodon*, *Itatodon*, *Simpsonodon*;

(?) Not preserved: *Gondtherium*.

Megacauda = 1

Castorocauda = 1

38. Cusp ee (sensu Zhou et al. 2019; = cusp “e” of Averianov et al. 2010):
(0) Absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Woutersia*, *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon*, *Megacauda*, *Castorocauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Tashkumyrodon*, *Sibirotherium*, *Itatodon*, *Simpsonodon*;
(1) Present: *Tegotherium*, *Hutegotherium*, *Microdocodon* = 1, *Khorotherium* = 1, *Ergetiis* = 1
(?) Not preserved: *Gondtherium*.

Megacauda = 0
Castorocauda = 0

39. Mesio-lingual corner cingulid (width would be related with presence of cusp e, or cusp e’s position; Hu et al. 2007: character 17):

(0) Narrow or absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Woutersia*, *Docodon*, *Docofossor*, *Dsungarodon*, *Megacauda*, *Castorocauda*, *Microdocodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Itatodon*;
(1) Wide: *Haldanodon*, *Agilodocodon*, *Borealestes*, *Dobunnodon*, *Nujalikodon*, *Krusatodon*, *Tashkumyrodon*, *Simpsonodon*, *Khorotherium*, *Ergetiis*;
(?) Not preserved: *Gondtherium*.

Megacauda = 0
Castorocauda = 0

40. Line-like mesio-lingual cingulid: posterior extension from cuspule e or an equivalent position (Luo and Martin 2007: character 22, as revised by Averianov et al. 2010):

(0) Connected to cusp g: *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Delsatia*, *Woutersia*;
(1) Extending posteriorly to below the cusp g: *Haldanodon*, *Dsungarodon*, *Agilodocodon*, *Dobunnodon*, *Microdocodon*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Itatodon*, *Khorotherium*, *Ergetiis*;
(2) Absent or limited to the mesial part of the tooth: *Docodon*, *Docofossor*, *Megacauda*, *Castorocauda*, *Borealestes*, *Nujalikodon*, *Krusatodon*, *Simpsonodon*.
(?) Inapplicable: *Sinoconodon*, *Hadrocodium*, *Kuehneotherium*.
(?) Not preserved: *Gondtherium*.

Megacauda = 2
Castorocauda = 2

41. Height ratio of cusp b to cusp a (Martin and Averianov 2004: character 1; Luo and Martin 2007: character 23):

(0) distinct, well separated by a notch from cusp a: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Woutersia*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Microdocodon*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Itatodon*, *Simpsonodon*, *Khorotherium*, *Ergetiis*;
(1) Small, approximated to cusp a: *Docodon*, *Haldanodon*, *Docofossor*;
(2) Large (nearly half the size as cusp a): *Dsungarodon*, *Castorocauda*, *Megacauda*;

(?) Not preserved: *Gondtherium*.

Megacauda = 2

Castorocauda = 2

42. Cusps b-a separation (cusp b placement (Hu et al. 2007: ch 2; Averianov et al. 2010: character 15):

(0) Close to cusp a: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Woutersia*, *Docodon*, *Docofossor*;

(1) Well-separated from cusp a by a deep notch: *Haldanodon*, *Dsungarodon*, *Megacauda*, *Castorocauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Microdocodon*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Itatodon*, *Simpsonodon*, *Khorotherium*, *Ergetiis*.

(?) Not preserved: *Gondtherium*.

Megacauda = 1

Castorocauda = 1

43. The “docodont cusp f” (Postero-lingually positioned as defined by Martin and Averianov 2004: figs. 3 and 5, and differing from mesio-labially positioned cusp f; Luo and Martin 2007: character 24; distribution revised from Meng et al. 2015):

(0) Absent: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Woutersia*, *Delsatia*, *Dsungarodon*, *Megacauda*, *Castorocauda*;

(1) Present: *Haldanodon*, *Docodon*, *Docofossor*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Tashkumyrodon*, *Sibirotherium*, *Itatodon*, *Simpsonodon*;

(2) Present and crest-like: *Microdocodon*, *Tegotherium*, *Hutegotherium*, *Khorotherium* = 2 (crest-like), *Ergetiis* = 2 (crest-like);

(?) Not preserved: *Gondtherium*.

Megacauda = 0

Castorocauda = 0

44. The “standard cuspule e” (mesio-labially positioned, as defined by Kielan-Jaworowska et al. 2004: fig. 5.9: ‘mesiolabial cusp’. We follow Luo & Martin 2007 [character 25] in regarding this cusp to be different from cusp g in postero-lingual position):

(0) Absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Hadrocodium*, *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon*, *Megacauda*, *Castorocauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Microdocodon*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Itatodon*, *Simpsonodon*, *Khorotherium*, *Ergetiis*;

(1) Present: *Megazostrodon*, *Kuehneotherium*, *Delsatia*, *Woutersia*;

(?) Unknown: *Gondtherium*.

Megacauda = 0

Castorocauda = 0

45. The b-e crest (crescent of Sigogneau-Russell 2003; Martin and Averianov 2004: character 6; Luo and Martin 2007: character 26):

- (0) Absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Woutersia*, *Haldanodon*, *Docodon*, *Nujalikodon*;
 (1) Present and continuous from cusp b to the cingulid: *Dsungarodon*, *Megacauda*, *Castorocauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Tashkumyrodon*, *Itatodon*, *Simpsonodon*;
 (2) Present, as a part of the pseudotalonid rim: *Microdocodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Khorotherium*, *Ergetiis*;
 (?) Not preserved: *Gondtherium*, *Docofossor* (worn).

Megacauda = 1

Castorocauda = 1

46. Anterior basin (Hu et al. 2007: character 18):

- (0) No basin: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Woutersia*;
 (1) Small concavity: *Haldanodon*, *Docodon*, *Docofossor*, *Nujalikodon*;
 (2) Pseudotalonid basin: *Dsungarodon*, *Megacauda*, *Castorocauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Microdocodon*, *Tashkumyrodon*, *Tegotherium*, *Sibirotherium*, *Itatodon*, *Simpsonodon*, *Khorotherium*, *Ergetiis*;
 (?) Unknown: *Gondtherium*.

Megacauda = 2

Castorocauda = 2

47. Upper molars distal basin (better assessed on middle molars if available: Hu et al. 2007: character 20):

- (0) Absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Woutersia*;
 (1) Present: *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon*, *Megacauda*, *Castorocauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Microdocodon*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Itatodon*, *Simpsonodon*, *Khorotherium*, *Ergetiis*;

(?) Not preserved: *Gondtherium*.

Megacauda = 1

Castorocauda = 1

48. Width ratio of anterior basin vs. distal basin (modified from Hu et al. 2007: character 21, measured at the level of cusps/crests on occlusal surface):

- (0) Posterior basin narrower than anterior basin (or anterior part of the tooth): *Dsungarodon*, *Megacauda* (scored on m3), *Castorocauda* (scored on m3), *Agilodocodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Microdocodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Itatodon*, *Simpsonodon*, *Khorotherium*, *Ergetiis*;
 (1) Posterior basin wider than anterior basin: *Haldanodon*, *Docodon*, *Docofossor*, *Tashkumyrodon*;
 (?) Not applicable: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Woutersia*;
 (?) Not preserved: *Gondtherium*.

Megacauda = 0 (scored on m3)
Castorocauda = 0 (scored on m3)

49. Lower molar antero-posterior length proportion. The anterior portion defined as the distance from the apex of primary cusp a to the mesial margin; the posterior portion defined as distance from primary cusp to the distal margin of the molar. Most suitable molars for this metric measurement are the middle to penultimate molar. Character states may be treated as ordered in phylogenetic search.

(0) Antero-posterior proportion is 70% - 90% (anterior portion is 70% of the posterior portion in length):

Sinoconodon, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Docodon*, *Docofossor*;

(1) Antero-posterior proportion is 100% - 125%: *Woutersia*, *Nujalikodon*, *Haldanodon*, *Megacuada*, *Castorocauda*, *Dobunnodon*, *Borealestes*, *Krusatodon*, *Tashkumyrodon*;

(2) Antero-posterior proportion is 140% - 160%: *Dsungarodon*, *Itatodon*, *Agilodocodon*, *Simpsonodon*, *Microdocodon*, *Tegotherium*, *Hutegotherium*;

(3) Antero-posterior proportion is over 180%: *Sibirotherium*, *Khorotherium*, *Ergetiis*.

(?) Not preserved: *Gondtherium*.

Megacuada = 1
Castorocauda = 1

50. Interlock of lower molars (Luo and Martin 2007: character 27; Averianov et al. 2010: character 31; character state definition and distribution revised from Meng et al. 2015):

(0) No interlock: *Sinoconodon*, *Hadrocodium*;

(1) d-b-e interlock: *Morganucodon*, *Dinnetherium*, *Dsungarodon*, *Megacauda*, *Castorocauda*, *Nujalikodon*, *Tashkumyrodon*;

(2) d – ‘standard’-f-e interlock: *Megazostrodon*, *Kuehneotherium*, *Delsatia*, *Woutersia*;

(3) d-e overlap: *Agilodocodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Microdocodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Itatodon*, *Simpsonodon*, *Khorotherium* = 3 (d-e overlap);

(4) d-b overlap: *Docodon*, *Haldanodon*, *Docofossor*, *Ergetiis*;

(?) Not preserved: *Gondtherium*.

Megacauda = 1
Castorocauda = 1

51. Placement of lower cusp e (Luo and Martin 2007: character 29, scoring modified according to Averianov et al. 2010):

(0) Lingual position: aligned straight with main cusps, or lingual to the median axis of the lower molar: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Delsatia*, *Woutersia*, *Haldanodon*, *Docodon*, *Docofossor*, *Megacauda*, *Castorocauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Itatodon*;

(1) Cusp e labially shifted: *Dsungarodon*, *Microdocodon*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Simpsonodon* (revised from Zhou et al. 2019), *Khorotherium*, *Ergetiis*.

(?) Unknown: *Gondtherium*.

Megacauda = 0
Castorocauda = 0

52. Cusp triangulation (cusp triangulation between the a-c crest and the a-b crest following Butler 1997; Sigogneau-Russell and Godefroit 1997; Luo and Martin 2007: character 28):

- (0) Absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*;
- (1) Present: *Kuehneotherium*, *Delsatia*, *Woutersia*, *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon*, *Megacauda*, *Castorocauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Microdocodon*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Itatodon*, *Simpsonodon*, *Khorotherium*, *Ergetiis*;
- (?) Unknown: *Gondtherium* (the lower dentition is not known).

Megacauda = 1
Castorocauda = 1

53. Degree of triangulation of cusps g-a-c (distribution revised from Meng et al. 2015):

- (0) Obtuse triangle (>80 degrees): *Dsungarodon*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Tashkumyrodon*, *Itatodon*, *Simpsonodon*;
- (1) Acute triangle (≤80 degrees): *Haldanodon*, *Docodon*, *Docofossor*, *Megacauda*, *Castorocauda*, *Microdocodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Khorotherium*, *Ergetiis*;
- (?) Not applicable: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium* (not applicable to *Kuehneotherium* that has triangle by b-a-c), *Woutersia*, *Delsatia*.
- (?) Not preserved: *Gondtherium*.

Megacauda = 1
Castorocauda = 1

54. Gibbousness of crown base overhanging the roots at crown-root junction (scored at the middle molar[s] if multiple molars are known):

- (0) Absent: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Woutersia*, *Haldanodon*, *Docodon*, *Docofossor*, *Megacauda* (especially anterior molars), *Castorocauda*;
- (1) Present: *Dsungarodon*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Dobunnodon*, *Nujalikodon*, *Microdocodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium*, *Itatodon*, *Simpsonodon*, *Khorotherium*, *Ergetiis*;
- (?) Not preserved: *Delsatia*, *Gondtherium*.

Megacauda = 0
Castorocauda = 0

55. Number of upper molariform roots (Averianov and Lopatin 2006: character 4; Luo and Martin 2007: character 30):

- (0) Two: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Woutersia*;

(1) Three: *Haldanodon*, *Docodon*, *Docofossor*, *Megacauda*, *Dsungarodon*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*, *Tegotherium*, *Hutegotherium*, *Sibirotherium* (scored from Averianov and Lopatin 2006), *Gondtherium* (Prasad and Manhas 2002 stated that this taxon likely had three roots), *Simpsonodon*, *Khorotherium*;
(?) Unknown: *Delsatia*, *Castorocauda* (not exposed), *Itatodon*, *Tashkumyrodon*, *Dobunnodon*, *Nujalikodon*, *Ergetiis*.

Megacauda = 1

Castorocauda = ? (not exposed)

56. Number of lower canine roots (Ji et al. 2006; Averianov and Lopatin 2006: character 11; Luo and Martin 2007: character 31):

(0) One: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Kuehneotherium*;

(1) Two: *Hadrocodium* (incipient division of roots), *Haldanodon*, *Docodon*, *Docofossor*, *Dsungarodon*, *Megacauda*, *Castorocauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Sibirotherium*;

(?) Unknown: *Woutersia*, *Delsatia*, *Gondtherium*, *Simpsonodon*, *Dsungarodon*, *Itatodon*, *Tashkumyrodon*, *Tegotherium*, *Microdocodon*, *Dobunnodon*, *Nujalikodon*, *Khorotherium*, *Ergetiis*.

Megacauda = 1

Castorocauda = 1

57. Lower canine crown size:

(0) Lower canine trenchant, and taller (>125% in crown height) than adjacent incisors, and than the first premolar (if present): *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Haldanodon*, *Docodon*, *Docofossor*, *Megacauda*, *Castorocauda*, *Sibirotherium*;

(1) Lower canine forming a gradient with incisors and premolars, not taller than adjacent teeth: *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*;

(?) Unknown: *Woutersia*, *Delsatia*, *Gondtherium*, *Simpsonodon*, *Dsungarodon*, *Itatodon*, *Tashkumyrodon*, *Tegotherium*, *Microdocodon*, *Dobunnodon*, *Nujalikodon*, *Khorotherium*, *Ergetiis*.

Megacauda = 0

Castorocauda = 0

58. Count of lower premolar or premolar positions:

(0) 3 premolars or fewer: *Sinoconodon* (juvenile specimens may have one or two deciduous premolars); *Hadrocodium* (only one premolar in the only known specimen);

(1) 4 premolars: *Morganucodon*, *Dinnetherium*, *Docodon*, *Haldanodon*, *Docofossor*;

(2) 5 premolars: *Megazostrodon*, *Megacauda*, *Borealestes*, *Krusatodon*;

(3) 6 premolars or premolar positions: *Kuehneotherium* (following Gill et al. 2014), *Castorocauda*, *Agilodocodon*, *Microdocodon*;

(?) Premolars unknown or premolar region incomplete: *Woutersia*, *Delsatia*, *Gondtherium*, *Simpsonodon*, *Dsungarodon*, *Itatodon*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Dobunnodon*, *Nujalikodon*, *Khorotherium*, *Ergetiis*.

Megacauda = 2 (5 lower premolars)

Castorocauda = 3 (changed from “2”) after revision of previous “6” to 5 molars, for molar count of *Castorocauda*

59. Ultimate lower molar: pattern of two roots:

(0) Fully divided roots: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Docodon*, *Dsungarodon* (scored on “*Acuodulodon*” specimen, Hu et al. 2007 on synonymy proposed by Martin et al. 2010), *Megacauda*, *Castorocauda*, *Agilodocodon*, *Krusatodon*, *Microdocodon*, *Tegotherium* (Martin et al 2010: fig. 12), *Hutegotherium*, *Simpsonodon*, *Khorotherium*, *Ergetiis*;

(1) Roots become twinned, confluent or even single-rooted: *Hadrocodium*, *Kuehneotherium*, *Haldanodon*, *Docofossor*, *Borealestes*.

(?) Unknown: *Woutersia*, *Delsatia*, *Gondtherium*, *Tashkymyrodon*, *Tegotherium*, *Sibirotherium*, *Itatodon*, *Dobunnodon*, *Nujalikodon*.

Megacauda = 0

Castorocauda = 0

60. Profile of lower premolars (in either lateral or medial view)

(0) Trenchant cusp a (cusp a height from cingulid $\geq$ molar length of the premolar): *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Haldanodon*, *Docodon*, *Docofossor*, *Megacauda*, *Castorocauda*;

(1) lower profile (cusp a height from cingulid lower than premolar length): *Dsungarodon* (scored on isolated premolar referred to *Dsungarodon* by Martin et al. 2010), *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*, *Itatodon*, *Simpsonodon*, *Ergetiis*;

(?) Preservation incomplete: *Gondtherium*.

(?) Unknown: *Delsatia*, *Woutersia*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Dobunnodon*, *Nujalikodon*, *Khorotherium*.

Megacauda = 0

Castorocauda = 0

61. Ultimate premolar recurved vs. erect cusp a profile and orientation (scored on lower m1):

(0) Erect: *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Haldanodon*, *Docodon*, *Docofossor*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*, *Itatodon*, *Simpsonodon*;

(1) Recurved: *Castorocauda*, *Megacauda*, *Dsungarodon* (Martin et al. 2010 taxonomy, lower premolars of *Acuoduloson* Hu et al. 2007);

(?) Unknown: *Woutersia*, *Delsatia*, *Gondtherium*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Dobunnodon*, *Nujalikodon*, *Khorotherium*, *Ergetiis*.

Megacauda = 1

Castorocauda = 1

62. Diphyodont canine

(0) Absent (multiple replacements): *Sinoconodon*;

(1) Present (two generation, one replacement): *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Haldanodon*, *Docodon*, *Docofossor*, *Megacauda*, *Agilodocodon*, *Borealestes*, *Krusatodon*, *Microdocodon*, *Sibirotherium*;

(?) Unknown: *Woutersia*, *Delsatia*, *Dsungarodon*, *Castorocauda*, *Gondtherium*, *Tashkumyrodon*, *Tegotherium*, *Hutegotherium*, *Itatodon*, *Simpsonodon*, *Dobunnodon*, *Nujalikodon*, *Khorotherium*, *Ergetiis*.

Megacauda = 1

Castorocauda = ? (unknown)

(10) Phylogenetic Matrix: Nexus file

```
#NEXUS
[written Fri Jun 19 10:51:48 CDT 2026 by Mesquite version 3.70 (build 940)]

BEGIN TAXA;
  TITLE Taxa;
  DIMENSIONS NTAX=29;
  TAXLABELS
    Sinoconodon Morganucodon Dinnetherium Megazostrodon Haderocodium Kuehneotherium
    Delsatia Woutersia Gondtherium Nujalikodon Haldanodon Docodon Docofossor Dsungarodon
    Megacauda Castorocauda Itatodon Agilodocodon Simpsonodon Dobunnodon Borealestes Krusatodon
    Microdocodon Tashkumyrodon Sibirottherium Khorotherium Ergetiis Tegotherium Hutegotherium
  ;
END;

BEGIN CHARACTERS;
  TITLE 'Matrix in file "Microdo-phyl-Dec2017-tran.nex"';
  DIMENSIONS NCHAR=62;
  FORMAT DATATYPE = STANDARD RESPECTCASE GAP = - MISSING = ? SYMBOLS = " 0 1 2 3 4";
  CHARSTATELABELS
    1 'Mand-angle shape',
    2 'Mand-angle efflection',
    3 'Mand-ectot-groove',
    4 Med_ridge_protub,
    5 'Mand-grv convergence',
    6 Dent_lamina_groove,
    7 Shallow_symphysis,
    8 Wide_Upper_Molar,
    9 Cusp_X_Upper_Molar,
    10 'Ant-Up Mo A-X crest',
    11 'Post-Up M A-X crest',
    12 Up_Molar_Cusp_Y,
    13 Up_Molar_Cusp_C,
    14 'Post crest-cingjulum',
    15 Up_Mol_Cusp_E,
    16 Up_Mo_Waisted,
    17 Up_Mo_anterior_fovea,
    18 Protruding_stylar_lobe,
    19 Up_Mo_stylar_grv,
    20 Lw_mo_cusp_c,
    21 lwm_cusps_c & g morphs,
    22 'Lw a-c v-notch',
    23 Lw_Mo_cusp_g_patterns,
    24 'Lw cusp c-g size ratio',
    25 Lw_pseudotalonid,
    26 'Lw V-Notch a-g crest',
    27 'Lw crest b-g',
    28 'Lw crest c-d',
    29 'Lw cres c-df',
    30 Lw_cusp_d_position,
```

```

31 Lw_distal_cusp_df,
32 'Lw ultima/Penultima posterior reduction',
33 Lw_folding_enamel,
34 'Lw connecting a-d',
35 'crest a-d angulation',
36 'crest b-g',
37 cusp_e_size,
38 Cusp_ee,
39 mesiolingual_cingulid,
40 'line cingulid below g or g-position',
41 'b-a height ratio',
42 'b-a separation',
43 docodont_f,
44 standard_cuspule_e,
45 'b-e crest',
46 anterior_basin,
47 distal_basin,
48 basin_width_ratio,
49 'Lw A-P proportion',
50 'lo mo inter-lock',
51 e_cusp_shift,
52 'a-b-c triangulation',
53 'g-a-c triangle',
54 'Gibbousness/root constriction',
55 Upper_molar_roots,
56 Canine_root_#,
57 Low_canine_size,
58 lo_premo_loci_#,
59 Ult_mo_root_fusion,
60 Profile_of_lw_prem,
61 Recurved_premolar,
62 Diphyodonty ;

```

MATRIX

Sinoconodon	00001000000000000000??00?0????00000??000?0000000?0000?000000000
Morganucodon	00000000000000000000?010000??00000?000000000000?0100?000010001
Dinnetherium	20000000000000000000?010000??00000?000000000000?0100?000010001
Megazostrodon	20000000000000000000?010000??00000?000000001000?0200?000020001
Hadrocodium	00000110000000000000??00?0????00000??000?0000000?0000?001001001
Kuehneotherium	20000010000000000000??00?0????00000??000?0001000?0201?000031001
Delsatia	????????????????????1002100??00000?000000001000?0201???????????
Woutersia	????????1000010100001002100??00000?000000001000?1201?00?????????
Gondtherium	????????110000010?????????????????0?????????????????????????????
Nujalikodon	????0????????????????100311111001?0111001201100110110101?????????
Haldanodon	1111101111211210101103032110010110210111110011114011011011001
Docodon	1111101111211211101113032111010110210021010011104011011010001
Docofossor	1111101111211210101013132110010010210021010?11104011011011001
Dsungarodon	11?1????111101?10??1004111100111010210012100121021110111?011?
Megacauda	111110110120111101004111101011020110022100121011011011020011
Castorocauda	111??10?????????????10041111010110201100221001210110110?103001?
Itatodon	????11?????????????10041210110100201100101101210230101?????10?
Agilodocodon	1111111110101110111004121121110121100110110121023010111130101
Simpsonodon	????11?111110110010100412112101012011012011012102311011???010?
Dobunnodon	????????????????????100301112001?0111001101101210130101?????????
Borealestes	1111011111101111101003011120010010110120110121013010111121101
Krusatodon	11110111110101110101003011120010011110120110121013010111120101
Microdocodon	111111111110111011100411110111101000101012022102311111?130101
Tashkumyrodon	????????????????????1003?21111011020?001101101211111101?????????
Sibirotherium	????111111101110111003121001011020000010110221033111110?????1
Khorotherium	????10?110010111011100302002111002100111012022103311111????0???
Ergetiis	?11?00?????????????10030200211100210011101202210341111????01??
Tegotherium	????11?111110111???100412100111102000101012022102311111????0???
Hutegotherium	????11?111110111011100412100111102000101012022102311111????0???

```

;

END;
BEGIN ASSUMPTIONS;
    OPTIONS DEFTYPE = unord PolyTcount = MAXSTEPS;
    TYPESET * UNTITLED = unord: 1- 62;

END;

BEGIN MacClade;
    Version 4.0 84;
    LastModified 2082823737;
    FileSettings editor '0' '0' '1' '1';
    Singles 000;
    Editor 000110011111110010001001 '0' '24' Geneva '9' '100' '1' all;
    EditorPosition '44' '45' '819' '1371';
    TreeWindowPosition '46' '6' '843' '1390';
    ListWindow Characters closed Geneva '9' '50' '10' '129' '388' 000;
    ListWindow Taxa closed Geneva '9' '50' '10' '225' '490' 100000;
    ListWindow Trees closed Geneva '9' '50' '10' '276' '490';
    ListWindow TypeSets closed Geneva '9' '50' '10' '276' '490';
    ListWindow WtSets closed Geneva '9' '50' '10' '276' '490';
    ListWindow ExSets closed Geneva '9' '50' '10' '276' '490';
    ListWindow CharSets closed Geneva '9' '50' '10' '276' '490';
    ListWindow TaxSets closed Geneva '9' '50' '10' '276' '490';
    ListWindow CharPartitions closed Geneva '9' '50' '10' '276' '490';
    ListWindow CharPartNames closed Geneva '9' '50' '10' '276' '490';
    ListWindow WtSets closed Geneva '9' '50' '10' '276' '490';
    ChartWindowPosition '52' '30' '818' '1380';
    StateNamesSymbols closed Geneva '9' '10' '50' '30' '148' '220';
    WindowOrder Data;
    OtherSymbols & / 00 ? -;
    Correlation '0' '0' '1000' '0' '0' 10011010;
    Salmo 00000001;
    EditorFile '2';
    ExportHTML _ MOSS '100' 110000;
    PrettyPrint 10;
    EditorToolsPosition '596' '972' '115' '165';
    TreeWindowProgram 10;
    TreeWindow 0000;
    Continuous '0' '3' 1;
    Calculations 0000001;
    SummaryMode '0' '0' 0;
    Charts Geneva '9' ( normal ) 0010;
    NexusOptions '0' '0' '50' 001011011;
    TipLabel '1';
    TreeFont Geneva '9' ( normal );
    TreeShape 0.7 1.0 0100;
    TraceLabels 0101;
    ChartColors '0' '0' '65535' '9' '0' 1;
    ChartBiggestSpot 1;
    ChartPercent 10;
    ChartBarWidth '10' 1;
    ChartVerticalAxis 10101;
    ChartMinMax '0';
    TraceAllChangesDisplay '1' 1;
    BarsOnBranchesDisplay '0' '0' '60000' '10000' '10000' '10000' '10000' '60000'
'65000' '65000' '65000' '6' '1' 0000101;
    ContinuousBranchLabels 0;
    AllStatesBranchLabels 1;
    IndexNotation '2' 1;
    PrintTree 10.00 '2' '2' '2' '2' '2' '2' '2' '2' '2' '2' '2' '2' Geneva '9' ( normal )
Geneva '10' ( normal ) Geneva '9' ( normal ) Geneva '9' ( normal ) Geneva '9' ( bold )

```

```

Geneva '9' ( normal ) Geneva '9' ( normal ) '0' '0' '0' '0' '0' '0' '0' '0' '0' '0' '0' '0' '0' '0' '0' '0'
'0' '0' '0' '0' '0' '0' '0' '0' '0' '0' '0' '0' '0' '0' '0' '0' '0' '0' '1' '1' '1' '1'
'25971' '176' '-39' '4' '-40' '0' '1' '2' '1' '8' '0' '0' '0' '0' '2'
1000111000000000000100000111000;
    MatchChar 00 .;
    EntryInterpretation 01;
    ColorOptions 00;
    TreeTools '0' '5' '4' '0' '10' '4' '0' 00100111111101110;
    EditorTools '0' '0' '0' '1000' '0' '0' '6' '3' '0' 100000101110001;
    PairAlign '2' '2' '3' '2' '1' '1' '2' '1' '3' 1010;
    BothTools '1';

END;
BEGIN MESQUITECHARMODELS;
    ProbModelSet * UNTITLED = 'Mk1 (est.)': 1- 62;
END;

Begin MESQUITE;
    MESQUITESCRIPTVERSION 2;
    TITLE AUTO;
    tell ProjectCoordinator;
    timeSaved 1781884308968;
    getEmployee #mesquite.minimal.ManageTaxa.ManageTaxa;
    tell It;
        setID 0 170156751319261612;
        tell It;
            setDefaultOrder 0 2 4 3 5 6 7 8 9 28 18 19 24 16 25 11 20 23 22
27 17 21 12 10 15 26 31 13 14;
            attachments ;
        endTell;
    endTell;
    getEmployee #mesquite.charMatrices.ManageCharacters.ManageCharacters;
    tell It;
        setID 0 4053522984695825337;
        tell It;
            setDefaultOrder 0 1 2 50 3 4 51 5 6 7 8 9 10 11 12 13 58 52 53
14 59 15 16 17 18 19 20 21 22 23 24 60 25 26 27 28 29 54 30 31 32 33 34 35 36 37 38 39 61
40 41 42 43 44 45 46 47 48 49 55 56 57;
            attachments ;
        endTell;
        mqVersion 370;
        checksumv 0 3 3286294886 null getNumChars 62 numChars 62 getNumTaxa 29
numTaxa 29 short true bits 31 states 31 sumSquaresStatesOnly 10087.0 sumSquares
10087.0 longCompressibleToShort false usingShortMatrix true NumFiles 1 NumMatrices 1;
        mqVersion;
    endTell;
    getWindow;
    tell It;
        suppress;
        setResourcesState false false 100;
        setPopoutState 300;
        setExplanationSize 0;
        setAnnotationSize 0;
        setFontIncAnnot 0;
        setFontIncExp 0;
        setSize 1614 781;
        setLocation 35 25;
        setFont SanSerif;
        setFontSize 10;
        getToolPalette;
        tell It;
        endTell;
    desuppress;

```

```

endTell;
getEmployee #mesquite.charMatrices.BasicDataWindowCoord.BasicDataWindowCoord;
tell It;
    showDataWindow #4053522984695825337
#mesquite.charMatrices.BasicDataWindowMaker.BasicDataWindowMaker;
    tell It;
        getWindow;
        tell It;
            setExplanationSize 30;
            setAnnotationSize 20;
            setFontIncAnnot 0;
            setFontIncExp 0;
            setSize 1514 709;
            setLocation 35 25;
            setFont SanSerif;
            setFontSize 10;
            getToolPalette;
            tell It;
                setTool
mesquite.charMatrices.BasicDataWindowMaker.BasicDataWindow.ibeam;
            endTell;
            setTool
mesquite.charMatrices.BasicDataWindowMaker.BasicDataWindow.ibeam;
            colorCells #mesquite.charMatrices.NoColor.NoColor;
            colorRowNames
#mesquite.charMatrices.TaxonGroupColor.TaxonGroupColor;
            colorColumnNames
#mesquite.charMatrices.CharGroupColor.CharGroupColor;
            colorText #mesquite.charMatrices.NoColor.NoColor;
            setBackground White;
            toggleShowNames on;
            toggleShowTaxonNames on;
            toggleTight off;
            toggleThinRows off;
            toggleShowChanges on;
            toggleSeparateLines off;
            toggleShowStates on;
            toggleReduceCellBorders off;
            toggleAutoWCharNames on;
            toggleAutoTaxonNames off;
            toggleShowDefaultCharNames off;
            toggleConstrainCW on;
            toggleBirdsEye off;
            toggleColorOnlyTaxonNames off;
            toggleShowPaleGrid off;
            toggleShowPaleCellColors off;
            toggleShowPaleExcluded off;
            togglePaleInapplicable on;
            togglePaleMissing off;
            toggleShowBoldCellText off;
            toggleAllowAutosize on;
            toggleColorsPanel off;
            toggleDiagonal on;
            setDiagonalHeight 80;
            toggleLinkedScrolling on;
            toggleScrollLinkedTables off;
        endTell;
        showWindow;
        getWindow;
        tell It;
            forceAutosize;
        endTell;
    getEmployee #mesquite.charMatrices.AlterData.AlterData;

```

```

tell It;
    toggleBySubmenus off;
endTell;
getEmployee #mesquite.charMatrices.ColorByState.ColorByState;
tell It;
    setStateLimit 9;
    toggleUniformMaximum on;
endTell;
getEmployee #mesquite.charMatrices.ColorCells.ColorCells;
tell It;
    setColor Red;
    removeColor off;
endTell;
getEmployee #mesquite.categ.StateNamesStrip.StateNamesStrip;
tell It;
    showStrip off;
endTell;
getEmployee #mesquite.charMatrices.AnnotPanel.AnnotPanel;
tell It;
    togglePanel off;
endTell;
getEmployee
#mesquite.charMatrices.CharReferenceStrip.CharReferenceStrip;
tell It;
    showStrip off;
endTell;
getEmployee
#mesquite.charMatrices.QuickKeySelector.QuickKeySelector;
tell It;
    autotabOff;
endTell;
getEmployee
#mesquite.charMatrices.SelSummaryStrip.SelSummaryStrip;
tell It;
    showStrip off;
endTell;
getEmployee
#mesquite.categ.SmallStateNamesEditor.SmallStateNamesEditor;
tell It;
    panelOpen true;
endTell;
endTell;
showExtraDataWindow #4053522984695825337
#mesquite.charMatrices.BasicDataWindowMaker.BasicDataWindowMaker;
tell It;
    getWindow;
    tell It;
        setExplanationSize 30;
        setAnnotationSize 20;
        setFontIncAnnot 0;
        setFontIncExp 0;
        setSize 1514 709;
        setLocation 35 25;
        setFont SanSerif;
        setFontSize 10;
        getToolPalette;
        tell It;
            setTool
mesquite.charMatrices.BasicDataWindowMaker.BasicDataWindow.ibeam;
        endTell;
        setActive;
        setTool
mesquite.charMatrices.BasicDataWindowMaker.BasicDataWindow.ibeam;

```

```

        colorCells #mesquite.charMatrices.NoColor.NoColor;
        colorRowNames
#mesquite.charMatrices.TaxonGroupColor.TaxonGroupColor;
        colorColumnNames
#mesquite.charMatrices.CharGroupColor.CharGroupColor;
        colorText #mesquite.charMatrices.NoColor.NoColor;
        setBackground White;
        toggleShowNames on;
        toggleShowTaxonNames on;
        toggleTight off;
        toggleThinRows off;
        toggleShowChanges on;
        toggleSeparateLines off;
        toggleShowStates on;
        toggleReduceCellBorders off;
        toggleAutoWCharNames on;
        toggleAutoTaxonNames off;
        toggleShowDefaultCharNames off;
        toggleConstrainCW on;
        toggleBirdsEye off;
        toggleColorOnlyTaxonNames off;
        toggleShowPaleGrid off;
        toggleShowPaleCellColors off;
        toggleShowPaleExcluded off;
        togglePaleInapplicable on;
        togglePaleMissing off;
        toggleShowBoldCellText off;
        toggleAllowAutosize on;
        toggleColorsPanel off;
        toggleDiagonal on;
        setDiagonalHeight 80;
        toggleLinkedScrolling on;
        toggleScrollLinkedTables off;
    endTell;
    showWindow;
    getWindow;
    tell It;
        forceAutosize;
    endTell;
    getEmployee #mesquite.charMatrices.AlterData.AlterData;
    tell It;
        toggleBySubmenus off;
    endTell;
    getEmployee #mesquite.charMatrices.ColorByState.ColorByState;
    tell It;
        setStateLimit 9;
        toggleUniformMaximum on;
    endTell;
    getEmployee #mesquite.charMatrices.ColorCells.ColorCells;
    tell It;
        setColor Red;
        removeColor off;
    endTell;
    getEmployee #mesquite.categ.StateNamesStrip.StateNamesStrip;
    tell It;
        showStrip off;
    endTell;
    getEmployee #mesquite.charMatrices.AnnotPanel.AnnotPanel;
    tell It;
        togglePanel off;
    endTell;
    getEmployee
#mesquite.charMatrices.CharReferenceStrip.CharReferenceStrip;

```

```

        tell It;
            showStrip off;
        endTell;
        getEmployee
#mesquite.charMatrices.QuickKeySelector.QuickKeySelector;
        tell It;
            autotabOff;
        endTell;
        getEmployee
#mesquite.charMatrices.SelSummaryStrip.SelSummaryStrip;
        tell It;
            showStrip off;
        endTell;
        getEmployee
#mesquite.categ.SmallStateNamesEditor.SmallStateNamesEditor;
        tell It;
            panelOpen true;
        endTell;
    endTell;
endTell;
getEmployee #mesquite.charMatrices.ManageCharacters.ManageCharacters;
tell It;
    showCharacters #4053522984695825337
#mesquite.lists.CharacterList.CharacterList;
    tell It;
        setData 0;
        getWindow;
        tell It;
            useTargetValue off;
            setTargetValue ;
            newAssistant
#mesquite.lists.DefaultCharOrder.DefaultCharOrder;
            newAssistant
#mesquite.lists.CharListInclusion.CharListInclusion;
            newAssistant
#mesquite.lists.CharListPartition.CharListPartition;
            newAssistant
#mesquite.parsimony.CharListParsModels.CharListParsModels;
            setExplanationSize 30;
            setAnnotationSize 20;
            setFontIncAnnot 0;
            setFontIncExp 0;
            setSize 1514 709;
            setLocation 35 25;
            setFont SanSerif;
            setFontSize 10;
            getToolPalette;
            tell It;
                setTool
mesquite.lists.CharacterList.CharacterListWindow.arrow;
            endTell;
        endTell;
        showWindow;
        getEmployee
#mesquite.lists.CharListAnnotPanel.CharListAnnotPanel;
        tell It;
            togglePanel off;
        endTell;
    endTell;
endTell;
endTell;
end;

```


(11) Maximum Parsimony and Bayesian Analyses: Comments & Summary

(1) Phylogenetic matrix

The matrix of this study consists of 62 dental and mandibular characters and 29 taxa, with 20 docodontan genera (including *Nujalikodon*) and nine outgroups. The character list and taxon scores are adopted with updates from previous analyses, successively expanded and updated in several rounds of analyses on docodontan interrelationship. These studies are (from the recent to the earlier studies): Patrocínio et al. (2025), Panciroli et al. (2024), Averianov et al. (2024), Panciroli et al. (2021), Panciroli et al. (2019), Zhou et al. (2019), Averianov et al. (2010); Luo and Martin (2007). This succession of updates are necessitated by the discoveries of new docodontans (e.g. Averianov et al. 2024; Patrocínio et al. 2025).

(2) Maximum parsimony analyses

The main parsimony analysis on this matrix was by PAUP Heuristic Search in 50,000 replicates; with all characters equal weight, multi-state characters run as un-ordered. The heuristic replicates are run with the following parameters: branch-swapping algorithm of tree-bisection-reconnection (TBR) (reconnection limit = 8); steepest descent option in effect; branches collapsed if maximum branch length is zero; 'MulTrees' option not in effect; only 1 tree will be saved per replicate; No topological constraints in effect; Trees are unrooted.

PAUP Heuristic Search (50,000 replicates) resulted in 23 Equally Parsimonious Trees (EPTs); each equally parsimonious tree with 173 steps, Consistency Index (CI) = 0.497, and Retention Index (RI) = 0.800. Our preferred consensus tree topology is the Adam's consensus tree (of the 23 EPTs), as presented in Figure 5.

The Adam's consensus tree from these PAUP searches returns the monophyletic Docodonta (including *Nujalikodon* as proposed by Patrocínio et al. 2025). The focus of our study - *Megacauda* and *Castorocauda* are united in the monophyletic Megacaudidae, with *Dsungarodon* as the family's sister taxon – a clade recovered both by Adam's consensus tree and by the strict consensus tree. The two other family-level clades, Docodontidae (sensu Luo et al. 2015) and Tegotheeriidae (sensu Averianov et al. 2010; as modified by Panciroli et al. 2019 and Zhou et al. 2019), are also well-supported by both the Adam's consensus and the strict consensus. Our Adam's consensus and strict consensus trees also recovered (*Borealestes*, *Krusatodon*, and *Dobunnodon*) as a clade, as originally proposed by Panciroli et al. (2024), with branch support of Bremer = 1.

(3) Branch Support Estimates

We optioned to use PAUP and TNT to run bootstrap heuristic search and to estimate the Bremer index for branch support, because TNT is faster than PAUP in estimating the branch support. The clade of Docodonta (including *Nujalikodon*) is recovered with a weak support of Bremer = 1. The Docodontidae, the Megacaudidae, and the Tegotheeriidae (Averianov et al. 2010; Panciroli et al. 2019)

are the three subclades with better Bremer/Bootstrap values (see Figure 5 and summary of branch support). Aside from these, other clades are all weakly supported.

Gondtherium, a late Early Jurassic taxon represented by a single upper molar, was commonly assumed to be a sister taxon to the Docodonta (Luo and Martin 2007 and some subsequent studies). But it has unstable positions in various iterations of our phylogenetic analyses. This is a prominent weakness of our phylogenies. *Gondtherium* is excluded from the Docodonta clade in the 50% majority consensus tree of the 23 EPTs from PAUP search. But in our preferred Adam consensus tree, it forms an unresolved trichotomy with *Nujalikodon* and the rest of docodontans. We suspect that instability of *Gondtherium* is caused by the fact that it is a single upper molar (therefore missing all characters of lower molars) and *Nujalikodon* is represented by a single lower molar (missing all characters of the upper molars). None of the lower molar characters scored for *Nujalikodon* can be scored for *Gondtherium*, and vice versa. The missing data problems for *Gondtherium* and *Nujalikodon* is the cause for the uncertainty of *Gondtherium* phylogenetic placement.

(4) Bayesian analyses of docodontan relationships

The Bayesian Analyses of docodontans (including *Megacauda*) on our 29 taxa x 62 characters have adopted largely the same search protocols of the Patrocínio et al. (2025), but we used the Mkv model instead. Our 50% majority-rule consensus tree (details in log file of Bayesian analyses) has returned the clade of Docodonta (including *Nujalikodon*), the clade of (Megacaudidae+*Dsungarodon*), the clade of Tegotheiidae (*sensu* Averianov et al. 2010; Panciroli et al. 2021) and clade of Docodontidae (*sensu* Luo and Martin 2007; Luo et al. 2015).

Our Bayesian analysis has confirmed the clade of Docodonta (including *Nujalikodon*), to the exclusion of *Gontherium*. This is broadly consistent with the proposal that *Nujalikodon* is a docodontan (Patrocínio et al. 2025). However, by our matrix and in our Bayesian consensus trees, *Nujalikodon* is the sister-taxon to the Docodontidae, in contrast to placement of this fossil as basal-most taxon of docodontans by Patrocínio et al. (2025). In our maximum compatibility tree of 14995 post burn-in trees, *Nujalikodon*+Docodontidae is deeply nested in Docodonta. Given our matrix, the placement of *Nujalikodon* and Docodontidae is unstable. But the placement of the Megacaudidae and its sister-taxon *Dsungarodon* is stable.

Heuristic search settings:
 Optimality criterion = parsimony
 Character-status summary:
 Of 62 total characters:
 All characters are of type 'unord'
 All characters have equal weight
 1 character is parsimony-uninformative
 Number of parsimony-informative characters = 61
 Gaps are treated as "missing"
 Starting tree(s) obtained via stepwise addition
 Addition sequence: random
 Number of replicates = 50000
 Starting seed = generated automatically
 Number of trees held at each step = 1
 Branch-swapping algorithm: tree-bisection-reconnection (TBR) with reconnection limit = 8
 Steepest descent option in effect
 Initial 'Maxtrees' setting = 600 (will be auto-increased by 100)
 Branches collapsed (creating polytomies) if maximum branch length is zero
 'MulTrees' option not in effect; only 1 tree will be saved per replicate
 No topological constraints in effect
 Trees are unrooted

Heuristic search completed
 Total number of rearrangements tried = 266270020
 Score of best tree(s) found = 173
 Number of trees retained = 23
 Time used = 55.57 sec (CPU time = 55.91 sec)

Tree-island profile:

Island	Size*	First tree	Last tree	Score	First replicate	Times hit
1	1	1	1	173	406	3
2	1	2	2	173	546	54
3	1	3	3	173	796	23
4	1	4	4	173	1886	21
5	1	5	5	173	1910	11
6	1	6	6	173	3100	5
7	1	7	7	173	5789	13
8	1	8	8	173	6684	3
9	1	9	9	173	9233	7
10	1	10	10	173	9807	9
11	1	11	11	173	10347	7
12	1	12	12	173	12343	2
13	1	13	13	173	16826	2
14	1	14	14	173	18369	1
15	1	15	15	173	20339	5
16	1	16	16	173	23039	2
17	1	17	17	173	24190	5
18	1	18	18	173	25627	1
19	1	19	19	173	27126	2
20	1	20	20	173	27153	4
21	1	21	21	173	28438	4
22	1	22	22	173	29919	6
23	1	23	23	173	35488	1
24	1	-	-	174	4	1192**
25	1	-	-	175	20	3831**
26	1	-	-	176	3	7388**
27	1	-	-	177	13	9483**
28	1	-	-	178	7	8986**
29	1	-	-	179	6	7185**
30	1	-	-	180	29	5146**
31	1	-	-	181	17	3142**
32	1	-	-	182	12	1688**
33	1	-	-	183	2	924**
34	1	-	-	184	1	471**
35	1	-	-	185	144	199**
36	1	-	-	186	497	101**
37	1	-	-	187	2514	40**
38	1	-	-	188	3579	14**
39	1	-	-	189	8035	10**
40	1	-	-	190	3414	5**
41	1	-	-	191	13563	2**
42	1	-	-	192	4249	2**

Note(s):
 * Only one tree was saved per island; island structure is undetermined
 ** Multiple observations of the same score do not imply identity of the corresponding trees

paup> pscorers;

Lengths and fit measures of trees in memory:
 Character-status summary:
 Of 62 total characters:
 All characters are of type 'unord'
 All characters have equal weight
 1 character is parsimony-uninformative
 Number of parsimony-informative characters = 61

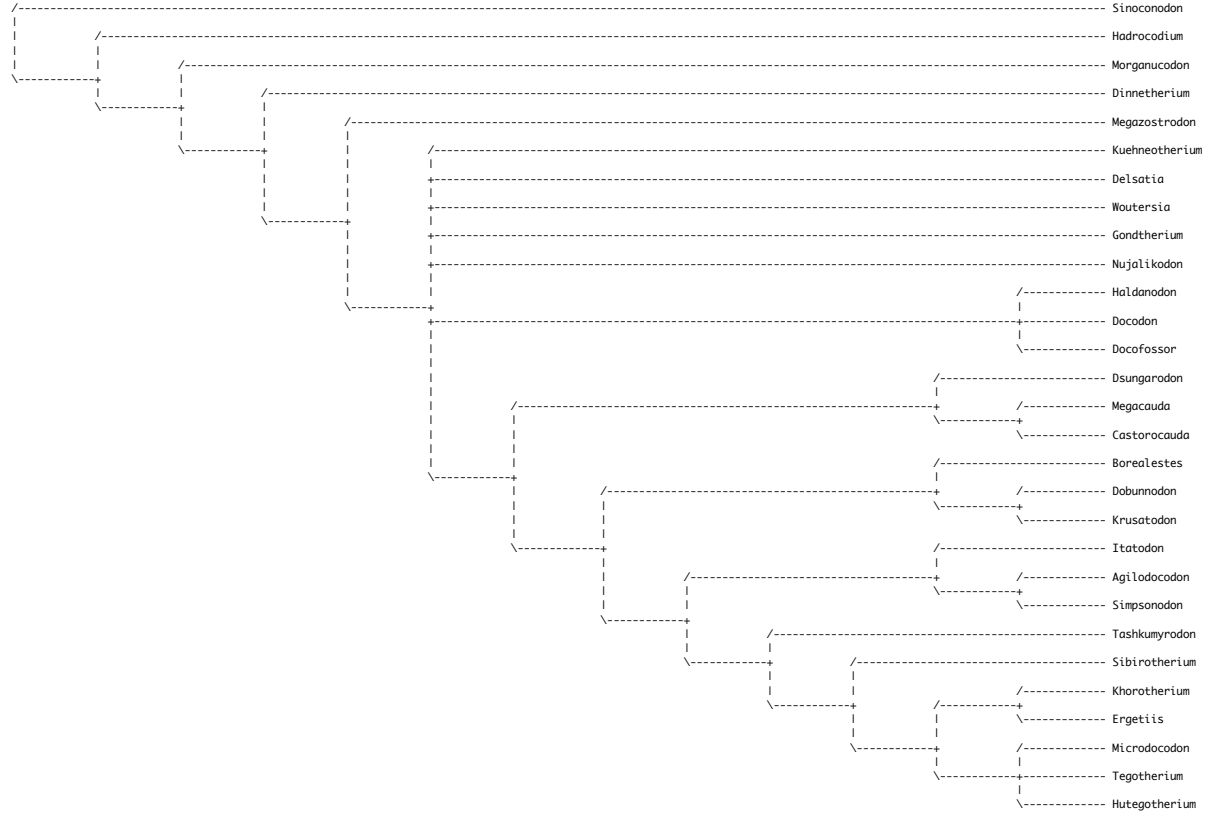
Gaps are treated as "missing"

Sum of min. possible lengths = 86
Sum of max. possible lengths = 521

Tree #	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Length	173	173	173	173	173	173	173	173	173	173	173	173	173	173	173	173	173	173	173	173	173	173	173
CI	0.497	0.497	0.497	0.497	0.497	0.497	0.497	0.497	0.497	0.497	0.497	0.497	0.497	0.497	0.497	0.497	0.497	0.497	0.497	0.497	0.497	0.497	0.497
RI	0.800	0.800	0.800	0.800	0.800	0.800	0.800	0.800	0.800	0.800	0.800	0.800	0.800	0.800	0.800	0.800	0.800	0.800	0.800	0.800	0.800	0.800	0.800

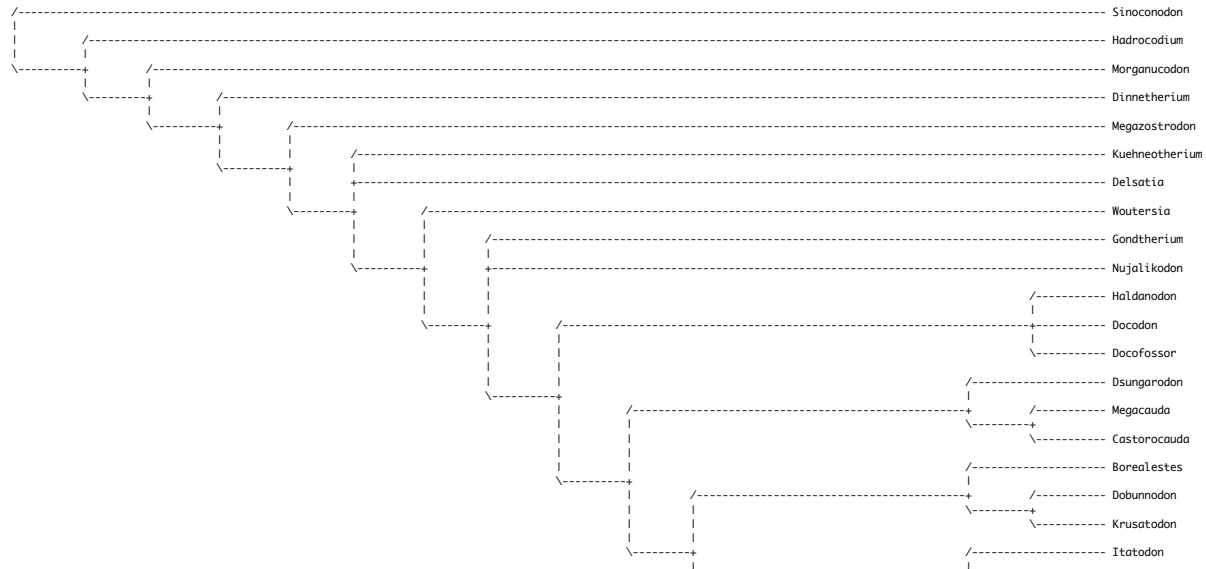
paup> contree;

Strict consensus of 23 trees:



paup> contree / strict=no adams;

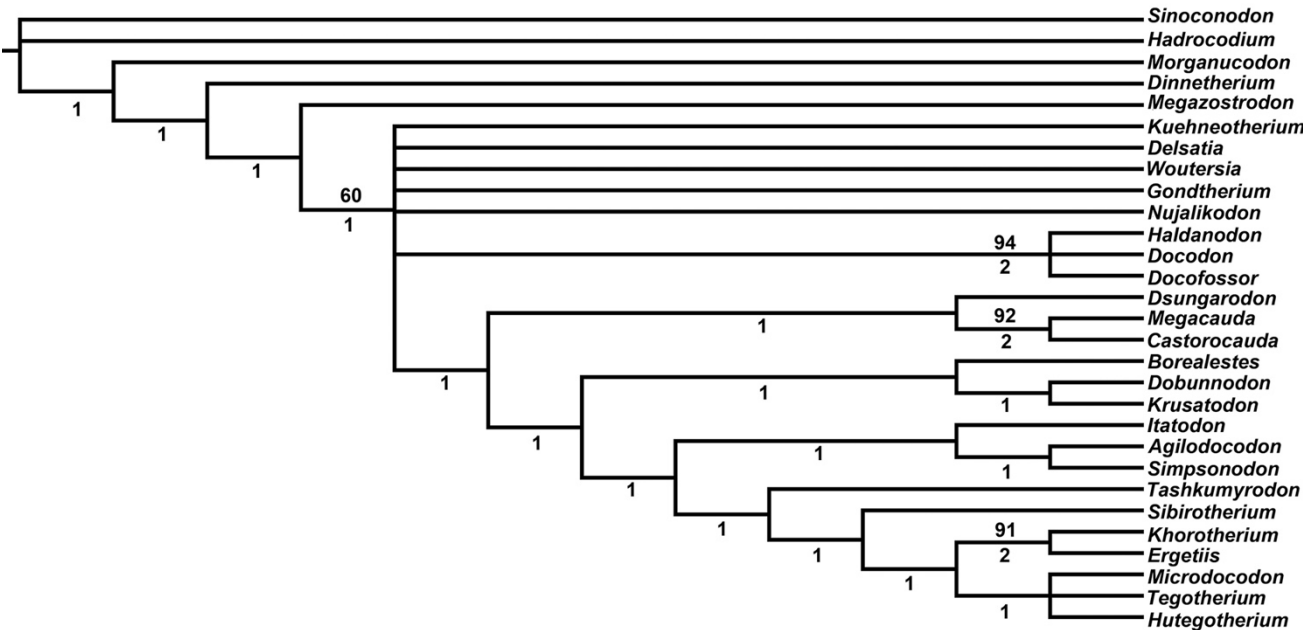
Adams consensus of 23 trees:



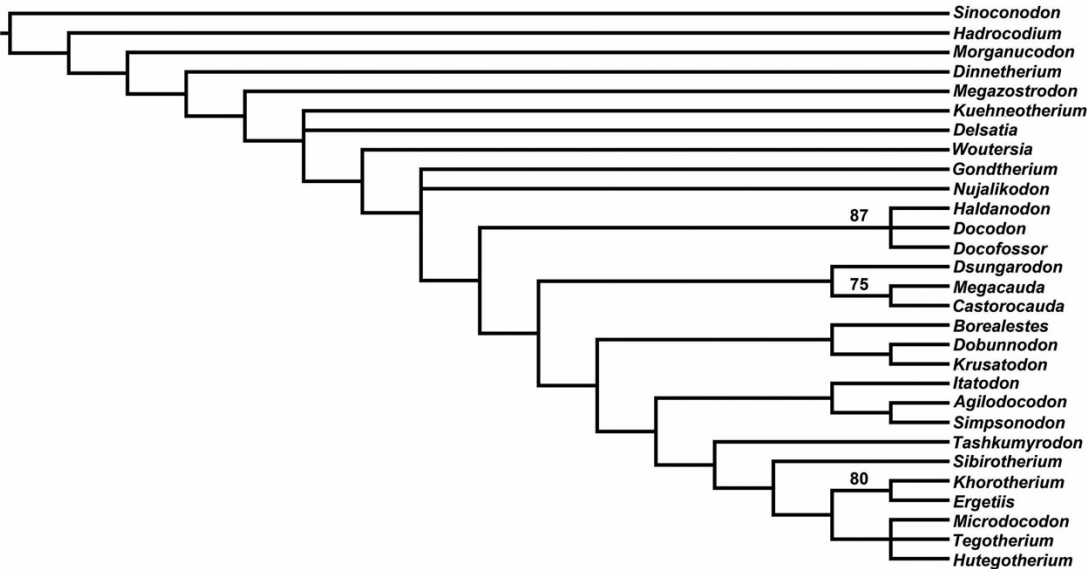
.....*****	19	82.61%
.....*****	16	69.57%
.....**.....	16	69.57%
.....*****	13	56.52%
.....*****	11	47.83%
.....**.....	7	30.43%
.....*.....*****	7	30.43%
.....*.....*****	6	26.09%
.....**.....	6	26.09%
.....*.....*****	6	26.09%
.....**.....	4	17.39%
.....*.....*****	3	13.04%
.....**.....	1	4.35%
.....*.....*****	1	4.35%

paup> log start;

Summary of Branch Supports (calculated from PAUP and TNT)



Maximum parsimony strict consensus with Bremer support (below branch) and Bootstrap value (above branch)
Only book strap values at 50% or higher are reported



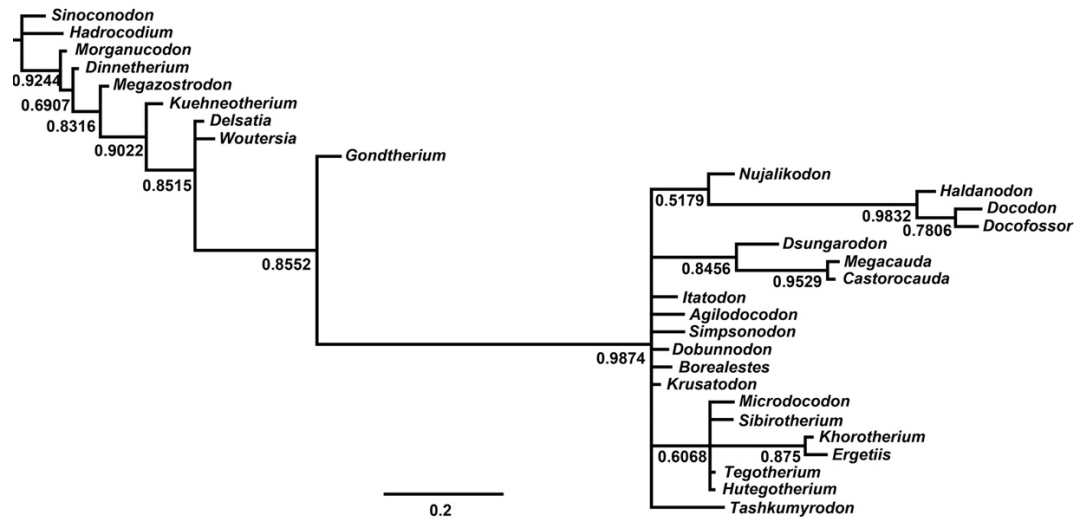
Adam's Consensus Tree with Branch Support of Bootstrap value (above branch)
Only bootstrap values at 50% or higher are reported

Summary of Bayesian Analyses (MrBayes)

MrBayes, 50% majority-rule consensus tree.

Command:

```
execute .../.../Megac-19-06-2026.nex;
lset coding=variable rates=gamma;
mcmc ngen=10000000 nrun=4 nchain=4 samplefr=2000 printfr=10000 diagnfr=10000;
sumt;
sump;
```

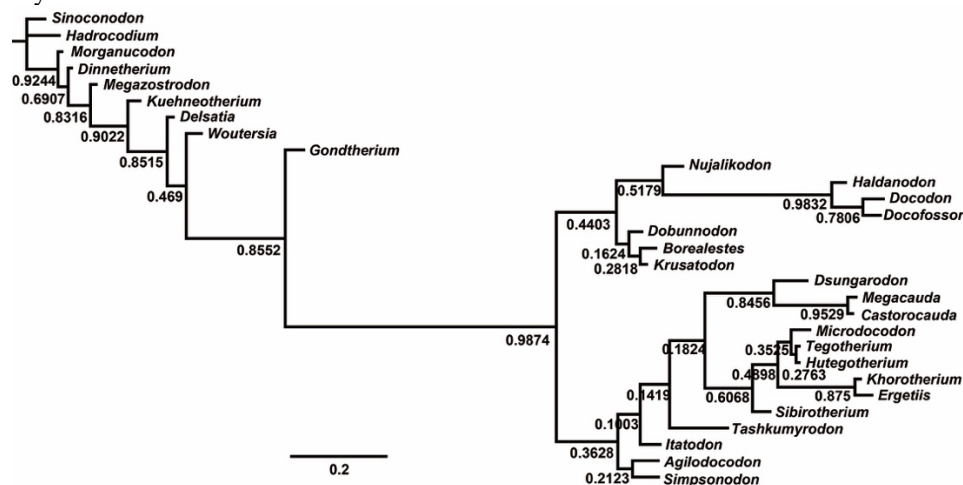


MrBayes, maximum compatibility tree.

Command:

```
execute .../.../Megac-19-06-2026.nex;
lset coding=variable rates=gamma;
mcmc ngen=10000000 nrun=4 nchain=4 samplefr=2000 printfr=10000 diagnfr=10000;
sumt contype=Allcompat;
sump;
```

Maximum compatibility tree of 14995 post burn-in trees in Bayesian analysis; the value below the node representing the posterior probability.



(13) References cited in Supplementary Information

Cited References in Text and Supplementary Information

1. Kielan-Jaworowska, Z., R. L. Cifelli, & Z.-X. Luo. *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure*. (Columbia University Press, 2004)
2. Luo, Z.-X. Transformation and diversification in the early mammalian evolution. *Nature* **450**, 1011–1019 (2007).
3. Martin, T. Mesozoic mammals – early mammalian diversity and ecomorphological adaptations. In *Handbook of Zoology, Mammalia, Mammalian Evolution, Diversity and Systematics* (eds F. E. Zachos & R. J. Asher) 199–299 (De Gruyter, 2018)
4. Bishop, P. J. & Pierce, S. E. The fossil record of appendicular muscle evolution in Synapsida on the line to mammals: Part II—Hindlimb. *Anatomical Record* **307**, 1826–1896 (2023).
5. Luo, Z.-X., & Manley, G. A. Origins and evolution of mammalian ears and hearing function. In *The Senses – A Comprehensive Reference (Volume 2) (Second Edition)* (eds Fritzsche, B. & Grothe, B) Chapter 2, 207–252. (Elsevier Academic Press, 2020). (<https://doi.org/10.1016/B978-0-12-805408-6.00033-6>).
6. Rawson, J. R. G., Martinelli, A. G., Gill, P. G. Soares, M. B., Schultz, C. L., & Rayfield, E. J. Brazilian fossils reveal homoplasy in the oldest mammalian jaw joint. *Nature* **634**, 381–388 (2024).
7. Grossnickle, D. M., Chen, M., Wauer, J. G. A., Pevsner, S. K., Weaver, L. N., Meng, Q.-J., Liu, D., Zhang, Y.-G. & Luo, Z.-X. Incomplete convergence of gliding-mammal skeletons. *Evolution* **74**, 2662–2680 (2020). (DOI: 10.1111/evo.14094).
8. Zhou, C.-F., Bhullar, B.-A.S., Neander, A.I., Martin, T. & Luo, Z.-X. New Jurassic mammaliaform sheds light on early evolution of mammal-like hyoid bones. *Science* **365**, 276–279 (2019).
9. Meng, Q.-J., Grossnickle, D. M., Liu, D., Zhang, Y.-G., Neander, A. I., Ji, Q., & Z.-X. Luo. New gliding mammaliaforms from the Jurassic. *Nature* **548**, 291–296 (2017).
10. Meng, Q.-J., Ji, Q., Zhang, D., Liu, D. M. Grossnickle, & Luo Z.-X. An arboreal docodont from the Jurassic and mammaliaform ecological diversification. *Science* **347**, 764–768 (2015).
11. Martin, T. Postcranial anatomy of *Haldanodon exspectatus* (Mammalia, Docodonta) from the Late Jurassic (Kimmeridgian) of Portugal and its bearing for mammalian evolution. *Zoological Journal of the Linnean Society* **145**, 219–248 (2005).
12. Luo, Z.-X., Meng, Q.-J. Ji, Q., Liu, D. Zhang, Y.-G. & Neander, A. I. Evolutionary development in basal mammaliaforms as revealed by a docodontan. *Science* **347**, 760–764 (2015)
13. Ji, Q., Luo, Z.-X., Yuan, C.-X. & Tabrum, A. R. A swimming mammaliaform from the Middle Jurassic and ecomorphological diversification of early mammals. *Science* **311**, 1123–1127 (2006).
14. Jia, J., Anderson, J. S. & Gao, K.-Q. Middle Jurassic stem hynobiid from China shed light on the evolution of basal salamanders. *iScience* **24**, 102744. (2021) (doi.org/10.1016/j.isci.2021.102744).
15. Huang, D. Y., Cai, C.-Y., Xu, X, Wang, X.-L., Su, Y.-T., Liao, H.-Y., Jiang J.-Q. & Sha, J.-G. Daohugou fossil beds and Daohugou biota (Chapter 3). Pp. 37–70. In, Huang, D. Y. (ed.). *The Daohugou Biota* (Shanghai Scientific and Technical Publishers, 2016).
16. Panciroli, E., Benson, R. B.J. Fernandez, V., Fraser, N. C., Humpage, M., Luo, Z.-X., Newham, E. & Walsh, S. Jurassic fossil juvenile reveals prolonged life history in early mammals. *Nature* **632**, 815–22 (2024).
17. Luo, Z.-X. & Martin, T. Analysis of molar structure and phylogeny of docodontan genera. *Bulletin of the Carnegie Museum of Natural History* **39**, 27–47 (2007). ([doi:10.2992/0145-9058](https://doi.org/10.2992/0145-9058))

18. Averianov, A. O., Martin, T., Lopatin, A. V., Skutschas, P. P., Vitenko, D. D., Schellhorn, R. & Kolosov, P. N. Docodontans from the Lower Cretaceous of Yakutia, Russia: New insights into diversity, morphology, and phylogeny of Docodonta. *Cretaceous Research* **158**, 105836 (2024)
19. Patrocínio, S., Panciroli, E., Rotatori, F.M., Mateus, O., Milàn, J., Clemmensen, L.B. & Crespo, V.D. The oldest definitive docodontan from central East Greenland sheds light on the origin of the clade. *Papers in Palaeontology*, **11**, e70022 (2025).
20. Butler, P. M. Docodont molars as tribosphenic analogues (Mammalia, Jurassic). In: Russell, D. E., Santoro, J.-P., and Sigogneau-Russell, D. (eds.) *Teeth Revisited: Proceedings of the VIIth International Symposium on Dental Morphology. Mémoires du Muséum national d'Histoire naturelle* **C53**, 329–340 (1988).
21. Luo, Z.-X., Q. Ji & Yuan, C.-X. Convergent dental evolution in pseudotribosphenic and tribosphenic mammals. *Nature* **450**, 93–97 (2007).
22. Mao, F.-Y., Li, Z., Wang, Z., Zhang, C., Rich, T. H., Vickers-Rich, P. & Meng, J. Jurassic shuotheriids show earliest dental diversification of mammaliaforms. *Nature*, **628**, 569–575 (2024). <https://doi.org/10.1038/s41586-024-07258-7>.
23. Jones, M. E. (2023) Over-eruption in marsupial carnivore teeth: compensation for a constraint. *Proceedings of Royal Society B* **290**, 20230644. (<https://doi.org/10.1098/rspb.2023.0644>)
24. Orr, C. M., Delezenne, L. K., Scott, J. E., Tocheri, M. W. & Schwartz, G. T. The comparative method and the inference of venom-delivery systems in fossil mammals. *Journal of Vertebrate Paleontology* **27**, 541–546 (2007).
25. Schultz, J. A., Bhullar, B. A. S. & Z.-X. Luo. Re-examination of the Jurassic mammaliaform *Docodon victor* by computed tomography and occlusal functional analysis. *Journal of Mammalian Evolution*. **26**, 9–38 (2017).
26. Grossnickle, D.M., Weaver, L.N., Jäger K.R.K. & Schultz, J.A. The evolution of anteriorly directed molar occlusion in mammals. *Zoological Journal of the Linnean Society*, **194**, 349–365 (2022).
27. Stilson K. T., Luo Z.-X., Li, P., Olson, S. & Ross, C. F. Three-dimensional mandibular kinematics of mastication in the marsupial *Didelphis virginiana*. *Philosophical Transactions of Royal Society, Series B*. **378**, 20220548 (2023). (doi.org/10.1098/rstb.2022.0548).
28. Rose, K. D. *The Beginning of Age of Mammals*. (Johns Hopkins University Press, 2006).
29. Hocking, D. P., Evans, A. R. & Fitzgerald, E. M. G. Leopard seals (*Hydrurga leptonyx*) use suction and filter feeding when hunting small prey underwater. *Polar Biology* **36**, 211–222 (2013) (DOI 10.1007/s00300-012-1253-9).
30. Luo, Z.-X. Developmental patterns in Mesozoic evolution of mammal ears. *Annual Review of Ecology, Evolution and Systematics* **42**, 355–80 (2011). (10.1146/annurev-ecolsys-032511-142302).
31. Allin, E. F. & Hopson, J. A. Evolution of the auditory system in Synapsida (“mammal-like reptiles” and primitive mammals) as seen in the fossil record. In, *The Evolutionary Biology of Hearing* (eds Webster, D. B., Fay, R. R., & Popper, A. N.) 587–614 (Springer-Verlag, 1992).
32. Evans, H. E. & De Lahunta, A. *Miller's Anatomy of the Dog (4th Edition)*. (Elsevier-Saunders, 2013).
33. Li, P., Ross, C. F. & Luo, Z.-X. Morphological disparity and evolutionary transformations in the primate hyoid apparatus. *Journal of Human Evolution* **162**, 103094 (2022). Published online 2021 (<https://doi.org/10.1016/j.jhevol.2021.103094>).
34. German, R. Z., Campbell-Malone, R., Crompton, A. W., Ding, P., Holman, S., Konow, N. & Thexton, A. J. The concept of hyoid posture. *Dysphagia* **26**, 97–98 (2011).

35. Li, P., Ross, C. F., Luo, Z.-X. & Gidmark, N. J. Head posture impacts mammalian hyoid position and suprahyoid muscle length: implication for swallowing biomechanics. *Philosophical Transactions of Royal Society B* **378**, 20220552 (2023) (doi.org/10.1098/rstb.2022.0552).
36. Li, P., Sellers, K. C., Orsbon, C. P., Laurence-Chasen, J. D., Gumidyala, R., Yuan, M., Huerta, G., Lever, T. E., Gidmark, N. J., Luo, Z.-X. & Ross, C. F. Diverse tongue base retraction strategies drive bolus propulsion during mammalian swallowing. *Integrative and Comparative Biology* **65**, 1416–1436 (2025) (<https://doi.org/10.1093/icb/icaf016>).
37. Mayerl, C. J. & German, R. Z. Evolution, diversification and function of the maternal–infant dyad in mammalian feeding. *Philosophical Transactions of the Royal Society B: Biological Sciences* **378**, 20220554(2023).
38. Hiiemae, K. M. & Crompton A. W. Mastication, food transport, and swallowing. In, *Functional Vertebrate Morphology* (eds M. Hildebrand, D. M. Bramble, K. F. Liem, & Wake, D. B.) 262–290 (Belknap, Cambridge, MA, 1985).
39. Smith, K. K. The evolution of the mammalian pharynx. *Zoological Journal of the Linnean Society* **104**, 313–349 (1992).
40. Lillegraven, J. A. & Krusat, G. Cranio-mandibular anatomy of *Haldanodon exspectatus* (Docodontia; 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 (1991).
41. Martinelli, A. G. & Rougier, G. W. On *Chalimnia musteloides* (Eucynodontia: Trithelodontidae) from the Late Triassic of Argentina, and a phylogeny of Ictidosauria. *Journal of Vertebrate Paleontology* **27**, 442–460 (2007).
42. Crompton, A. W., Musinsky, C., Bonaparte, J. F., Bhullar B.-A. & Owerkowicz, T. Evolution of the mammalian fauces region and the origin of suckling. *Published by Digital Access to Scholarship at Harvard* [DASH.HARVARD.EDU], (2018) (<https://nrs.harvard.edu/URN-3:HUL.INSTREPOS:37364482>).
43. Luo, Z.-X., Zhou, C.-F., Li, P. & Neander, A. I. Cranial and middle ear structures of Early Cretaceous mammal *Origolestes* (Spalacotherioidea, Trechnotheria, Mammalia). *Palaeobiodiversity and Palaeoenvironments* **105**, 883–915 (2025) (<https://doi.org/10.1007/s12549-025-00683-0>).
44. Kielan-Jaworowska, Z. Skull structure and affinities of the Multituberculata. *Palaeontologia Polonica* **25**, 5–41 (1971).
45. Wible, J. R. & Rougier, G. W. Cranial anatomy of *Kryptobaatar dashzevegi* (Multituberculata, Mammalia) from the Mongolian Late Cretaceous, and its bearing on the evolution of mammalian characters. *Bulletin of American Museum of Natural History* **247**, 1–124 (2000). ([doi:10.1206/0003-0090](https://doi.org/10.1206/0003-0090))
46. Barghusen, H. R. On the evolutionary origin of the therian Tensor Veli Palatini and Tensor Tympani muscles. In *The Ecology and Biology of Mammal-like Reptiles* (eds Hotton III, N., MacLean, P. D., Roth, J. J., & Roth, E. C.) 253–262 (Smithsonian Institution Press, 1986).
47. Diogo, R. & Powell, V. The origin and evolution of mammalian head muscles with special emphasis on the facial myology of primates and modern humans. In, *Heads, Jaws, and Muscles, Fascinating Life Sciences* (eds Ziermann, J. M., Diaz, R. E., Jr, & Diogo, R.) 253–293. (Springer Nature Switzerland AG, 2012).
48. Gambaryan, P. P., Aristov, A. A., Dixon, J. M. & Zubitsova, G. Y. Peculiarities of the hind limb musculature in monotremes: an anatomical description and functional approach. *Russian Journal of Theriology* **1**, 1–36 (2002).
49. Howell, A. B. *Aquatic Mammals*. (Charles C. Thomas, 1930).

50. Koretsky, I. A., Barnes, L. G. & Rahmat, S. J. Re-evaluation of morphological characters questions current views of pinniped origins. *Vestnik zoologii* **50**(4), 327–354 (2016).
51. Fish, F. E., Rybczynski N., Lauder, G. V. & Duff, C. M. The role of the tail or lack thereof in the evolution of tetrapod aquatic propulsion. *Integrative and Comparative Biology* **61**, 398–413 (2021). (doi:10.1093/icb/icab021).
52. Thewissen, J. G. M. & Fish, F. E. Locomotor evolution in the earliest cetaceans: functional model, modern analogues, and paleontological evidence. *Paleobiology* **23**, 482–490 (1997).
53. Sennikov, A. G. Some morphofunctional features of the tail of early archosaurs related to swimming adaptations. *Paleontological Journal* **57**, 432–451 (2023).
54. Kielan-Jaworowska, Z. & Gambaryan, P. P. Postcranial anatomy and habits of Asian multituberculate mammals. *Fossils and Strata* **36**, 1–92 (1994).
55. Rose, K. D. & von Koenigswald, W. An exceptionally complete skeleton of *Palaeosinopa* (Mammalia, Cimolesta, Pantolestidae) from the Green River formation, and other postcranial elements of the Pantolestidae from the Eocene of Wyoming (USA). *Palaeontographica A* **273**(3–6), 55–96 (2005).
56. Hand, S. J., Wilson, L. A. B., López-Aguirre, C., Houssaye, A., Archer, M., Bevitt, J. J., Evans, A. R., Halim, A. Y., Hung, T. & Beck, R. M. D. Bone microstructure supports a Mesozoic origin for an amphibious lifestyle in monotremes (Mammalia). *Proceedings of the National Academy of Sciences U.S.A.* **122**, e2413569122 (2025)
57. Phillips, M. J., Bennett, T. H. & Lee, M. S. Y. Molecules, morphology, and ecology indicate a recent, amphibious ancestry for echidnas. *Proceedings of National Academy of Sciences U.S.A.* **106**, 17089–17094 (2009).
58. Hood, G. A. *Semi-aquatic Mammals: Ecology and Biology*. (Johns Hopkins University Press, 2020).
59. Rybczynski N. Castorid phylogenetics: implications for the evolution of swimming and tree-exploitation in beavers. *Journal of Mammalian Evolution* **14**, 1–35 (2007) (DOI 10.1007/s10914-006-9017-3).
60. Law, C. J., Slater, G. J. & Mehta R. S. Lineage diversity and size disparity in Musteloidea: testing patterns of adaptive radiation using molecular and fossil-based methods. *Systematic Biology* **67**, 127–144 (2018).

Methods References

61. Butler, P. M. An alternative hypothesis on the origin of docodont molar teeth. *Journal of Vertebrate Paleontology* **17**, 435–439 (1997).
62. Sigogneau-Russell D. & Godefroit P. A primitive docodont (Mammalia) from the Upper Triassic of France and the possible therian affinities of the order. *Comptes Rendus de l'Académie des Sciences*, **324**, 135–140 (1997).
63. Brinkkötter, J. J. *Molar dentition of the docodontan Haldanodon (Mammaliaformes) as functional analog to tribosphenic teeth*. (Doctoral dissertation, Rheinische Friedrich-Wilhelms-Universität Bonn, 2018) (<https://nbn-resolving.org/urn:nbn:de:hbz:5n-54872>)
64. Averianov, A. O., Lopatin, A. V., Krasnolutskii, S. A. & Ivantsov, S. V. New docodontans from the Middle Jurassic of Siberia and reanalysis of Docodonta interrelationships. *Proceedings of the Zoological Institute of the Russian Academy of Sciences* **314**, 121–148 (2010).
65. Panciroli, E., Benson, R.B.J., & Luo, Z.-X. The mandible and dentition of *Borealestes serendipitus* (Docodonta) from the Middle Jurassic of Skye, Scotland. *Journal of Vertebrate Paleontology* **39**, e1621884 (2019).

66. Panciroli, E., Benson, R.B.J., Fernandez, V., Butler, R.J., Fraser, N.C., Luo, Z.-X., & Walsh, S.L. New species of mammaliaform and the cranium of *Borealestes* (Mammaliaformes: Docodonta) from the Middle Jurassic of the British Isles. *Zoological Journal of Linnean Society* **192**, 1323–1362 (2021).
67. Averianov, A.O., Lopatin, A.V., & Leshchinskiy, S.V. New interpretation of dentition in Early Cretaceous docodontan *Sibirotherium* based on microcomputed tomography. *Journal of Mammalian Evolution* **30**, 811–817. <https://doi.org/10.1007/s10914-023-09682-4> (2023).
68. Swofford, D. L. *PAUP* Phylogenetic analysis using parsimony (* and other methods)*, 459 4.0b10a. (Sinauer Associates, 2003).
69. Goloboff, P.A., Catalano, S.A., TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* **32**, 221e238 (2016).
70. Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A., & J. P. Huelsenbeck. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**, 539–542 (2012).

Additional References in Supplementary Information

71. Rowe, T. B. Definition, diagnosis, and origin of Mammalia. *Journal of Vertebrate Paleontology* **8**, 241–264 (1988).
72. Kretzoi, M. On Docodonta, a new order of Jurassic mammals. *Annales Historico-Naturales Musei Nationalis Hungarici* **39**, 108–111 (1946).
73. Hu, Y.-M. Postcranial morphology of *Repenomamus* (Eutriconodonta, Mammalia): implications for the higher-level phylogeny of mammals. *PhD thesis, The City University of New York*, pp. 1–405 (available from ProQuest.Com, 2006).
74. Martin, T., Averianov, A. O., and Pfretzschner, H.U. Mammals from the Late Jurassic Qigu Formation in the southern Junggar Basin, Xinjiang, Northwest China. *Palaeobiodiversity and Palaeoenvironments* **90**, 295–319 (2010).
75. Ren, D., Gao, K.-Q., Guo, Z. and S.-A. Ji, Stratigraphic division of the Jurassic in the Daohugou area, Ningcheng, Inner Mongolia. *Geological Bulletin of China* **2**, 584–588 (2002).
76. Huang, D. Y. Jurassic integrative stratigraphy and timescale of China. *Science China Earth Science* **62**, 223–255 (2019).
77. Huang, D.-Y., Cai, C.-Y., Jia, J.-J., Su, W. T., and Liao, H.-Y. Fossil record of Daohugou fossiliferous beds and its bottom conglomerate layer. *Acta Palaeontologica Sinica* **54**, 351–357 (2015).
78. Wang, S., Hethke, M., Wang, B., Tian, Q., Yang, Z, and Jiang, B. High-resolution taphonomic and palaeoecological analyses of the Jurassic Yanliao Biota of the Daohugou area, northeastern China. *Palaeogeograph, Palaeoclimatology and Palaeoecology* **530**, 200–216 (2019).
79. Zhou, C.-F., Wu, S., Martin, T. and Luo, Z.-X. A Jurassic mammaliaform and the earliest mammalian evolutionary adaptations. *Nature* **500**, 163–168. (2013) (doi:10.1038/nature12429).
80. Xu, X., Zhou, Z.-H., Sullivan, C., Wang, Y., and Ren, D. An updated review of the Middle–Late Jurassic Yanliao Biota: Chronology, taphonomy, paleontology and paleoecology. *Acta Geologica Sinica* **90**, 2229–2243 (2016) ([doi:10.1111/1755-6724.13033](https://doi.org/10.1111/1755-6724.13033))
- 81 Liu, Y.-Q., Liu, S., Ji, Z., Yang, U. Pb zircon age for the Daohugou Biota at Ning-Cheng of Inner Mongolia and comments on related issues. *Chinese Science Bulletin* **51**, 2634–2644 (2006). ([doi:10.1007/s11434-006-2165-2](https://doi.org/10.1007/s11434-006-2165-2))

82. Liu Y.-Q., Kuang, H. W., Jiang, X. J., Peng, N., Xu, H. and Sun, H. Y. Timing of the earliest known feathered dinosaurs and transitional pterosaurs older than the Jehol Biota. *Palaeogeography, Palaeoclimatology, Palaeoecology* **323**, 1–12 (2012).
83. Chang, S.-C., Zhang, H., Hemming, S. R., Mesko, G. T., and F. Yan. ⁴⁰Ar/³⁹Ar age constraints on the Haifanggou and Lanqi formations: When did the first flowers bloom? *Geological Society London Special Publications* **378**, 277–284 (2014). (doi:10.1144/SP378.1)
84. Meng, J. Hu, Y., Wang, Y., Wang, X., and Li, C. A Mesozoic gliding mammal from northeastern China. *Nature* **444**, 889–893 (2006).
85. Zheng, X., Bi, S., Wang, X. & Meng, J. A new arboreal haramiyid shows the diversity of crown mammals in the Jurassic period. *Nature* **500**, 199–202 (2013).
86. Martin, T. and Schultz, J. A. Deciduous dentition, tooth replacement, and mandibular growth in the Late Jurassic docodontan *Haldanodon expectatus* (Mammaliaformes). *Journal of Mammalian Evolution* **30**, 507–531 (2023). (<https://doi.org/10.1007/s10914-023-09668-2>)
87. Parrington, F. R. On the Upper Triassic mammals. *Philosophical Transactions of the Royal Society B* **261**, 231–272 (1971).
88. Luo, Z.-X., Bhullar, B.-A. S., Crompton, A.W., Neander, A. I., and Rowe, T. B. Reexamination of the mandibular and dental morphology of the Early Jurassic mammaliaform *Hadrocodium wui*. *Acta Palaeontologica Polonica* **67**, 95–113 (2022). (doi.org/10.4202/app.00949.2021)
89. Luo, Z.-X. Meng, Q.-J., Liu, D., Y.-G. Zhang, and Yuan, C. X. Cruro-pedal structure of the paulchoffatiid multituberculate *Rugosodon eurasiaticus* and evolution of the multituberculate ankle. *Palaeontologia Polonica* **67**, 149–169 (2016). ([dx.doi.org/10.4202/pp.2016.67_149](https://doi.org/10.4202/pp.2016.67_149))
90. Bi, S.-D., Wang, Y.-Q., Guan J., Sheng, X. and Meng, J. Three new Jurassic euharamiyidan species reinforce early divergence of mammals. *Nature* **514**, 579–584 (2014).
91. Luo, Z.-X., Meng, Q.-J., Grossnickle, D. M., Liu, D., Zhang, Y.-G., Neander, A. I., and Q, Ji. New evidence for mammaliaform ear evolution and feeding adaptation in a Jurassic ecosystem. *Nature* **548**, 326–329 (2017) (doi:10.1038/nature23483).
92. Foster JR. Preliminary mass estimates for mammalian genera of the Morrison Formation (Upper Jurassic; North America). *PaleoBios* **28**, 114–122 (2009).
93. Gingerich, P. D. and Smith, B. H. Allometric scaling in the dentition of primates and insectivores. Pp. 257–272. In W. L. Jungers (Editor), *Size and Scaling in Primate Biology* (Plenum Press, New York, 1984).
94. Van Dyck, S., Gynther, I., and Baker, A. (eds.) Field Companion to the Mammals of Australia. (Australia, New Hollander Publishers, 2013).
95. Campione, N. and Evans, D. C. A universal scaling relationship between body mass and proximal limb bone dimensions. *BMC Biology* **10**, 60 (2012) (doi:10.1186/1741-7007-10-60).
96. Huttenlocker, A. K., Grossnickle, D. M., Kirkland, J. I., Schultz, J. A., and Z.-X. Luo Late-surviving stem mammal links the lowermost Cretaceous of North America and Gondwana. *Nature* **558**, 108–112 (2018). ([doi:10.1038/s41586-018-0126-y](https://doi.org/10.1038/s41586-018-0126-y))
97. Kermack, K. A., Lee, A. J., Lees, P. M., and Mussett, F. A new docodont from the Forest Marble. *Zoological Journal of the Linnean Society* **89**, 1–39 (1987). ([doi:10.1111/j.1096-3642.1987.tb01342.x](https://doi.org/10.1111/j.1096-3642.1987.tb01342.x))
98. Pfretzschner, H. U, Martin, T., Maisch, M., Matzke, A., and Sun, G. A new docodont from the Late Jurassic of the Junggar Basin in Northwest China. *Acta Palaeontologica Polonica* **50**, 799–808 (2005).

99. Martin, T., Averianov, A. O., and Pfretzschner, H.U. Mammals from the Late Jurassic Qigu Formation in the southern Junggar Basin, Xinjiang, Northwest China. *Palaeobiodiversity and Palaeoenvironments* **90**, 295–319 (2010).
100. Fox, R. C., and Scott, C. S. First evidence of a venom delivery apparatus in extinct mammals. *Nature* **435**, 1091–1093 (2005).
101. Fox, R. C. Scott, C. S. *Bisonalveus gracilis* n. sp. (Pentacodontidae, Cimolesta): novel dental adaptations and their paleobiological implications in a small Paleocene mammal. *Palaeontographica A* (2020), 67–119 (2020).
102. Cuenca-Bescós and Rofes 2007; Cuenca-Bescós, G. and Rofes, J. First evidence of poisonous shrews with an envenomation apparatus. *Naturwissenschaften* **94**, 113–116 (2007).
103. Furió, M., Agustí, J., Mouskhelishvili, A., Sanisidro, Ó. and Santo-Cubedo, A. The paleobiology of the extinct venomous shrew *Beremendia* (Soricidae, Insectivora, Mammalia) in relation to the geology and paleoenvironment of Dmanisi (Early Pleistocene, Georgia). *Journal of Vertebrate Paleontology* **30**, 928–942 (2010).
104. Folinsbee, K. A., Müller, J. and Reisz, R. R. Canine grooves: morphology, function, and relevance to venom. *Journal of Vertebrate Paleontology* **27**, 547–551 (2007).
105. Turvey, S. T. Evolution of non-homologous venom delivery systems in West Indian insectivores? *Journal of Vertebrate Paleontology* **30**, 1294–1299 (2010).
106. Rofes, J., and Cuenca-Bescós, G. A new genus of red-toothed shrew (Mammalia, Soricidae) from the Early Pleistocene of Gran Dolina (Atapuerca, Burgos, Spain), and a phylogenetic approach to the eurasiatic Soricinae. *Zoological Journal of the Linnean Society* **155**, 904–925 (2009).
107. Dufton, M. J. Venomous mammals. *Pharmacology & Therapeutics* **53**, 199–215 (1992).
108. McDowell S. B. The greater antillean insectivores. *Bulletin of American Museum of Natural History* **115** (3), 115–214 (1958).
109. Nowak, R. M. Walker's Mammals of the World, 6th edition. (Johns Hopkins University Press, 1999).
110. Pournelle, G. H. Classification, biology, and description of the venom apparatus of insectivores of the genera *Solenodon*, *Neomys*, and *Blarina*; pp. 31–42 in W. B. Sutherland, E. E. Buckley, and V. Deulofeu (eds.), *Venomous Animals and Their Venoms*. (Academic Press, 1968).
111. Hotton, N. C., III. The nature and diversity of synapsids: prologue to the origin of mammals. In: Schultze, H.-P. and Trueb, L. (eds.) *Origins of the Higher Groups of Tetrapods: Controversy and Consensus* (Comstock, 1991).
112. Benoit, J., Norton, L. A., Manger, P. R., and Rubidge, B. S. Reappraisal of the envenoming capacity of *Euchambesia mirabilis* (Therapsida, Therocephalia) using μ CT-scanning techniques. *PLoS ONE* **12**(2), e0172047 (2017) (doi:10.1371/journal.pone.0172047)
113. Liu, J., and Abdala, F. The emblematic South African therocephalian *Euchambesia* in China: a new link in the dispersal of late Permian vertebrates across Pangea. *Biology Letters* **18**, 20220222 (2022). (<https://doi.org/10.1098/rsbl.2022.0222>)
114. Ligabue-Braun, R., Verli, H., and Carlini, C. R. Venomous mammals: a review. *Toxicon* **59**, 680–695 (2012).
115. Kowalski, K., Marciniak, P. and Rychlik, L. A new, widespread venomous mammal species: hemolytic activity of *Sorex araneus* venom is similar to that of *Neomys fodiens* venom. *Zoological Letters* **Jun 7;8**(1):7 (2022). (<https://doi.org/10.1186/s40851-022-00191-5>)

116. Nekaris, K. A.-I., Moore, R. S., Rode, E. J., and Fry, B. G. Mad, bad and dangerous to know: the biochemistry, ecology and evolution of slow loris venom. *Journal of Venomous Animals and Toxins including Tropical Diseases* **19**, 2.1 (2013) (<http://www.jvat.org/content/19/1/21>)
117. Marín, L., S. Moreno, & F. Moreno. A systematic literature review and case report of bilateral two-rooted mandibular deciduous canines and their usefulness in forensic identification. *Dental Anthropology*, **33**, 23-29 (2020)
118. Kanadasamy, S., Balakrishnan, N. and Chnadraseskar M. A three-rooted permanent maxillary canine: a rare anatomical variant. *Journal of Pharmacy and Bioallied Sciences* **2019**, **11**(Suppl **2**), S485–S487 (2013). doi: [10.4103/JPBS.JPBS_292_18](https://doi.org/10.4103/JPBS.JPBS_292_18) (2019)
119. Gingerich, P. D. Molar occlusion and function in the Jurassic mammal *Docodon*. *Journal of Mammalogy* **254**, 1008–1013 (1973).
120. Berkovitz, B. and Shellis, P. *The Teeth of Mammalian Vertebrates*. (Elsevier A, 2018)
121. Rougier, G. W., Garrido, A., Gaetano, L., Puerta, P. F., Corbitt, C., and Novacek, H. J. First Jurassic triconodont from South America. *American Museum Novitates* **3580**, 1–17 (2007).
122. Gaetano L. C. and Rougier, G. W. New materials of *Argentoconodon fariassorum* (Mammaliaformes, Triconodontidae) from the Jurassic of Argentina and its bearing on triconodont phylogeny. *Journal of Vertebrate Paleontology* **31**(4), 829–843 (2012).
123. Gao, C.-L., Wilson, G. P., Luo, Z. X., Maga, A. M., Meng, Q. J., and Wang, X.-R. A new mammal skull from the Lower Cretaceous of China with implications for the evolution of obtuse angled molars and amphilestid eutriconodonts. *Proceedings of Royal Society (London) Series B (Biological Sciences)* **277**, 237–246 (2009). (doi:10.1098/rspb.2009.1014)
124. Signogneau-Russell 1995 Sigogneau-Russell, D. Two possibly aquatic triconodont mammals from the Early Cretaceous of Morocco. *Acta Palaeontologica Polonica* **40**, 149–162 (1995).
125. Sprague, J. M. The hyoid region of placental mammals with especial reference to the bats. *American Journal of Anatomy* **72**, 385–472 (1943). ([doi:10.1002/aja.1000720304](https://doi.org/10.1002/aja.1000720304))
126. Sprague, J. M. The hyoid region in the Insectivora. *American Journal of Anatomy* **74**, 175–216 (1944). ([doi:10.1002/aja.1000740203](https://doi.org/10.1002/aja.1000740203))
127. Gasc, J.-P. (1967) Squelette hyobranchial. In: Grassé, P. P. (ed.) *Traité de Zoologie Anatomie, Systématique, Biologie*, **Tome XVI, Fascicle I**, 550–583; 1103–1106. Masson.
128. Edmonds, C. E., Catchpole, E. A., Gould, F. D. H., Bond, L. E., Stricklen, B. M., German, R. Z., & Mayerl, C. J. Preterm birth impacts the timing and excursion of oropharyngeal structures during infant feeding. *Integrative Organismal Biology*, **2**(1), obaa028 (2020).
129. Weissengruber, G. E., Forstenpointner, G., Peters, G., Kübber-Heiss, A., and Fitch, W. T. Hyoid apparatus and pharynx in the lion (*Panthera leo*), jaguar (*Panthera onca*), tiger (*Panthera tigris*), cheetah (*Acinonyx jubatus*) and domestic cat (*Felis silvestris* f. *catus*). *Journal of Anatomy* **201**(3):195–209 (2002). ([doi:10.1046/j.1469-7580.2002.00088.x](https://doi.org/10.1046/j.1469-7580.2002.00088.x))
130. Mao, F.-Y., Liu, C., Chase, M. H., Smith, A., and Meng, J. Exploring ancestral phenotypes and evolutionary development of the mammalian middle ear based on Early Cretaceous Jehol mammals. *National Science Review* **8**(5), nwaa188 (2020). (doi.org/10.1093/nsr/nwaa188)
131. Kuhn, H.-J. Die Entwicklung und Morphologie des Schädels von *Tachyglossus aculeatus*. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **528**, 1–192 (1971).

132. Wheelhouse, J., Vogelnest, L. and Nicoll, R. G. Skeletal radiographic anatomy of echidnas: insights into unusual mammals. *Journal of Mammalogy* **103**(4), 920–931 (2022). (<https://doi.org/10.1093/jmammal/gyab138>)
133. Vogelnest, L. and Graeme, A. *Radiology of Australian Mammals*. (CSIRO Publishing 2015).
134. Ruf, I., Luo, Z.-X. and Martin, T. Re-investigation of the basicranium of *Haldanodon expectatus* (Docodonta, Mammaliaformes). *Journal of Vertebrate Paleontology* **33**, 382–400 (2013).
135. Sues, H.-D. The skull and dentition of two tritylodontid synapsids from the Lower Jurassic of western North America. *Bulletin of the Museum of Comparative Zoology* **151**, 217–268 (1986).
136. Bonaparte, J. F., Martinelli, A. G., and Schultz, C. L. New information on *Brasilodon* and *Brasilitherium* (Cynodontia, Probainognathia) from the Late Triassic of southern Brazil. *Revista Brasileira de Paleontologia* **8**, 25–46 (2005).
137. Crompton, A. W., and Z.-X. Luo. The relationships of the Liassic mammals *Sinoconodon*, *Morganucodon oehleri* and *Dinnetherium*. Pp. 30-44. In: *Mammal Phylogeny (Volume 1)* (F. S. Szalay, M. J. Novacek, and M. C. McKenna , eds.) (Springer-Verlag, New York (1993)).
138. Kermack, K. A., Mussett, F., and Rigney, H. W.. The skull of *Morganucodon*. *Zoological Journal of the Linnean Society* **71**, 1–158 (1981).
139. Hopson, J. A. and Barghusen, H. An analysis of therapsid relationships. In: Hotton, N. III, MacLean, P. D., Roth, J. J., and Roth, E. C. (eds.) *The Ecology and Biology of Mammal-like Reptiles*, pp. 83–106. (Smithsonian Institution Press, 1986).
140. Hopson, J. A. The mammal-like reptiles: A study of transitional fossils. *The American Biology Teacher* **49**(1), 16–26 (1987).
141. Luo, Z.-X., Crompton, A. W., and Sun, A.-L. A new mammal from the Early Jurassic and evolution of mammalian characteristics. *Science* **292**, 1535–1540 (2001).
142. Huttenlocker, A. K., Grossnickle, D. M., Kirkland, J. I., Schultz, J. A., and Z.-X. Luo Late-surviving stem mammal links the lowermost Cretaceous of North America and Gondwana. *Nature* **558**, 108–112 (2018). ([doi:10.1038/s41586-018-0126-y](https://doi.org/10.1038/s41586-018-0126-y))
143. Wang, Y.-Q., Hu, Y.-M., Meng, J., and Li, C.-K. An ossified Meckel's cartilage in two Cretaceous mammals and origin of the mammalian middle ear. *Science* **294**, 357–361 (2001).
144. Martin, T., Marugán-Lobón, J., Vullo, R., Martín-Abad, H., Luo, Z.-X., and Buscalioni, A. D. A Cretaceous eutriconodont and integument evolution of early mammals. *Nature* **526**(7573), 380–384 (2015).
145. Li, C.K., Wang ,Y.Q., Hu, Y.M. and Meng, J. A new species of *Gobiconodon* (Triconodonta, Mammalia) and its implication for the age of Jehol Biota. *Chinese Science Bulletin* **48**(11), 1129-1134 (2003).
146. Hahn, G. Neue Beobachtungen zum Schädel- und Gebiss-Bau der Paulchoffatiidae (Multituberculata, Ober-Jura). *Palaeovertebrata* **17**, 155–196 (1987).
147. Rougier, G. W., Wible J. R., Hopson, J. A. Reconstruction of the cranial vessels in the Early Cretaceous mammal *Vincelestes neuquenianus*: implications for the evolution of the mammalian cranial vascular system. *Journal of Vertebrate Paleontology* **12**(2), 188–216 (1992).
148. Rougier, G. W. *Vincelestes neuquenianus Bonaparte (Mammalia, Theria) un primitivo mamífero del Cretácico Inferior de la Cuenca Neuquina*. 720 pp. Ph. D. dissertation, (Universidad Nacional de Buenos Aires, Buenos Aires, 1993).
149. Rougier, G. W, Martinelli, A. G, and Forasiepi, A. M. *Mesozoic Mammals from South America and Their Forerunners*. (Springer, 2021).

150. Krause, D. W., Hoffmann, S., Wible, J. R., Kirk, E. C., Schultz, J. A., von Koenigswald, W., Groenke, W. J. R., Rossie, J. B., O'Connor, P. M., Seiffert, E. R., Dumont, E. R., Holloway, W. L., Rogers, R. R., Rahantarisoa, L. J., Kemp, A. D., and Andriamialison, H. First cranial remains of a gondwanatherian mammal reveal remarkable mosaicism. *Nature* **515**, 512–517 (2014).. ([doi:10.1038/nature13922](https://doi.org/10.1038/nature13922))
151. Krause D. W, Hoffmann, S., Lyson, T. R., Dougan, L. G, Petermann, H., Tecza, A., Chester, S. G. B, and Miller, I. M. New skull material of *Taeniolabis taoensis* (Multituberculata, Taeniolabididae) from the Early Paleocene (Danian) of the Denver Basin, Colorado. *Journal of Mammalian Evolution* **28**, 1083–1143 (2021).
152. Miao, D. Skull morphology of *Lambdopsalis bulla* (Mammalia, Multituberculata). *Contributions to Geology, University of Wyoming, Special Paper* **4**, 1–104 (1988).
153. Kielan-Jaworowska, Z., Hurum, J. H., and Lopatin, A.V. Skull structure in *Catopsbaatar* and the zygomatic ridges in multituberculate mammals. *Acta Palaeontologica Polonica* **50**, 487–512 (2005).
154. Hopson, J. A. and Kitching, J. W. A probainognathian cynodont from South Africa and the phylogeny of nonmammalian cynodonts. In: Jenkins, F. A. Jr., Owerkowicz, and Shapiro, M. D. (eds.) *Studies in Organismic and Evolutionary Biology in Honor of A. W. Crompton. Bulletin of the Museum of Comparative Zoology* **156**, 5–35 (2001).
155. Gambaryan, P. P. and Kielan-Jaworowska, Z. Masticatory musculature of Asian taeniolabidid multituberculate mammals. *Acta Palaeontologica Polonica* **40(1)**, 45–108 (1995).
156. Harrington, R. M. pterygopharyngeus and its relation to m. palatopharyngeus. *The Laryngoscope* **55**, 499–508 (1945).
157. Tsumori, N., Abe, S., Agematsu, H., Hashimoto, M. and Ide, Y. Morphologic characteristics of the superior pharyngeal constrictor muscle in relation to the function during swallowing. *Dysphagia* **22**, 122–129 (2007).
158. Sumida et al., Sumida, K., Ando, K., Seki, S., Yamashita, K., Fujimura, A., Baba, O., and Kitamura, S. Anatomical status of the human palatopharyngeal sphincter and its functional implications. *Surgical and Radiologic Anatomy* **39**, 1191–1201 (2017).
159. Reiss, K. Z. Myology of the feeding apparatus of myrmecophagid anteaters (Xenarthra: Myrmecophagidae). *Journal of Mammalian Evolution* **4(2)**, 87–117 (2017).
160. Yoshida, M., Kitoh, J. Yanagita, N. Structure of the palate and pharynx in the house musk shrew (*Suncus murinus*). *Cells Tissues Organs* **171**, 286–292 (2002)
161. Tachimura T, Okuno K, Ojima M, and Nohara K. Change in levator veli palatini muscle activity in relation to swallowing volume during the transition from the oral phase to pharyngeal phase. *Dysphagia* **21(1)**, 7–13 (2006). ([doi:10.1007/s00455-005-9005-4](https://doi.org/10.1007/s00455-005-9005-4))
162. Parrington F. R. and Westoll, T. S. On the evolution of the mammalian palate. *Philosophical Transactions of the Royal Society of London B* **571(230)**, 305–355 (1940).
163. Crompton, A. W. Masticatory function in nonmammalian cynodonts and early mammals. In J. J. Thomason (ed.), *Functional Morphology in Vertebrate Paleontology*, 55–75. (Cambridge University Press, Cambridge, 1995).
164. Fourie, S. The cranial morphology of *Thrinaxodon liorhinus* Seeley. *Annals of the South African Museum* **65**, 337–400 (1974).
165. Luo, Z.-X., Kielan-Jaworowska, Z. and Cifelli, R. L. In quest for a phylogeny of Mesozoic mammals. *Acta Palaeontologica Polonica* **47**, 1-78 (2002).
166. Diogo, R., Powell, V. The Origin and Evolution of Mammalian Head Muscles with Special Emphasis on the Facial Myology of Primates and Modern Humans. In: Ziermann, J., Diaz Jr,

- R., Diogo, R. (eds) *Heads, Jaws, and Muscles*. (Fascinating Life Sciences. Springer, Cham, 2019). https://doi.org/10.1007/978-3-319-93560-7_11.
167. Standring, S. Gray's Anatomy – The Anatomical Basis of Clinical Practices (40th Edition). (Churchill Livingstone Elsevier, 2008).
 168. Tillmann, B. N. Atlas of Human Anatomy (Clinical Edition). (New York: Mud Puddle Books 2012).
 169. McWhorter, A. J., Rowley, J. A., Eisele, D. W., Smith, P. L and Schwartz, A. R. The effect of tensor veli palatine stimulation on upper airway patency. *Archive of Otolaryngology Head and Neck Surgery* **125(9)**, 937–940 (1999) (DOI: 10.1001/ARCHTOL. 125.9.937).
 170. Takada, Y. Izumi M. and Gotoh, K. Comparative anatomy of the hyoid apparatus of carnivores. *Mammal Study* **34**, 213–218 (2009)
 171. Adachi, T., Kogo, M., Lida, S., Hamaguchi, M., and Matsuya, T. Measurement of velopharyngeal movements induced by isolated stimulation of levator veli palatini and pharyngeal constrictor muscles. *Journal of Dental Research* **76(11)**, 1745-50 (1997). doi: 10.1177/00220345970760110501. PMID: 9372791.
 172. Ziermann, J. M., Diaz, R. E., Jr., and Diogo, R. *Heads, Jaws, and Muscles - Anatomical, Functional, and Developmental Diversity in Chordate Evolution*. (Springer Nature Switzerland, 2019).
 173. Mayerl, C.J., Steer, K.E., Chava, A.M., Bond, L.E., Edmonds, C.E., Gould, F.D.H., Stricklen, B.M., Hieronymous, T.L., and German, R.Z. The contractile patterns, anatomy and physiology of the hyoid musculature change longitudinally through infancy. *Proceedings of Royal Society, Series B* **288**, 20210052 (2021). <https://doi.org/10.1098/rspb.2021.0052>
 174. Panciroli, E., Benson, R. B. J., Fernandez, V., Humpage, M., Martín-Serra, A., Walsh, S., Luo, Z.-X., and Fraser, N. C. Postcrania of *Borealestes* (Mammaliformes, Docodonts) and the emergence of ecomorphological diversity in early mammals. *Palaeontology* **65(1)**: e12577 (2022). (<https://doi.org/10.1111/pala.12577>)
 175. Gambaryan, P. P., Kuznetsov, A. N., Panyutine, A. A., and Gerasimov, S. V. Shoulder girdle and forelimb myology of extant monotremes. *Russian Journal of Theriology* **12(1)**, 1-56 (2015).
 176. Regnault, S., Fahn-Lai, P., Norris, R. M., and Pierce, S. E. Shoulder muscle architecture in the echidna (Monotremata: *Tachyglossus aculeatus*) indicates conserved functional properties. *Journal of Mammalian Evolution* **27**, 591–603 (2020).
 177. Hildebrand, M. Digging of quadrupeds. In: Hildebrand, M. Bramble, D. M., Liem, K. F., and Wake, D. B. (eds.) *Functional Vertebrate Morphology*, pp 89–109 (Belknap, 1985).
 178. Martin, T. Mammalian postcranial bones from the Late Jurassic of Portugal and their implications for forelimb evolution. *Journal of Vertebrate Paleontology* **33**, 1432–1441 (2013).
 179. Samuels, J. X., B. Van Valkenburgh. Skeletal indicators of locomotor adaptations in living and extinct rodents. *Journal of Morphology* **269**, 1387-1411 (2008).
 180. Chen, M. and Wilson, G. P. A multivariate approach to infer locomotor modes in Mesozoic mammals. *Paleobiology* **41**, 280–312 (2015). ([doi:10.1017/pab.2014.14](https://doi.org/10.1017/pab.2014.14))
 181. Martin, T. Early mammalian evolutionary experiments. *Science* **311**, 1109–1110 (2006).
 182. Hopson, J. A. Patterns of evolution in the manus and pes of non-mammalian therapsids. *Journal of Vertebrate Paleontology* **15(3)**, 615–639 (1995).
 183. Bi, S.-D., Wang, Y.-Q., Guan J., Sheng, X. and Meng, J. Three new Jurassic euharamiyidan species reinforce early divergence of mammals. *Nature* **514**, 579–584 (2014).
 184. Macleod, N. and Rose, K. D. Inferring locomotor behavior in Paleogene mammals via eigenshape analysis. *American Journal of Science* **293(A)**, 300–355 (1993).

185. Maiolino et al. 2023. Maiolino, S. A., Chester, S. G. B., Boyer, D. M., and Bloch, J. I. Functional morphology of plesiadapiform distal phalanges and implications for the evolution of arboreality in Paleogene euarchontans. *Journal of Mammalian Evolution* **30**, 1107–1153 (2023).
186. Organ, J. M. Structure and function of platyrrhine caudal vertebrae. *Anatomical Record*, **293**, 730–745 (2010). ([doi:10.1002/ar.21129](https://doi.org/10.1002/ar.21129) [Medline](#))
187. Russo, G. A. Postsacral vertebral morphology in relation to tail length among primates and other mammals. *Anatomical Record* **298**, 354–375 (2015). ([doi:10.1002/ar.23004](https://doi.org/10.1002/ar.23004))
188. Hofmann, R. Lehmann, T. Warren, D. L., and Ruf, I. the squirrel is in the detail: Anatomy and morphometry of the tail in Sciuromorpha (Rodentia, Mammalia). *Journal of Morphology* **282**, 1659–1682 (2021).
189. Warburton, N. M., Malric, A., Yakovleff, M., Leonard, V., and Cailleau, C. Hind limb myology of the southern brown bandicoot (*Isodon obesulus*) and greater bilby (*Macrotis lagotis*) (Marsupialia: Peramelemorphia). *Australian Journal of Zoology* **63**, 147–162 (2015). (<http://dx.doi.org/10.1071/ZO14087>)
190. Zavodszky, A. M. and Russo, G. A. Comparative and functional morphology of chevron bones among mammals. *Journal of Mammalogy* **101**(2), 403–416 (2020). ([doi:10.1093/jmammal/gyaa010](https://doi.org/10.1093/jmammal/gyaa010))
191. Dawson, R., Milne, N. and Warburton, N. M. Muscular anatomy of the tail of the western grey kangaroo, *Macropus fuliginosus*. *Australian Journal of Zoology* **62**, 166–174 (2014). (<http://dx.doi.org/10.1071/ZO13085>)
192. Argot, C. Functional-adaptive anatomy of the axial skeleton of some extant marsupials and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. *Journal of Morphology* **255**, 279–300 (2003).
193. Ercoli et al. 2013 Ercoli, M. D., Echarri, S. Busker, F. Álvarez, A., Morales, M. M. and Turazzini, G. F. The Functional and phylogenetic implications of the myology of the lumbar region, tail, and hind limbs of the lesser grison (*Galictis cuja*). *Journal of Mammalian Evolution* **20**, 309–336 (2013) ([doi:10.1007/s10914-012-9219-9](https://doi.org/10.1007/s10914-012-9219-9))
194. Gregory, W. K. The monotremes and the palimpsest theory. *Bulletin of the American Museum of Natural History* **88**, 1–52 (1947).
195. Gregory 1951 Gregory, W. K. *Evolution Emerging* (Volumes 1 and 2). (Macmillan, 1951).
196. Lessertisseur, J. and Saban, R. Squelette axial, In: Grassé, P. P. (ed.), *Traité de Zoologie. Tome XVI (Fascicule I). Mammifères: Teguments et Squelette*. pp. 586–706 (Masson, 1967a).
197. Jenkins, F. A., Jr. and Parrington, F. R. The postcranial skeleton of the Triassic mammals *Eozostrodon*, *Megazostrodon* and *Erythrotherium*. *Philosophical Transactions of the Royal Society B* **273**, 387–431 (1976).
198. Kühne, W. G. The Liassic Therapsid *Oligokyphus*. (British Museum [Natural History], London, 1956).
199. Sues, H.-D. and Jenkins, F. A., Jr., The postcranial skeleton of *Kayentatherium wellsi* from the Lower Jurassic Kayenta Formation of Arizona and the phylogenetic significance of postcranial features in tritylodontid cynodonts. In: M. T. Carrano, R. W. Bloch, T. J. Gaudin, and J. R. Wible (eds.) *Amniote Paleobiology: Perspectives on the Evolution of Mammals, Birds and Reptiles*, pp. 114–152 (University of Chicago Press, 2006).
200. Sullivan, C., Liu, J., Roberts, E. M., Huang, T. D., Yang, C., and Zhong, S. Pelvic morphology of a tritylodontid (Synapsida: Eucynodontia) from the Lower Jurassic of China, and some functional and phylogenetic implications. *Comptes Rendus Palevol* **12**, 505–518 (2013).

201. Guignard, M. L., Martinelli, A. G., and Soares, M. B. The postcranial anatomy of *Brasilodon quadrangularis* and the acquisition of mammaliaform traits among non-mammaliaform cynodonts. *PLoS ONE* **14**(5), e0216672 (2019). (doi.org/10.1371/journal.pone.0216672)
202. Luo, Z.-X., and Q. Ji. New study on dental and skeletal features of the Cretaceous mammal *Zhangheotherium*. *Journal of Mammalian Evolution* **12**, 337–357 (2005).
203. Li, G. and Luo, Z.-X. A Cretaceous symmetrodont therian with some monotreme-like postcranial features. *Nature* **439**, 195–200 (2006).
204. Hu, Y.-M. (2006) Postcranial morphology of *Repenomamus* (Eutriconodonta, Mammalia): implications for the higher-level phylogeny of mammals. *PhD thesis, The City University of New York*, pp. 1–405 (available from ProQuest.Com)
205. Chen, M., Luo, Z.-X. and Wilson, G. P. The postcranial skeleton of *Yanoconodon allini* from the Early Cretaceous of Hebei, China and its implications for locomotor adaptation in eutriconodontan mammals. *Journal of Vertebrate Paleontology* **37**(3), e1315425 (23 pages) (2017) ([doi:10.1080/02724634.2017.1315425](https://doi.org/10.1080/02724634.2017.1315425))
206. Jäger, K. R. K., Luo, Z.-X., and Martin, T. Postcranial skeleton of *Henkelotherium guimarotae* (Cladotheria, Mammalia) and locomotor adaptation. *Journal of Mammalian Evolution* **3**, 349–372 (2019). (<https://doi.org/10.1007/s10914-018-09457-2>)
207. Galliari F. C. and Carlini, A. A. Xenarthran synsacrum morphology and evolution. *Journal of Mammalian Evolution* **26**, 493–504 (2019). (<https://doi.org/10.1007/s10914-018-9442-0>)
208. Hoffmann, S., Hu, Y., and Krause, D. W. Postcranial morphology of *Adalatherium hui* (Mammalia, Gondwanatheria) from the Late Cretaceous of Madagascar. In: Krause, D. W. and Hoffmann, S. (eds.) *Adalatherium hui* (Mammalia, Gondwanatheria) from the Late Cretaceous of Madagascar. *Society of Vertebrate Paleontology Memoir (Journal of Vertebrate Paleontology Supplement)* **21**, 133–213 (2020).
209. Spence, A. P. *Basic Human Anatomy* (Benjamin/Cummings Publishing Company Inc. Redwood City, California, 1990).
210. Crouch, J. E. *Text-Atlas of Cat Anatomy* (Lea & Febiger, 1969).
211. Lessertisseur J, and Saban, R. Squelette appendiculaire. In: Grassé, P. P. (ed.). *Traité de Zoologie XVI* (1), pp. 708–1123 (Masson, 1967b).
212. Hargaden, M. and Singer, L. Chapter 20 – anatomy, physiology, and behavior. In: Suckow, M. A., Stevens, K. A., and Wilson, R. P. (eds.) *The Laboratory Rabbit, Guinea Pig, Hamster, and Other Rodents* pp. 575–602 (American College of Laboratory Animal Medicine, 2012).
213. Walton, D. W. and Walton, G. M. Post-cranial osteology of bats. *Fondren Science Series* **1**(11), **Article 7**, 1–34 (1970).
214. Guignard, M. L., Martinelli, A. G., and Soares, M. B. Reassessment of the postcranial anatomy of *Prozostrodon brasiliensis* and implications for postural evolution of non-mammaliaform cynodonts. *Journal of Vertebrate Paleontology* **38**(3), 1–18 (2018).
215. Jenkins, F. A., Jr. The postcranial skeleton of African cynodonts. *Bulletin of the Peabody Museum of Natural History* **36**, 1–216 (1971).
216. Bishop P. J. and Pierce, S. E. Reconstructions of hindlimb musculature in extinct pre-therian synapsids. *Bulletin of the Museum of Comparative Zoology* **163**(9), 417–471 (2024a).
217. Rybczynski, N. Pabst, D, and McLellan, W. Soft-tissue structure in tail of *Castor*: toward inferring tail specialization in extinct, semiaquatic mammals. *Journal of Vertebrate Paleontology* **25**(3 Supplement), 107A–107A (2005).

218. Grassé, P.-P. Ordre des Monotrèmes. In: Grassé, P. P. (ed.) *Traité de Zoologie: Anatomie, Systématique, Biologie*, **Tome XVII**, Mammifères. Les Ordres: Anatomie, Ethologie, Systématique, pp. 47–92. (Masson, 1955).
219. Grassé, P.-P. Ordre des Marsupiaux. In: Grassé, P. P. (ed.) *Traité de Zoologie: Anatomie, Systématique, Biologie*, **Tome XVI**, Mammifères. Les Ordres: Anatomie, Ethologie, Systématique, pp. 93–171. (Masson, 1956).
220. Hickman, G. C. The mammalian tail: A review of functions. *Mammal Review* **9**, 143–157 (1979). ([doi:10.1111/j.1365-2907.1979.tb00252.x](https://doi.org/10.1111/j.1365-2907.1979.tb00252.x))
221. Hori, H., Fukutani, T., Nakane, H., Iino, S., and Nojyo, Y. Participation of ventral and dorsal tail muscles in bending movements of rat tail. *Anatomical Science International* **86**, 194–203 (2011) (DOI 10.1007/s12565-011-0110-1).
222. Thomas, J., Handasyde, K.A., Parrott, M. L., and Temple-Smith, P. The platypus nest: burrow structure and nesting behaviour in captivity. *Australian Journal of Zoology* **65** (6), 347–356 (2017) <https://doi.org/10.1071/ZO18007>.
223. Thomas, J., Parrott, M. L., Handasyde, K.A., and Temple-Smith, P. Burrow use by juvenile platypuses (*Ornithorhynchus anatinus*) in their natal home range. *Journal of Mammalogy* **100**(4), 1182–1190 (2019).
224. Krause, D. W. and Jenkins, F. A. (1983) The postcranial skeleton of North American multituberculates. *Bulletin of the Museum of Comparative Zoology* 150:199–246.
225. Yuan, C.-X., Ji, Q., Meng, Q.-J. and Z.-X. Luo. Earliest evolution of multituberculate mammals revealed by a new Jurassic fossil. *Science* **341**, 779–783 (2013).
226. Ji, Q., Z.-X. Luo, X.-L. Zhang, C.-X. Yuan, and L. Xu Evolutionary development of the middle ear in Mesozoic therian mammals. *Science*. **326**, 278–231. (2009) (DOI:10.1126/science.1187501).
227. Chen, M. and Luo, Z.-X. Postcranial skeleton of the Cretaceous mammal *Akidolestes cifellii* and its locomotor adaptations. *Journal of Mammalian Evolution* **20**, 159–189 (2013) (doi: 10.1007/s10914-012-9199-9)
228. Bishop, P. J. and Pierce, S. E. Late acquisition of erect hindlimb posture and function in the forerunners of therian mammals. *Science Advances* **10**, eadr2722 (2024b). ([dx.doi.org/10.1126/sciadv.adr2722](https://doi.org/10.1126/sciadv.adr2722))
229. Szalay, F. S. *Evolutionary History of the Marsupials and an Analysis of Osteological Characters* (Cambridge University Press, 1994).
230. Hurum, J. H., Luo, Z.-X., and Kielan-Jaworowska, Z. Were mammals originally venomous? *Acta Palaeontologica Polonica* **51**(1), 1–11 (2006).
231. Griffiths M. *The Biology of the Monotremes*. (Academic Press, 1978).
232. Whittington, C. M. K. and Belov, K. Tracing monotreme venom evolution in the genomics era. *Toxins* **6**, 1260–1273 (2014). (doi:10.3390/toxins6041260)
233. Q. Ji, Z.-X. Luo, S.-A. Ji, A Chinese triconodont mammal and mosaic evolution of the mammalian skeleton. *Nature* **398**, 326–330 (1999).
234. Berta, A., Sumich, J. L., and Kovacs, K. M. (2015) Musculoskeletal system and locomotion. Pp. pp. 211–268. In: Berta, A., Sumich, J.L., Kovacs, K.M. (eds.) *Marine Mammals: Evolutionary Biology (Third edition)* (Elsevier, 2015). (<https://dx.doi.org/10.1016/C2011-0-07338-6>)
235. Adam, P. Hindlimb anatomy. Pp. 470–472. In: Würsig, B. Thewissen, J. G. M., and Kovac, K. M. (eds.) *Encyclopedia of Marine Mammals (Third Edition)* (Academic Press, 2018). (<https://www.sciencedirect.com/book/edited-volume/9780128043271/>).

236. Würsig, B., Thewissen, J. G. M., and Kovacs, K. M. (2018) *Encyclopedia of Marine Mammals (3rd Edition)*. Academic Press.
237. Pridmore, P. A. Terrestrial locomotion in monotremes (Mammalia: Monotremata). *Journal of Zoology* **205**, 53–73 (1985).
238. Gambaryan, P. P. and Kuznetsov, A. N. An evolutionary perspective on the walking gait of the long-beaked echidna. *Journal of Zoology* **290**(1), 1–10 (2013). (doi:10.1111/jzo.12014)
239. Jenkins, F. A., Jr. Limb movements in monotremes (*Tachyglossus aculeatus*): a cineradiographic analysis. *Science* **168**, 1473–1475 (1970).
240. Weisbecker, V. and Nilsson, M. Integration, heterochrony, and adaptation in pedal digits of syndactylous marsupials. *BMC Evolutionary Biology* **8**:160 (2008) (doi:10.1186/1471-2148-8-160)
241. Griffiths M. The Platypus. *Scientific American* **258**(5), 84–91 (1988).
242. Augee, M. L., Gooden, B., and Musser, A. *Echidna: Extraordinary Egg-laying Mammal*. (Colingwood, Australia: CSIRO Publishing, 2006).
243. Kielan-Jaworowska, Z. and Hurum, J. H. Limb posture in early mammals: sprawling or parasagittal. *Acta Palaeontologica Polonica* **51**(3), 393–406 (2006).
244. Fish, F. E. Influence of hydrodynamic design and propulsive mode on mammalian swimming energetics. *Australian Journal of Zoology* **42**:79–101 (1993).
245. Fish, F. E. Secondary evolution of aquatic propulsion in higher vertebrates: validation and prospect. *Integrative and Comparative Biology* **56**, 1285–97 (2016).
246. von Koenigswald v. W. Das Skelett eines Pantolestiden (Proteutheria, Mamm.) aus dem Mittleren Eozän von Messel bei Darmstadt. *Paläontologische Zeitschrift* **54**, 267–287 (1980).
247. Pfretzschner, H. U. Muscle reconstruction and aquatic locomotion in the Middle Eocene *Buxolestes piscator* from Messel near Darmstadt. *Kaupia* **3**, 75–87 (1993).
248. Pfretzschner, H. U. *Buxolestes minor* n. sp.—ein neuer Pantolestide (Mammalia, Proteutheria) aus der eozänen Messel-Formation. *Courier Forschungsinstitut Senckenberg* **216**, 19–29 (1999).
249. von Koenigswald W. and Storch, G. *Leptictidium tobieni* n. sp., ein dritter Pseudorhyncocyonide (Proteutheria, Mammalia) aus dem Eozän von Messel. *Courier Forschungsinstitut Senckenberg* **91**, 107–116 (1987).
250. Fish, F. E. Association of propulsive swimming mode with behavior in river otters (*Lutra canadensis*). *Journal of Mammalogy* **75**, 989–97 (1994).
251. Fish, F. E. Secondary evolution of aquatic propulsion in higher vertebrates: validation and prospect. *Integrative and Comparative Biology* **56**, 1285–97 (2016).
252. Fish, F. E. Biomechanics and energetics in aquatic and semiaquatic mammals: platypus to whale. *Physiological and Biochemical Zoology* **73**(6), 683–698 (2000). (<http://dx.doi.org/10.1086/318108>)
253. Mori, K., Suzuki, S., Koyabu, D., Kimura, J., Han, S.-Y., and Endo, H. Comparative functional anatomy of hindlimb muscles and bones with reference to aquatic adaptation of the sea otter. *Journal of Veterinary Medical Science* **77**(5), 571–578 (2015)
254. Sánchez-Villagra, M. R. and Asher, R. J. Cranio-sensory adaptations in small faunivorous semiaquatic mammals, with special reference to olfaction and the trigeminal system. *Mammalia* **66**(1), 93–110 (2022). (doi: [10.1515/mamm.2002.66.1.93](https://doi.org/10.1515/mamm.2002.66.1.93))
255. Miyamae, J. A., Benoit, J., Ruf, I., Sibiya, Z., and Bhullar, B.-A. S. Synapsids and sensitivity: Broad survey of tetrapod trigeminal canal morphology supports and evolutionary trend of

- increasing facial tactile specialization in the mammal lineage. *The Anatomical Record* **2025**, 1–48 (2025). (doi: 10.1002/ar.25604)
256. Crumpton, N. and Thompson, R. S. The holes of moles: osteological correlates of the trigeminal nerve in Talpidae. *Journal of Mammalian Evolution* **20**, 213–225 (2013). (doi: 10.1007/s10914-012-9213-2)
 257. Dunstone, N. Adaptations to the semi-aquatic habit and habitat. In: Dunstone, N. and Gorman, M. L. (eds) *Behaviour and Ecology of Riparian Mammals. Symposia of the Zoological Society (London)* **71**, 1–16 (1998).
 258. Voss, R. S. Systematics and ecology of ichthyomine rodents (Muroidea): Patterns of morphological evolution in a small adaptive radiation. *Bulletin of the American Museum of Natural History* **188**, 259–493 (1988).
 259. Richard, P. B. The sensorial world of the Pyrenean desman, *Galemys pyrenaicus*. *Acta Zoolgica Fennica* **173**, 255–258 (1985).
 260. Sendral, M. and Santos, M. Conservation of a threatened semi-aquatic mammal: Insights from a systematic review on the Pyrenean Desman (*Galemys pyrenaicus*). *Journal for Nature Conservation* **86**, 126923 (2025). <https://doi.org/10.1016/j.jnc.2025.126923>
 261. Muchlinski, M. N. The relationship between the infraorbital foramen, infraorbital nerve, and maxillary mechanoreception: Implications for interpreting the paleoecology of fossil mammals based on infraorbital foramen size. *The Anatomical Record* **291(10)**, 1221–1226 (2008). <https://doi.org/10.1002/ar.20742>
 262. Muchlinski, M. N., Wible J. R., Corfe I. Sullivan, M., J. And Grant R. A. Good Vibrations: The Evolution of Whisking in Small Mammals. *The Anatomical Record* **303**, 89–99 (2020).
 263. Rowe, T. B., Rich, T. H., Vickers-Rich, P., Springer, M., and Woodburne, M. O., (2008) The oldest platypus and its bearing on divergence timing of the platypus and echidna clades. *Proceedings of the National Academy of Sciences* **105 (4)**, 1238–1242.
 264. Rich, T. H., Hopson, J. A., Gill, P. G. Trusler, P., Rogers-Davidson, S., Morton, S., Cifelli, C. L., Pickering, D., Kool, L., Siu, K., Burgmann, F. A., Senden, T., Evans, A. R., Wagstaff, B. E., Seegets-Villiers, D., Corfe, I. J., Flannery, T. F., Walker, K., Musser, A. M., Archer, A., Pian, R. and Vickers-Rich, P. The mandible and dentition of the Early Cretaceous monotreme *Teinolophos trusleri*. *Alcheringa* **40(4)**, 475–501 (2016)
 265. Kilbourne, B. M. Differing limb functions and their potential influence upon the diversification of the mustelid hindlimb skeleton. *Biological Journal of the Linnean Society* **132**, 685–703 (2021).
 266. Grossnickle, D. M., Brightly, W. H., Weaver, L. N., Stanchak, K. E. and Roston, R. A. Challenges and advances in measuring phenotypic convergence. *Evolution* **78(8)**, 1355–1371 (2024) (<https://doi.org/10.1093/evolut/qpae081>)
 267. Butler, P. M. The teeth of Jurassic mammals. *Proceedings of the Royal Society of London B* **109(3-4)**: 329–356 (1939). (<https://doi.org/10.1111/j.1096-3642.1939.tb00719.x>)
 268. Averianov, A. O. Interpretation of the Early Cretaceous mammal *Peraiocynodon* (Docodonta) and taxonomy of some British Mesozoic docodonts. *Russian Journal of Theriology* **3(1)**, 1–4 (2004).
 269. Sigogneau-Russell, D. Docodonts from the British Mesozoic. *Acta Palaeontologia Polonica* **48**, 357–374 (2003).
 270. Datta, P. Earliest mammal with transversely expanded upper molar from the Late Triassic (Carnian) Tiki Formation, South Rewa Gondwana Basin, India. *Journal of Vertebrate*

- Paleontology* **25(1)**, 200–207 (2005). ([https://doi.org/10.1671/0272-4634\(2005\)025\[0200:EMWTEU\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2005)025[0200:EMWTEU]2.0.CO;2))
271. Averianov, A. O. and Voyta, L. L. Putative Triassic stem mammal *Tikitherium copei* is a Neogene shrew. *Journal of Mammalian Evolution* **31(10)**, 1-6 (2024).