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# Original Article

# A new euharamiyidan, *Mirusodens caii* (Mammalia: Euharamiyida), from the Jurassic Yanliao Biota and evolution of allotherian mammals

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**ABSTRACT**

Allotheria are an extinct group of mammaliaforms that originally comprised multituberculates, to which 'haramiyidans' and gondwanatherians were later added. Phylogenetic relationships of allotherians have remained controversial since the first reports of the allotherian fossils in the 1800s. Here we report a new euharamiyidan based on a skeletal specimen from the Jurassic Daohugou phase of the Yanliao Biota, China. The superb specimen preserves impressions of differentiated hairs. The pes with impressions of toe skin and claw sheath represents the first such evidence in Mesozoic mammaliamorphs. The remarkable tooth morphologies surpass in complexity any Mesozoic mammals previously known. Phylogenetic analyses place the new species within euharamiyidans from Eurasia and support euharamiyidans, multituberculates, and gondwanatherians as a tripartite monophyletic Allotheria within mammals. This clade is supported not only by their similar molar pattern, but also by many shared derived features of the dental system recognized from discoveries during the last two decades. Allotherians and therians represent the two most successful groups of mammals that are characterized by distinct dental systems. They originated at the latest in the Late Triassic and became diversified in the Middle Jurassic, representing two directions of ecomorphological adaptation during early evolution of mammals.

**Keywords:** allotherian synapomorphies; dental system; haramiyidans; integument; mammalian evolution; multituberculates; phylogeny and definition

## INTRODUCTION

Fossils of allotherians, such as the haramiyidan *Thomasia* ('*Microlestes*') Plieninger, 1847 and multituberculate *Plagiaulax* Falconer, 1857, are among the earliest reported Mesozoic mammals. While their dental similarities were recognized long ago, the relationship between 'haramiyidans' and multituberculates has been controversial since their discoveries (Owen 1871, Simpson 1928). This is partly due to the fragmentary material known in the two groups, particularly 'haramiyidans'. For decades, the main evidence that unites 'haramiyidans' and multituberculates as allotherians is the gross similarity of their molar teeth (Butler 2000) and diverse views have been put forward: 'haramiyidans' have been considered either as the earliest multituberculates (Hahn 1973, Sigogneau-Russell 1989), as a sister-group of the multituberculates (Butler and MacIntyre 1994, Gambaryan and Kielan-Jaworowska 1995), as a paraphyletic group that gave rise to multituberculates (Van Valen 1976, Hahn *et al.* 1989, Butler 2000, Butler and Hooker 2005, Hahn and Hahn 2006, Bi *et al.* 2014, Han *et al.* 2017), or as a group that does not share the most recent common ancestor with multituberculates but is placed outside of mammals (Luo *et al.* 2015, 2017, Huttenlocker *et al.* 2018). Nonetheless, most recent studies have recognized euharamiyidans as a monophyletic group that is clustered with multituberculates and gondwanatherians to form Allotheria within Mammalia

(Wang *et al.* 2019, 2021, Krause *et al.* 2020a, Mao *et al.* 2020, 2021, this study). Because Late Triassic haramiyidan fossils are among the earliest records of mammaliaforms, their phylogenetic placement is critical to understand the origin of mammals and affect the trajectory in interpreting mammalian evolution.

Recent discoveries of euharamiyidans have greatly enriched our knowledge about haramiyidan morphology and biology. These discoveries have not only added new morphological information and species diversity to this otherwise poorly known group, but also corrected misinterpreted morphologies and taxonomy of 'haramiyidans' (Mao *et al.* 2022). With all the new data, Allotheria (multituberculates, 'haramiyidans', and gondwanatherians) as a clade of mammals gains increasing support.

Here we report a new euharamiyidan based on a skeletal specimen from the late Middle Jurassic Daohugou phase of the Yanliao Biota, China. The superb preservation of the specimen displays remains of claw sheath and fur and toe skin impressions. The animal also shows remarkable tooth morphologies, particularly the incisors and ultimate premolars, that perhaps surpass in complexity any Mesozoic mammals previously known. This casts new light on the dental evolution within allotherians. The new species is closely clustered with the coeval euharamiyidans in Eurasia and furnishes additional evidence for phylogenetic relationship of 'haramiyidans' and multituberculate. Based on this report and the discoveries made during the last two decades, we have summarized the morphological features shared by allotherians that support the close relationship of 'haramiyidans', multituberculates, and gondwanatherians as the clade of allotherians within mammals. Allotherians and therians represent the two most successful groups of mammals that have lived on earth. The two groups are best characterized and differentiated by their dental and jaw morphologies, which evolved in two directions of functions for food processing.

## MATERIAL AND METHODS

### Specimens and provenance
The holotype specimen (HT-B-PM-0001) was collected from the Daohugou site, Nincheng County, Inner Mongolia, China; the age of the strata is Bathonian–Callovian (168 to 164 Mya). It is the only unequivocal euharamiyidan from the Daohugou site or the Daohugou phase; other euharamiyidans are from the Linglongta phase of the Yanliao Biota (see: Ren *et al.* 2019, Gao *et al.* 2021, Mao *et al.* 2021, Yang *et al.* 2021). *Megaconus* (Zhou *et al.* 2013) is also from the Daohugou site, but its taxonomy remains controversial (Meng *et al.* 2014). The holotype specimen of the new species, a skeleton preserved in the main part and counterpart of a split slab (HT-B-PM-0001A and B), has been deposited at the Hongtao Fossil Museum, Lingyuan, Liaoning. The provenances of the specimens were ascertained by the collectors on site, by the lithological match of the slabs to the strata of the sites, and by co-existence of invertebrate index fossils on the same slabs, respectively. The authors (F.M., Z.L., and J.M.) have field experience at this site. These specimens are accessible to researchers after its publication.

### Specimen preparation and sampling
The specimen embedded in the matrix was needle prepared to expose some details of the skeleton by Mr. Shuhua Xie (IVPP), one of the most skillful preparators for small vertebrates worldwide. After the initial CT-scan, the skull was removed from the skeleton along a fracture to allow higher-resolution CT scanning for detailed morphology.

### Measurements
Measurements were taken using digital callipers and double-checked using digital methods from the images. After these elements were reconstructed, linear measurements were taken using the Measurements Menu/Coordinate Measurement module in VG Studio Max 3.5 (Volume Graphics, Heidelberg, Germany) and rechecked using the measurement tool in ImageJ 1.49v.

### Imaging and figures
Optical images were taken using a Canon Digital camera with a macro lens installed in the Key Laboratory of Vertebrate Evolution and Human Origins, IVPP. High-resolution micro-CT scanning was conducted using a GE v|tome|x m dual tube 240/180kV system in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP). Specimens were scanned using the 240 kv microfocus tube at 5.9, 9.5, 11.7 μm/voxel resolution, 90,120, 240 kV and 90, 100, 200 μa. Where needed, a Cu filter of 0.1-mm was used to reduce beam hardening artefacts. To improve the signal-to-noise ratio, 1800 projections were collected, for 333–2000 ms and averaged two to three times. To accommodate the long specimen, two scans for two separate portions of the cranium in the Y-axis (multiscan) were conducted to obtain higher resolution. The scan data were reconstructed using Phoenix datos|x (General Electric, Wunstorf, Germany). Segmentation and the rendering of the CT scanning data were processed using VG Studio Max 3.5 (Volume Graphics, Heidelberg, Germany).

### Phylogenetic analysis
A total of 131 taxa, including *Mirusodens*, were chosen based on Mao *et al.* (2021, 2022). The taxa selection in Mao *et al.* (2021) focused on Mesozoic mammals, particularly 'haramiyidans', multituberculates, and tritylodontids. Mao *et al.* (2022) demonstrated that haramiyidan teeth previously assigned to the purported haramiyidan '*Eleutherodon*', '*Millsodon*', and '*Kirtlingtonia*' and the multituberculate *Kermackodon*, were actually teeth from different upper or lower dental loci of the same haramiyidan species *Kermackodon oxfordensis*. This recognition results in significant taxonomical modification of these allotherians and impacts on haramiyidan phylogeny given that some of these taxa have been used in phylogenetic analyses (Huttenlocker *et al.* 2018, Wang *et al.* 2021). In this study, we used the haramiyidan species based on the currently recognized species of 'haramiyidans'.

A total of 573 characters was used in our analyses. As the taxa selected, these characters are primarily from Mao *et al.* (2021), which focus on the Mesozoic groups and include some postcranial characters of *Haramiyavia*, a critical taxon for the subject treated in this study. To better understand the phylogenetic position of *Mirusodens*, as well as the allotherian

phylogeny within the mammaliamorphs, some dental characters used for reconstructing a haramiyidan phylogeny (Mao et al. 2022) were incorporated in the data matrix used in this study and noted as 'new' in the character list (Supporting Information, File S1). Also, because of reinterpretations of specimens previously assigned to *Kermackodon* (=*Eleutherodon*) *oxfordensis*, '*Millsodon*', and '*Kirtlingtonia*', as mentioned above, the character coding for *Kermackodon oxfordensis* has been altered significantly.

Phylogenetic analyses were conducted using parsimony-based analyses (PAUP*, v.4.0) (Swofford 2002). For parsimony analyses, the heuristic search was conducted with the following settings: all characters are unordered and with equal weight; gaps are treated as 'missing'; multistate taxa are interpreted as uncertainty; starting tree(s) is obtained via stepwise addition; addition sequence is random with starting seed generated automatically; tree-bisection-reconnection (TBR) is used and set up with reconnection limit equal to eight; 'MulTrees' option is not in effect and one tree is saved per replicate; steepest descent option is not in effect; no topological constraint is in effect; trees are unrooted; number of replicates is 100 000. Number of trees retained = 990, of which the strict consensus tree was saved and presented in the Supporting Information, File S1. Data matrix and apomorphic list for the strict consensus are also provided in the Supporting Information, File S1.

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**Systematic palaeontology**

**Class mammalia Linnaeus 1758**

**Subclass allotheria Marsh 1880**

**Suborder Euharamiyida Bi *et al.* 2014**

**Family Arboroharamiyidae Zheng *et al.* 2013**

**Genus *Mirusodens* gen. nov.**

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*Type species: Mirusodens caii* gen. et sp. nov.

*Etymology: Mirus*, Latin, amazing, remarkable; *dens*, tooth; in reference to the remarkable tooth morphology of the new genus.

*Diagnosis:* Dental formula I1-C0-P3-M2/i1-c0-p1-m2 (upper/lower incisor, canine, premolar, and molar); differ from other 'haramiyidans' in having the following features: the upper incisor considerably larger than molars and having complex and multiple cusps; three upper premolars identified as P2–P4; P4 having complex roots and a heart-shaped crown with numerous cusps that are regularly arranged in curved rows and decrease in size from outer row toward the basin centre; lower ultimate premolar (p4) twice the length of lower molars and having no distal cusp or heel but having serrations along the mesial half of the crown; upper molars with initial cusp Ax and row Ax; lower molars with cusp b1 that projects mesially from the mesiobuccal base of a1.

*Remarks:* The new genus is dentally distinctive from other 'haramiyidans' and other mammaliaforms so that there seems no need to present a differential diagnosis for establishment of the new species. In the description of the dentition, we have a comparison for each set of teeth, which furnishes additional information for species differentiation.

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**Species *Mirusodens caii* gen. et sp. nov.**

**(Figs 1–6)**

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*Holotype:* A skeleton preserved in the part and counterpart of a split slab: part A, the left slab with most cranial elements and part B, the right slab (Fig. 1; HT-b-Pm-0001, Hongtao Fossil Museum, Lingyuan, Liaoning).

*Etymology:* Species name is after Mr Hongtao Cai, who collected and curates the holotype specimen.

*Locality and age:* Daohugou site, Nincheng County, Inner Mongolia, China; Bathonian–Callovian (168–164 Mya) (Mao et al. 2021; see also: Ren *et al.* 2019, Gao *et al.* 2021, Yang *et al.* 2021).

*Diagnosis:* As for the genus, by monotypy.

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*Description*

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*Skull:* The crushed holotype skeleton is preserved in the main part and counterpart of a split slab (Figs 1, 2). The breakage runs though the right side of the skull so that the main part (part A) contains most (primarily the left side) of the skull. The left side of the skull is embedded in the matrix and thus well-preserved; its morphology is revealed by the CT-scan. In lateral view, the rostrum is deep to accommodate the enlarged upper incisor that has a strong and long root, similar to that of *Dactylopsila trivirgata* Gray, 1858. The nasals project anteriorly, overhanging the external nostril. The anterior root of the zygomatic arch extends laterally at the position lateral to P4 and then continues posteriorly; the arch is deeper anteriorly and gently arching dorsally. The zygoma to the rostrum transition is not gradual but step-like, with the anterior root of the arch extending laterally and then posteriorly. A vague suture indicates that the jugal is probably sizable, which differs from the small jugal on the medial surface of the arch in multituberculates (Hopson *et al.* 1989). There is one distinct and short infraorbital foramen. The orbit appears to be large. The glenoid fossa is orientated anteroposteriorly and does not have a postglenoid process, similar to that of multituberculates. The nuchal crest is prominent, projecting dorsoposteriorly. The mandible is typical of euharamiyidans, deep and short. The coronoid process inclines posteriorly. As in other euharamiyidans and multituberculates, the process extends on the labial side of m2 and blocks the tooth in lateral view. The mandible has a small angular process that bends medially. The mandibular condyle is lower than the occlusal surface of the dentition and the articular surface faces posterodorsally. The masseteric fossa extends anteriorly and reaches to the level below p4. As in other euharamiyidans the mental foramen is at the diastema between the lower incisor and p4.

*Dentition* (Figs 2–4)*:* The tooth morphology of *Mirusodens caii* is remarkable, particularly its upper incisors and ultimate premolars. Some of the teeth are exposed in the broken surface of
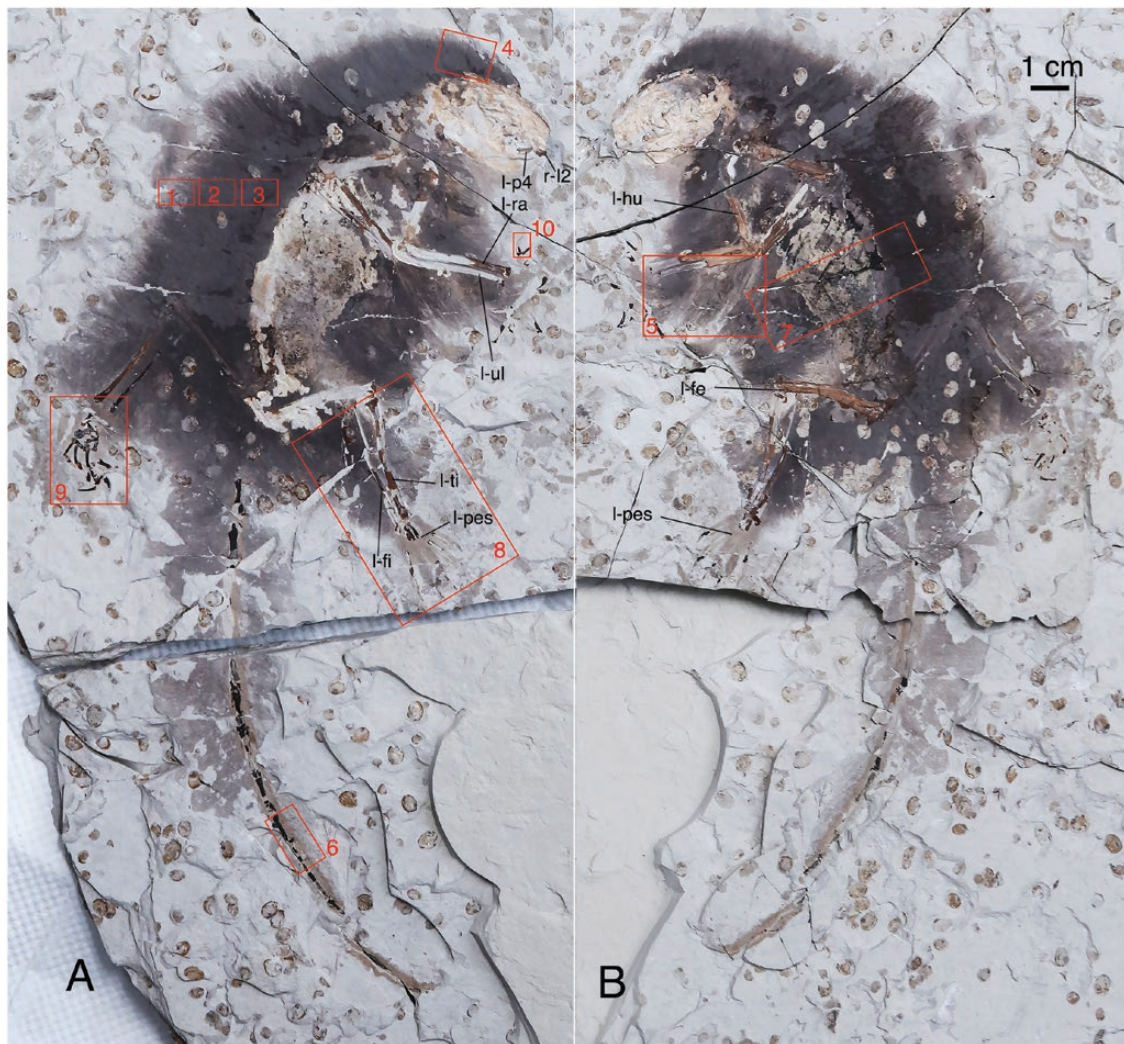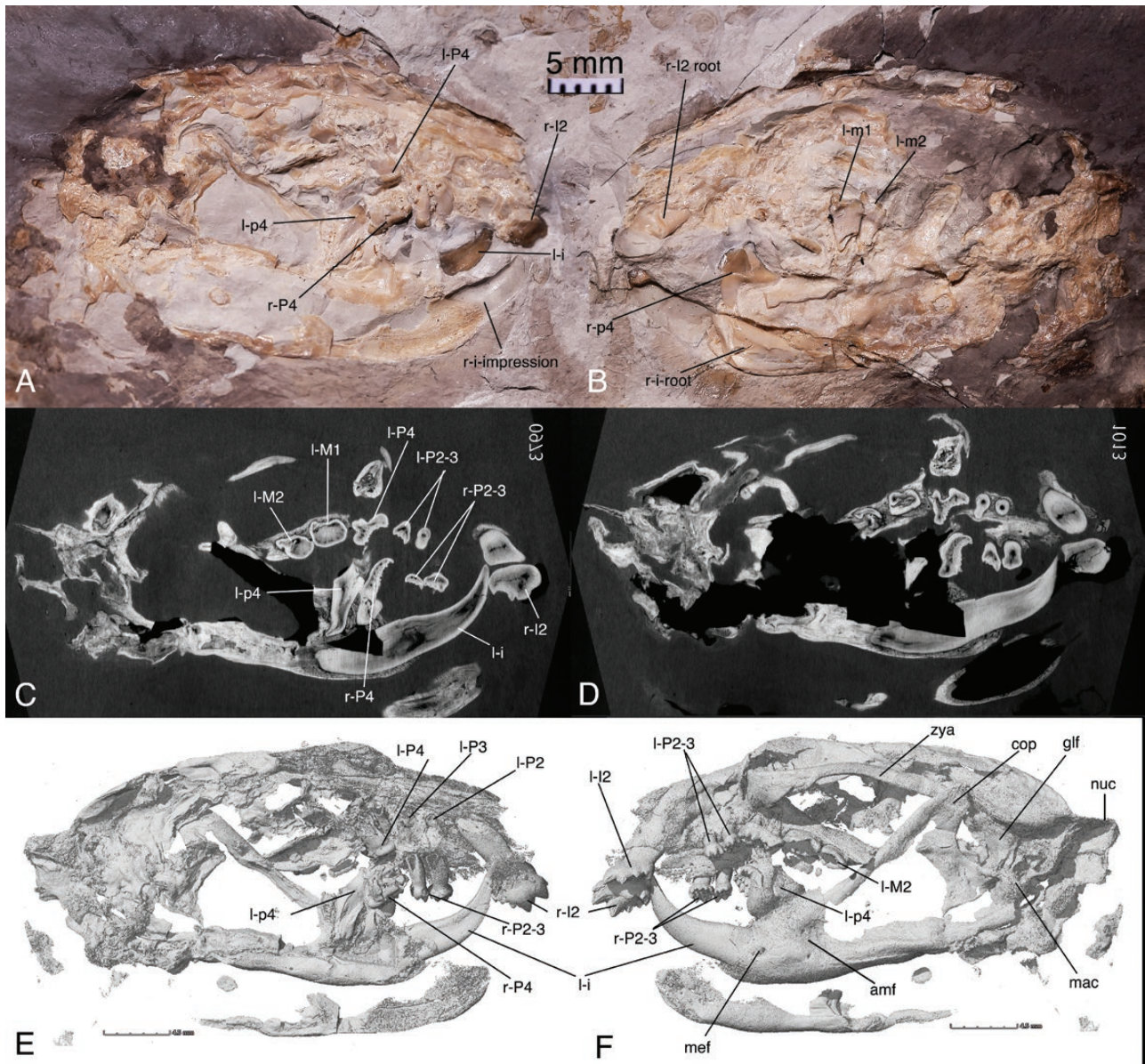
**Figure 1.** Holotype of *Mirusodens caii* gen. et sp. nov. (HT-B-PM-0001). A, main part (part A or 'left part' when referring to anatomic orientation of the split skeleton) in which most cranial structures and upper teeth were preserved; B, counterpart (part B or 'right part') in which most lower teeth were preserved. Red boxes 1–7 correspond to figure panels A–G in Figures 6 and 8–10 and to A–D in Figure 5. Note that the skeleton is preserved in association with numerous valves of conchostracans that are typical invertebrate fossils in the Daohugou strata. The dark area probably represents residues of the pelage, possibly the patagium (see Figs 5 and 6 for comparison with extant gliding mammals). Abbreviations: l-fe, left femur; l-fi, left fibula; l-hu, left humerus; l-I2, left and presumably the second upper incisor; l-ra, left radius; l-ti, left tibia; l-ul, left ulna; r-I2, right and presumably the second upper incisor.

the slab (Fig. 2) but most are embedded in the matrix so that they are preserved in good condition, as revealed by CT scan (Figs 2–4). The main slab (part A) contains the complete left upper dentition, the right upper incisor, P2–P4, and the left p4. The counterpart slab (part B) contains the right lower dentition, a segment of the incisor, the right M1–2, and the left m1–2. The lower jaws are partly preserved, which shows the general morphology and allows measurements of the mandible. The left upper dentition preserved in the main slab is interpreted as in its anatomic position. The teeth preserved in part B can be digitally re-associated to those in part A so that the upper and lower dentitions on both sides can be reconstructed. Measurements of teeth are in Table 1.

*Upper incisors: Mirusodens* has one pair of enlarged upper incisors, which are regarded as I2. The left incisor is smaller than the right one, showing a degree of asymmetry. The tooth crown is larger (mesiodistally longer) than all cheek teeth except for P4 and supported by a single robust root. The crown is multi-cusped and shaped almost like a molar. All cusps bear fine enamel ridges (flutings) so that the morphology of the upper incisor is in sharp contrast to the single-pointed and smoothly surfaced lower incisor. The mesial half of I2 has two main cusps, which, for convenient description, we denote as cusp 1 and 2. Cusp 1 is mesial to cusp 2. A minor cusp is immediately medial to cusp 1; similarly, another minor cusp is mesial to cusp 2; we consider this as a splitting of cusps, a unique feature that increases the cusps of the incisors. On the right I2, there is one more minor cusp on the labial side distal to cusp 2. The main and minor cusps are proportionally stronger on the right incisor. In lingual or buccal view, cusps 1 and 2 are high. Following cusp 2 are a few small cusps that decrease in height distally. Again, the number of the distal cusps differs on the two teeth. Except for the distal cusps, the cusps are on the buccal side of the tooth crown. The lingual
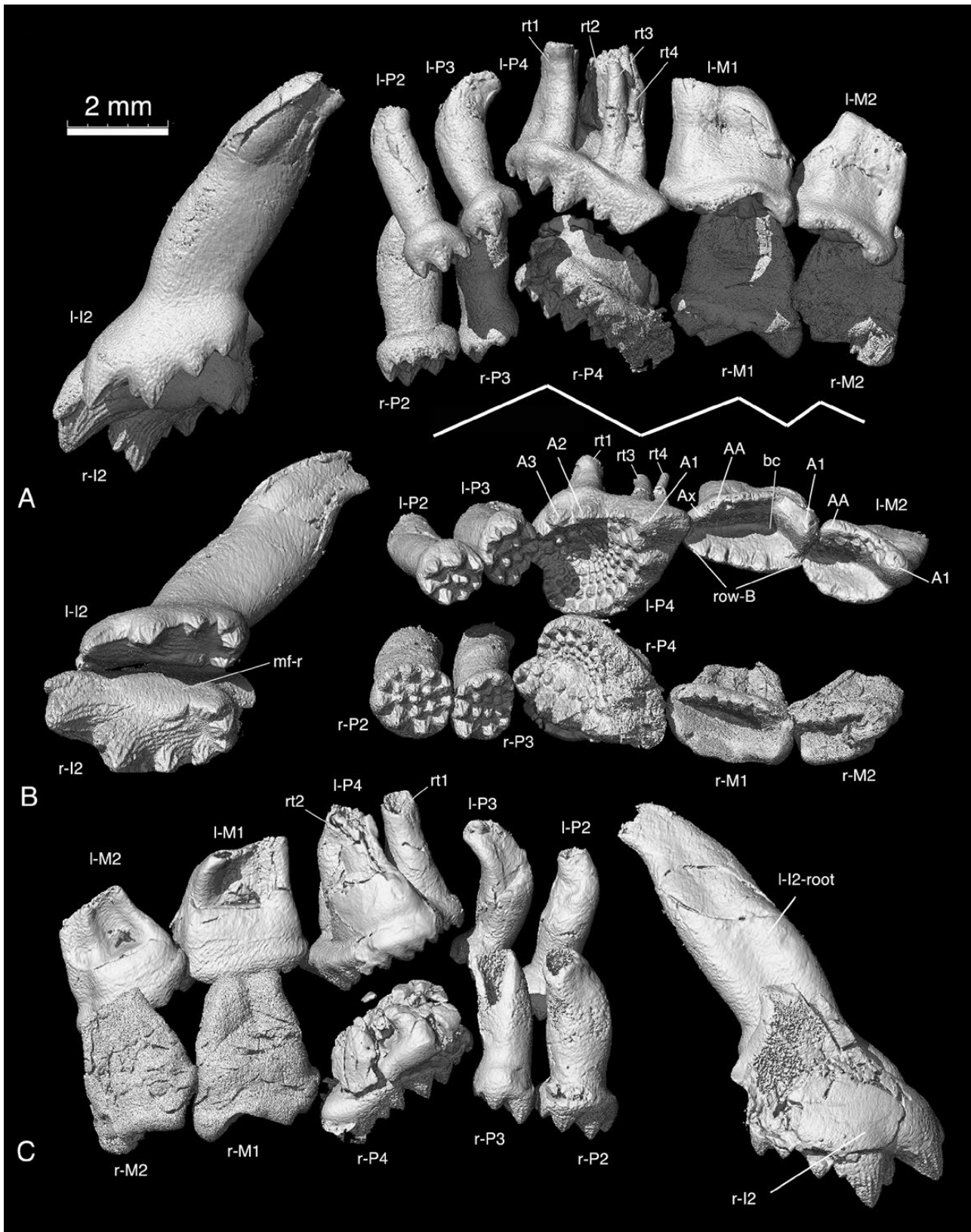
**Figure 2.** Skull of **Mirusodens caii** gen. et sp. nov. (holotype, HT-B-PM-0001). A, partial skull in the main part of the slab (part A) in which the left half of the skull and most teeth are preserved; B, partial skull in the counterpart of the slab (part B); C, D, two micro-CT slices through different positions of the partial skull in part A, showing the preserved condition of the specimen and the resolution of the scan; E, F, CT-rendered skull in preserved part A: E, the exposed or right side of the preserved skull in slab A, which is mostly broken; F, the left side of the skull that is embedded in the matrix and thus better preserved. Abbreviations: amf, anterior extremity of the masseteric fossa; cop, coronoid process; glf, glenoid fossa; l-i, left lower incisor; l-I2, left upper incisor (I2); l-M1, left upper first molar; l-m1, left lower first molar; l-m2, left second lower molar; l-M2, left second upper molar; l-P2, left second upper premolar; l-P3, left third upper premolar; l-p4, left ultimate premolar (p4); mac, mandibular condyle; mef, mental foramen; nuc, nuchal crest; r-I2, right upper incisor (I2); r-P2, right upper second premolar; r-P3, right upper third premolar; r-P4, right upper ultimate premolar (P4); zya, zygomatic arch.

side of the left I2 bears weak ridge-like cuspules, while the right I2 lacks lingual cusp. All cusps are on the buccal margin of the crown.

The lingual (medial) side of each I2 crown bears a large flat surface, which we interpret as the contact facet for the opposite I2, similar to other euharamiyidans, such as *Qishou* (Mao and Meng 2019a). The buccal side of the tooth is convex laterally. In life when the two incisors pair together, they formed a basin-shaped structure that was surrounded by rugged cusps, a good device for holding food items. There is a 'neck' that delimits the

transition of the crown and the root. The single root is robust and long, about twice the length of the crown length; it is implanted in the premaxilla at an angle of about 50° to the occlusal plane of the teeth.

The upper incisors of *Mirusodens* represent the extreme condition in known 'haramiyidans'. They are proportionally larger and more complex in structure than those of *Arboroharamiya* Zheng *et al.* 2013, *Shenshou* Bi *et al.* 2014, *Xianshou* Bi *et al.* 2014, *Qishou* , Wang *et al.* 2014 *Maiopatagium Wang et al. 2014,* and *Vilevolodon* Luo *et al.*

**Figure 3.** Upper teeth of *Mirusodens caii* gen. et sp. nov. (holotype, HT-B-PM-0001). A, upper dentition in left side view (labial for the left dentition and lingual for the right one); B, occlusal view of the upper teeth; C, upper teeth in right side view (labial for the right dentition and lingual for the left one). Note the root condition in each tooth. In (C) the root of the right incisor is broken, whereas the tooth crown of the left one is blocked by the right one. The teeth are restored digitally from the main and counterpart slabs and represent the preserved condition in the matrix. The white line outlines of the occlusal surfaces of the upper cheek teeth in lingual and buccal views, showing the en echelon (step-like) pattern, as first noted in *Haramiyavia* (Jenkins *et al.* 1997). Abbreviations: l-, indicates left side; mf-r, medial contact facet of the right upper incisor; r-, indicates right side; row-B, cusp row B of the upper molar; rt1–4, root 1, 2, 3, and 4 of the ultimate upper premolar (l-P4).
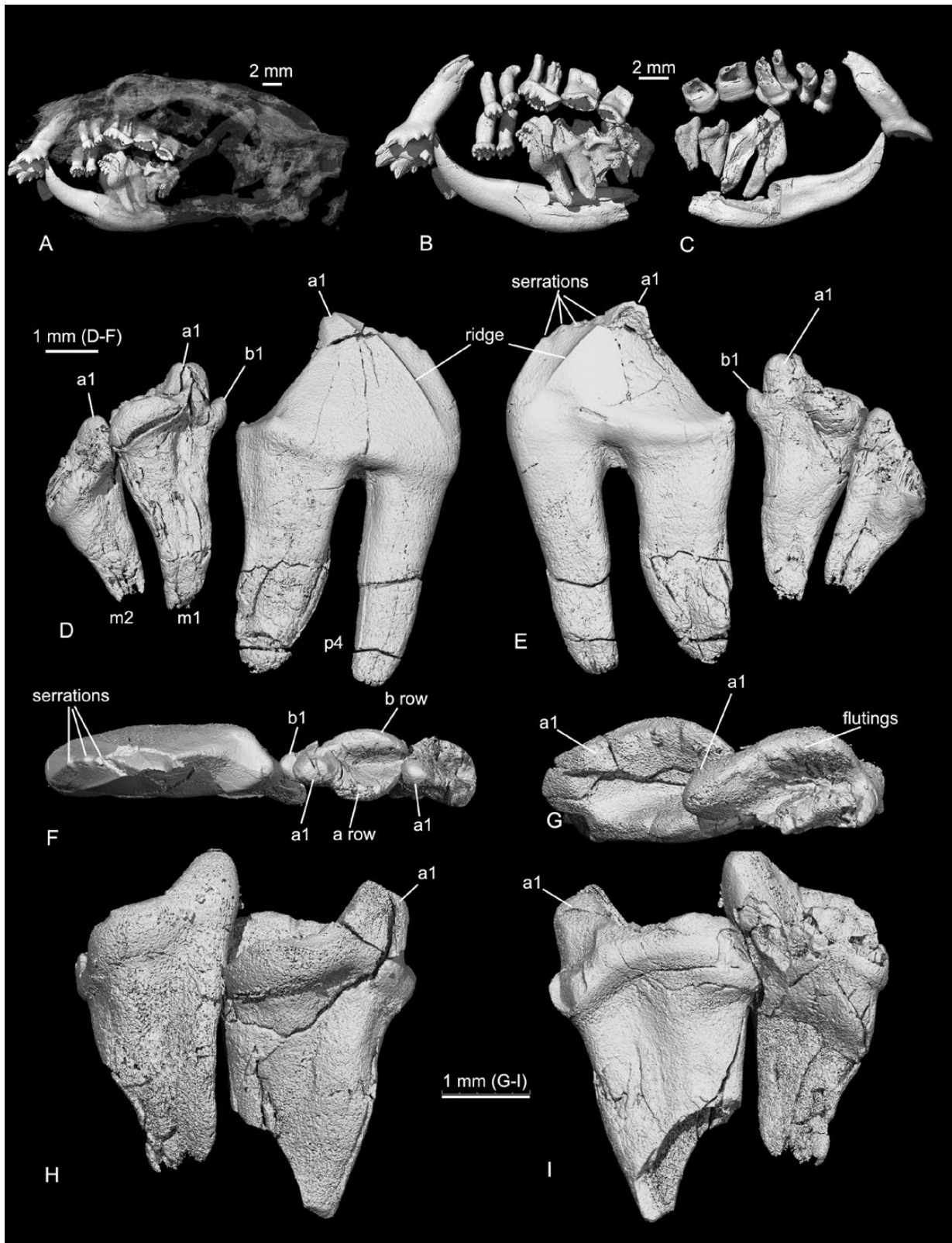
**Figure 4.** Lower teeth of *Mirusodens caii* gen. et sp. nov. (holotype, HT-B-PM-0001). A, skull (semi-transparent) in left side view, showing relationships of teeth in the skull; B, left side view of upper and lower teeth that are digitally restored from the main and counterpart slabs. Note that p4 is considerably longer than P4 and that the root of the lower incisor is on the lingual side of p4 roots; C, left upper and lower dentitions in lingual view; D–F, right lower p4–m2 in labial, lingual, and occlusal views. Note the position of cusp b1 in m1 (broken in m2); G–I, left lower m1–m2 in occlusal, lingual, and labial views; cusp b1 is broken in both m1 and m2.

**Table 1.** Measurements (in mm) of *Mirusodens caii* gen. et sp. nov. (holotype, HT-B-PM-0001). * = estimated = unknown

| Skull | | Left dentition (length/width) | | Right dentition (length/width) | |
|---|---|---|---|---|---|
| Cranial length | 34.17 | I | 3.56/1.64 | I | 4.05/1.67 |
| Left lower jaw length | 24.67 | P2 | 1.31/1.14 | P2 | 1.67/1.50 |
| Left lower jaw height | 11.64 | P3 | 1.34/1.46 | P3 | 1.22/1.43 |
| | | P4 | 3.34/2.60 | P4 | 3.25/2.39 |
| | | M1 | 2.80/1.58 | M1 | 2.65/1.44 |
| | | M2 | 2.34/1.53 | M2 | 2.49/1.20 |
| | | p4 | 4.14/1.28 | p4 | 4.36/1.40* |
| | | m1 | 2.38/1.39 | m1 | 2.47/1.36 |
| | | m2 | 1.91/1.24 | m2 | 2.00/1.19 |

*2017* from the Linglongta phase of Yanliao Biota; they are also more complex than the upper incisors of any known Triassic and Jurassic 'haramiyidans' and multituberculates (Hahn and Hahn 2006, Mao *et al.* 2022). In size and morphology; they are most similar to those of *Butlerodon* from the Middle Jurassic of United Kingdom (Mao *et al.* 2022). Such a large and complex tooth may have functioned as a set of multiple upper incisors in the marsupial *Dactylopsila trivirgata* and *Petaurus breviceps* Waterhouse, 1839 (Beck 2009, Burrows *et al.* 2020). As the right and left incisors fit together (in contact on their mesial surfaces), the pair forms a complex platform for sophisticated food picking and manipulation again the lower incisors (see comparison of lower incisors). The complex morphology of the upper incisors of *Mirusodens* is interpreted as a derived condition within euharamiyidans.

*Upper mesial and penultimate premolars (P2–3):* A large diastema separates the upper incisor and the mesial premolars, similar to other euharamiyidans. This diastema may be interpreted as being created by loss of I3, canine, and perhaps mesial premolar (P1), a condition present in all known euharamiyidans. Differing from all known euharamiyidans where the dentitions are known, *Mirusodens* is unique in having three upper premolars. The mesial and penultimate premolars are here interpreted as P2 and P3, which are similar in general morphology in having a rounded or oval profile in occlusal view. These teeth are single-rooted with a 'neck' delimiting the transition of the root and the crown. P3 has the distal end of the root bent distally. As in the upper incisors, the left P2–3 are smaller and have fewer cusps than the right ones. They are similar in that the three buccal cusps are the largest on the crown and cusps in the centre of the crown are the smallest. All cusps are conical and bear fine enamel ridges. The occlusal surface of the tooth crown is oval-shaped and shallowly basined.

The premolar loci of euharamiyidans are not fully resolved. In earlier studies, the ultimate premolar was denoted as P4 and the penultimate as P3 (Zheng *et al.* 2013, Bi *et al.* 2014, Luo *et al.* 2017, Meng *et al.* 2017). This is largely based on the assumption that the ancestral condition of the haramiyidan dentition has a full pack of premolars, as in *Haramiyavia* (Jenkins *et al.* 1997, Luo *et al.* 2015). Reduction of the premolars' number is a general trend in evolution of allotherians, which is best known in multituberculates (Kielan-Jaworowska *et al.* 2004). In 'haramiyidans', if *Haramiyavia* is considered as an ancestral

condition, reduction of teeth is also probably the evolutionary trend in 'haramiyidans'. Thus, presence of P2 in *Mirusodens* is probably a primitive condition. In other Yanliao euharamiyidans where the upper dentition is known, there are only two upper premolars, interpreted as P3 and P4 (Zheng *et al.* 2013, Bi *et al.* 2014, Han *et al.* 2017, Lou *et al.* 2017, Meng *et al.* 2017, Mao and Meng 2019a, Wang *et al.* 2021). P3 of *Mirusodens* is larger and more complex than that of *Qishou* sp. (Mao and Meng 2019a) and *Maiopatagium* (Meng *et al.* 2017), possibly *Shenshou* as well (the upper premolars were broken) (Bi *et al.* 2014), but smaller and simpler than that of *Arboroharamiya* (Zheng *et al.* 2013, Han *et al.* 2017), *Xianshou* (Bi *et al.* 2014), or *Vilevolodon* (Luo *et al.* 2017); nonetheless, P2 and P3 in combination in *Mirusodens* would form a more complex structure than P3 alone in other taxa.

The cheek teeth of an arboroharamiyid (PIN, nos. 5087/16 and 5087/10), originally identified as upper molariforms (Averianov *et al.* 2011: fig. 1), but believed to be upper premolars or P3s (Meng *et al.* 2014, Averianov *et al.* 2019, Mao and Meng 2019a), show some similarity to the left P3 of *Mirusodens* in general shape and cusp number of the tooth crown; this endorses the identification of those isolated teeth as upper premolars. Similarly, the tooth (BDUC J 562) identified as a left lower molar of an undetermined haramiyid (Butler and Hooker 2005: fig. 4B) was considered to be a P3 (Mao and Meng 2019b), which also shows similar general shape to the left P3 of *Mirusodens* but has fewer cusps. Presence of P2 and P3 in *Mirusodens* demonstrates the possibility that a similar condition could exist in other species, particularly the Triassic ones, such as *Thomasia*, which are represented only by isolated teeth that show diverse morphologies (Sigogneau-Russell 1989, Debuysschere 2015).

*Ultimate upper premolar (P4):* P4 of *Mirusodens* is a remarkable tooth compared to those of other 'haramiyidans' and perhaps even any of other mammaliaformes. It is the largest cheek tooth and characterized by crown and root morphologies. The CT-image of the right P4 is not well separated, but it can be seen that the cusp orientations and size are somewhat different from the left P4, but the general morphologies of the two P4 are comparable. The occlusal outline of P4 (based on the left one) is heart-shaped with the apex pointing distally; the lingual side is curved, whereas the buccal side is straight. The largest cusp is at the distobuccal corner that we denote as A1. Another two main cusps on the mesiobuccal side were denoted as A2 and

A3, although we do not assume any homology of these cusps in other species of euharamiyidans. Between A1 and A2, there are two minor cusps. On the crown surface, numerous cusps are arranged regularly as four or five parallel rows in a curved course from the lingual margin to the basin centre; the cusps decrease in size toward the centre. The buccal row bears larger cusps that form the buccal margin of the crown, whereas the row lingual to it consists of smaller cusps. At the very centre, the lowest area of the tooth basin, cusps are more randomly distributed and those in the deepest area are worn so that they became confluent. Such a remarkable arrangement of cusps on the broadly basined occlusal surface is unique; there seems no analogue to it, to our knowledge, in any known euharamiyidans or mammaliaformes. Such a cusp-floored basin is functionally similar to a coarse rasp so that food items can be firmly hold and then crushed as well as scraped against the main cusp of p4.

The complex crown is supported by four roots, denoted as root 1–4, that indicate considerable occlusal pressure sustained by the tooth. Root 1 supports the anterior one-third of the tooth crown; it is strong and anteroposteriorly compressed. The posterior two-thirds of the crown is supported by three roots. On the lingual side, root 2 as the strongest root is transversely compressed and obliquely extended, parallel to the oblique lingual edge of the tooth crown; there is no sign of division of this robust root, suggesting it is originally a single root. Labial to root 2 are two small, column-like roots of which the anterior one is longer and thicker. The two small roots are closely packed with a fused base. They support the mesiobuccal corner of the crown, primarily cusp A1. Such a complex root condition indicates considerable occlusal pressure sustained by P4.

P4 shows by far the most specialized structure in known euharamiyidans from the Yanliao Biota, including *Arboroharamiya jenkinsi* (Zheng *et al.* 2013, Meng *et al.* 2014), *Xianshou linglong*, *Shenshou lui* (paratype 1, WGMV-001), *Maiopatagium* (Meng *et al.* 2017), *Vilevolodon* (Luo *et al.* 2017), *Qishou jizantang*, and *Qishou* sp. (Mao and Meng 2019a, b) in the Yanliao Biota. Among those taxa, P4 of *Qishou* is proportionally the smallest, in relation to the molars, and simplest in crown structures in having several main cusps but lacking a broad basin filled with multiple cusps. The wear pattern indicates a longitudinal trench through the tooth crown, suggesting a relatively horizontal jaw movement during mastication. P4 of *Maiopatagium* is similar to that of *Qishou*, but its occlusal pattern is fundamentally different from the latter, as pointed out by Mao and Meng (2019b). Other aforementioned Yanliao taxa developed a proportionally larger and more complex P4, of which that of *Arboroharamiya jenkinsi* appears to be the most derived. The general pattern in these forms is that P4 has multiple main cusps and many cuspules; the tooth crown is transversely expanded (wider than long) and the distal end is concave for receiving the mesial end of M1. P4 of *Mirusodens* differs considerably from these forms. It is relatively larger, has more cusps that are arranged in a regular pattern on the crown. Its crown is triangular in shape in occlusal view and longer than wide with a pointed distal end. These differences in the Yanliao euharamiyidans can be viewed as derived features, compared to that of *Qishou*, perhaps adapted for different diets or food sources.

Outside of the Yanliao Biota, the left P4 (PIN 5087/101) of *Sharypovoia arimasporum* from the Middle Jurassic (Bathonian),

Western Siberia, Russia (Averianov *et al.* 2019: Fig. 2) appears to be simple, more similar to that of *Qishou* or *Maiopatagium*. Moreover, the holotype tooth of 'Kermackodon multicuspis' (Butler and Hooker 2005: Fig. 6; BMNH M46822), originally identified as a right M2 of a multituberculate, has been re-interpreted as P4 of an euharamiyidan (Mao *et al.* 2022). The heart-shaped outline and wear pattern of the tooth is unlike any M2 of multituberculates, but similar to P4 of euharamiyidans. The tooth identified as the right upper premolar of *Sineleutherus uyguricus* (Martin *et al.* 2010: Fig. 2H–J; SGP 2005/3) is conspicuous. As interpreted by the authors, the lingual side of the tooth crown is remarkably flat and almost completely covered by an extensive wear facet; in addition, the base of the large distal cusp occupies the distal half of the crown and its tip bends mesially. The wear facet suggests strong and vertical shear from the lower tooth that has a similarly vertical shearing facet on the labial surface of the tooth, a condition that is unknown in any known 'haramiyidans'. This tooth, if identified correctly, differs from all upper premolars of euharamiyidans preserved in associated dentitions and may represent a distantly related member of 'haramiyidans'.

*Upper molars:* As in other euharamiyidans, *Mirusodens* has two molars in each jaw quadrant. Each molar has one massive root that is transversely narrow. From the groove on the lateral surface of the root shaft, it can be inferred that the massive root was fused from two, mesiodistally arranged, roots. Unlike the upper incisor and premolars, the crown–root transition is not so distinct. M1 is longer and worn more deeply than M2, judging from cusp relief; minor cusps in the tooth basin of M1 are nearly erased by wear. As in other euharamiyidans, the distobuccal cusp (A1) is the largest of the tooth cusps and extends more distally than row B cusps. A concavity exists mesial to A1 and probably bears small cuspules, as in M2, but the cuspules are indistinct because of wear. There are two cusps on the mesiobuccal end of row A, denoted as cusp AA and Ax, which correspond to cusp BB and Bx in *Kermackodon* ('Eleutherodon') (see: Mao *et al.* 2022). Cusp AA is interpreted as homologous to the mesiobuccal cusp of M1 in other euharamiyidans, such as A5 in *Arboroharamiya jenkinsi* (Meng *et al.* 2014), A2 in *Sharypovoia arimasporum*, or A3 in *Maiopatagium sibiricum* [see Mao *et al.* (2022) for interpreting the cusp homologies]. Cusp Ax is weak, less developed than that in *Kermackodon oxfordensis* (Butler and Hooker 2005, Mao *et al.* 2022). Ax is followed by a weak ridge. The central valley of the tooth crown is relatively straight, which is bounded by a borad and gentle buccal wall, and a narrow and steep lingual wall. The valley is not even in depth; its deepest area is buccal to cusp B2. There are six (or seven) B cusps of which the middle ones are higher than those on the two ends. As in other euharamiyidans, except for *Maiopatagium* (Mao and Meng 2019b), the buccal side of cusp row B, the lingual and buccal sides of A1 bear wear. Whether cusp row A bears wear on its buccal side is unclear, but in our interpretation, it most likely does. M2 is shorter than M1 and displays more cuspules because of minor wear. Cusp row Ax is more discernible in M2. There are small enamel ridges that extend from the buccal side of the crown to the basin floor. The two molars of *Mirusodens* are aligned in a typical 'haramiyidan' pattern in that they are aligned mesiodistally, differing from multituberculates that have the buccal cusp row of M2 aligns distally
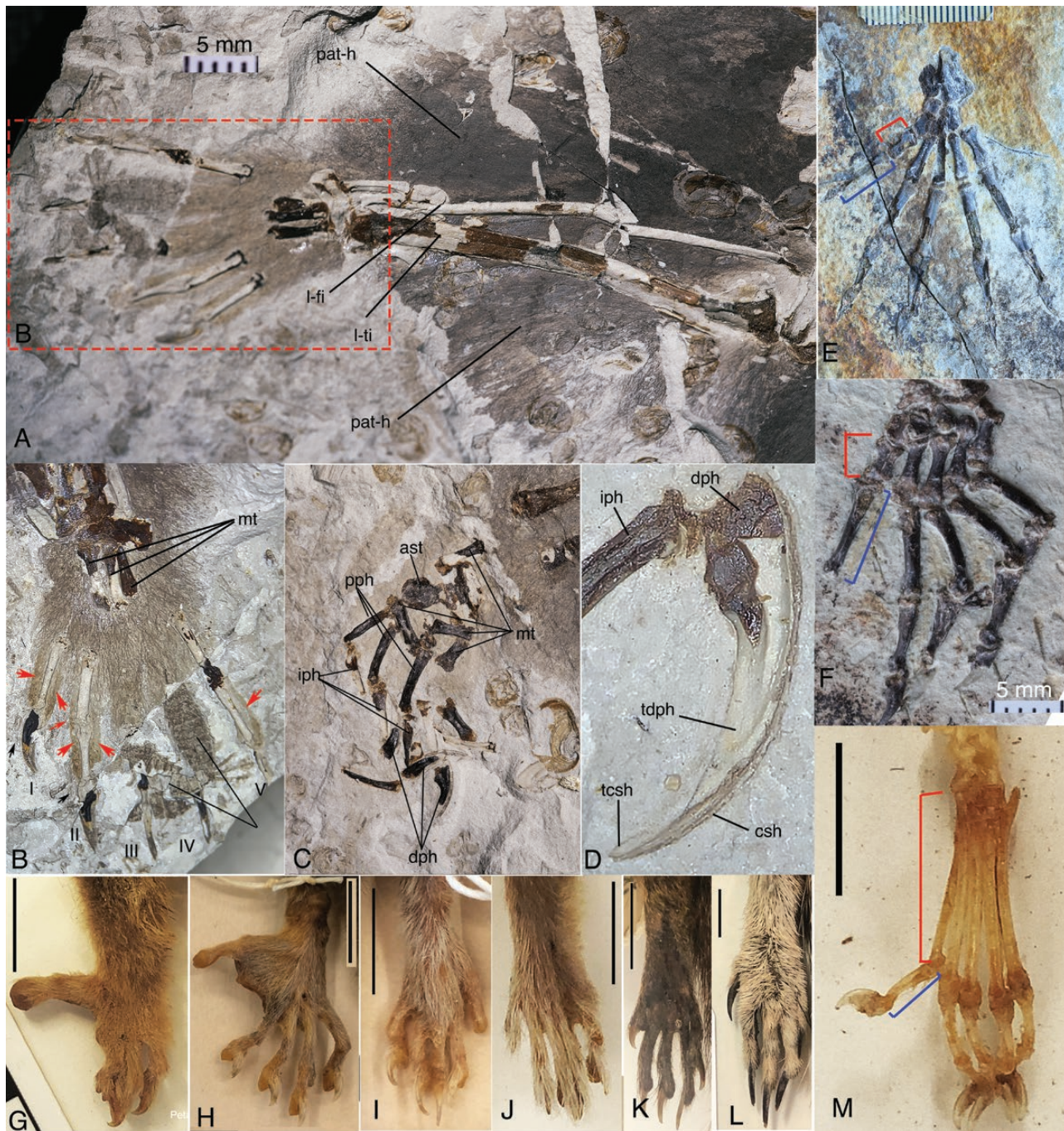
**Figure 5.** Pes and manus morphologies and soft tissues of *Mirusodens caii* gen. et sp. nov. (Holotype, HT-B-PM-0001) in comparison with those of extant mammals. A, C, D, correspond to red-boxed areas 8–10 in Figure 1. A, left hindlimb, showing the hair impressions in related to the limb bones. The hair distribution is narrowest at the ankle area and becomes much broad toward the knee; such an area does not seem to be all attributable to only hair because the hair impressions appear fine and short; it is most likely that the hair is on the patagium that stretched from the hindlimb to the tail and to the trunk of the body; B, the left pes in dorsal view, showing the toes, claws, potential impressions of the pedal skin or digital pads that outline the shapes of the toes that are long and well separated. Hair are short and fine on the instep and toes; C, disarticulated right pes, showing the shapes and relative lengths of the footbones; D, a claw in the manus, showing the remain and impression of keratinous claw and relationship of the phalanx (partial impression) and claw sheath; E, bony elements of the pes of euharamiyidan (**unpublished** figure) in ventral view, showing the relative length of the bony elements; F, the bony elements of the manus of *Shenshou*; G–I, pes morphologies of extant marsupials in dorsal view (G, gliding *Petaurus*, AMNH 196914; H, arboreal *Marmosa*, AMNH 266428; I, terrestrial *Monodelphis*, AMNH 263547); J–L, pes morphologies of extant placentals in dorsal view ( J, gliding *Glaucomys*, AMNH 188250; K, arboreal *Microsciurus*, AMNH 32497; L, terrestrial *Geosciurus*, AMNH 83652); M, bony elements of the pes of *Glaucomy* in dorsal view (AMNH 267293). Red arrows in (B) point to the edge of the toe skin edges. Red and blue lines in (E), (F), and (M) indicate the relative length of metapodial and proximal phalanx of digit I. Some images in (E–M) are photographically reversed for comparison. Abbreviations: ast, astragalus; csh, claw sheath (impression and remain); dph, distal phalanx (phalanges); iph, intermediate phalanx; I–V, digits from I to V; l-fi, left fibula; l-ti, left tibia; mt, metatarsal; pat-h, possible patagium around the hind limb; pph, proximal phalanx (phalanges); tcsh, tip of claw sheath; tdph, tip of distal phalanx (impression).

to the lingual row of M1, resulting in a different occlusal relationship for M1 and M2.

In lateral or medial view, the cheek teeth are not orientated with their occlusal surfaces horizontal; instead, they incline in different directions. For instance, the occlusal surfaces of P2 and P3 face ventroposteriorly, whereas that of P4 faces ventroanteriorly. Thus, the occlusal surfaces of the upper cheek teeth have the 'en echelon' (step-like) pattern (Fig. 3A, C), which was first recognized in the three upper molars of *Haramiyavia* (Jenkins *et al.* 1997, Luo *et al.* 2015). In *Mirusodens* the most pronounced step-like region is between P2–3 mesially and P4 distally, whereas in other euharamiyidans with the full upper dentition preserved, it is between P3 and P4. The inclined occlusal surface of P4 is the longest with the mesial end higher than the distal end in position. The steps are proportionally small on the molars of *Mirusodens*, as in other euharamiyidans. The en echelon pattern of the upper dentition is associated with the tall cusp a1 of the lower molars, and the pronounced region between the penultimate premolar(s) and P4 corresponds to the enlarged cusp a1 of p4.

Upper molars of *Mirusodens* are singled rooted; the root is thick at the cervical region and gradually tapers toward the distal end. This pattern is present in most known euharamiyidans. The upper molars of *Mirusodens* are similar to *Arboroharamiya* (Zheng *et al.* 2013, Meng *et al.* 2014), *Shenshou lui* (paratype 1, WGMV-001), *Maiopatagium furculiferum* (Meng *et al.* 2017), and *Qishou,* in having cusp A1 not so distally extended, contrasting to those in *Xianshou*, *Vilevolodon* (Luo *et al.* 2017), and *Sharypovoia* (Averianov *et al.* 2019). However, A1 of *Maiopatagium sibiricum* appears extended distally, but this is partly due to a reduced row B that bears only one or two cusps. In addition, the upper molar of *Mirusodens* has a relatively longer row B that bears more cusps than other euharamiyidans except for *Arboroharamiya jenkinsi*, which is probably one of the reasons that cusp A1 does not appear so distally extended in these taxa. The important feature of the upper molar of *Mirusodens*, however, is the initial development of cusp Ax and row Ax, which is absent in other Yanliao euharamiyidans. These extra cusps are well developed in *Kermackodon oxfordensis* ('*Eleutherodon*' *oxfordensis*) (Kermack *et al.* 1998, Butler and Hooker 2005, Mao *et al.* 2022) and weakly so in the holotype specimen (M2) of *Butlerodon* from the Woodeaton locality. In general morphology, M2 of *Mirusodens* is most similar to that of *Butlerodon* from the Middle Jurassic Woodeaton locality of England (Mao *et al.* 2022).

*Lower incisor:* As in other euharamiyidans, as well as in multituberculates and gondwanatherians, there is only one pair of enlarged lower incisors. CT-scan shows no tooth germ in the dentary. In buccal view, the incisor is in the shape of a curved dagger that tapers to a sharp tip that points dorsally. The buccal side of the tooth is convex and the lingual side is more flat. A sharp ridge extends along the dorsolabial rim of the crown, whereas the dorsolabial surface of the crown is rounded. From the exposed part, it is clear that the crown is covered entirely by enamel, and there seems to be no wear facet on the tip of the incisor. The root of the incisor is strong and extends backward to the level below m2; it is lingual to the roots of p4.

In general, the lower incisor is similar in all euharamiyidans, the only feature worth noting is that there is no indication of the lower incisor germ within the preserved dentary of *Mirusodens*, as in some euharamiyidans (Mao *et al.* 2019). Lack of the germ occurs in those that have relatively enlarged p4. The enlarged lower incisor and the deep mandible accommodating the enlarged tooth are highly similar to those of the marsupial *Dactylopsila trivirgata* and *Petaurus breviceps* (Beck 2009, Burrows *et al.* 2020). These arboreal animals use the lower incisors to extract wood-boring larvae (Cartmill 1974, Kay and Hylander 1978, Rawlins and Handasyde 2002), as well as to consume gums (Rawlins and Handasyde 2002). The highly similar lower jaw and incisor morphologies between these arboreal marsupials and *Mirusodens* (other euharamiyidans as well) suggest that the latter may have lived a similar life as the aforementioned extant arboreal animals, in the Jurassic forests, although these morphologies and lifestyles certainly evolved independently.

*Lower premolar:* As in other euharamiyidans that have the lower dentition preserved, there is only one lower premolar in each lower jaw of *Mirusodens*, and the tooth is denoted as p4 in correspondence with P4 in position and function. Both p4s are preserved in the holotype with the left p4 crown slightly crushed. The p4 is double-rooted and the roots are strong, with the distal root being thicker than the mesial one and the root of the molar. The roots are also long, ventrally passing the middle line of the incisor root on the lateral side of the latter. The tooth is implanted slightly inclined in the dentary, with the crown leaning mesially. The tooth crown is transversely compressed and in buccal and lingual views, the crown outline is triangular, nearly symmetrical. The crown is formed almost completely by the hypertrophied cusp a1, and there is no distal cusp or heel, except that there is a small concave area on the distolingual base of the crown. The p4 is much larger than the molars and its length is longer than the total length of m1–2, suggesting that p4, working along with P4, is the primary functional tooth in processing food. There are four or five serrations along the mesial half of the blade-like crown; the distal one ends at the summit in the middle point of the crown. On either the lingual and buccal sides, a fine ridge that extends from the summit mesioventrally in parallel to the mesial edge of the crown and delimits a narrow band that is flat or slightly concave on the mesiobuccal surface.

There are roughly two types of p4 in previously known euharamiyidans, except for *Kermackodon oxfordensis*: those (type I) that have a relatively small cusp a1 but large and multiple cusped distal portion (two rows of cusps) and a basin; the others (type II) have a large a1 but a simple heel with only a few small cuspules. Type I p4 is present in *Shenshou*, *Qishou*, *Sineleutherus* (Martin *et al.* 2010, Averianov *et al.* 2011), and *Sharypovoia* (Averianov *et al.* 2019), whereas type II p4 is present in *Arboroharamiya*, *Xianshou*, and *Vilevolodon*. Type I p4 is similar to that of *Thomasia* (Sigogneau-Russell 1989, Debuysschere 2015), although the identification of the isolated teeth in *Thomasia* is not certain (Mao *et al.* 2022). Type I p4 probably represents the plesiomorphic condition, whereas type II p4 is derived in euharamiyidans. The p4 of *Mirusodens* represents perhaps the most specialized condition among known euharamiyidans in which the tooth has an enlarged crown that is longer than the total length of m1 and m2 and cusp a becomes

predominant at the expenses of the distal heel and cusps. In addition, the blade-like crown has some serrations; in other euharamiyidans, p4 is transversely compressed but cusp a remains more or less conical, without any serration.

The p4 of *Mirusodens* is most similar to that of *Kermackodon oxfordensis* (BMNH M46684) (Butler and Hooker 2005) in their general shapes. In particular, p4 of *K. oxfordensis* has three or four serrations. The serrations in these two euharamiyidan p4s, however, are different from those in multituberculates in being few and uneven. In multituberculates, such as the Middle Jurassic *Tashtykia primaeva* (PIN 5087/52; Averianov *et al.* 2020: fig. 6), the p4 crown is relatively low and has a rounded or squared outline in buccal view; the serrations are many and evenly distributed along the entire crown. Fine ridges extend from the serrations on both lingual and buccal sides in parallel arrangement. In function, p4 of multituberculates is different from that of euharamiyidans in that it shears against the upper teeth (except for some more advanced cimonodontans), while in euharamiyidans p4 bites against the basined P4, primarily for crushing.

As recognized by Averianov *et al.* (2020), BMNH M46684 is unique in having mixed characters of euharamiyidans and multituberculates. Its high sectorial crown and posterior basin surrounded by small cusps are typical of euharamiyidans, whereas p4 of multituberculates lacks a posterior basin. In addition, the mesial end of BMNH M46684 lacks a vertical groove for holding the preceding premolar, another euharamiyidan feature. In BMNH M46684, there is still a small heel with multiple cuspules and the enamel ridges or serrations are on the distal half of the tooth crown. However, in p4 of *Mirusodens* the serrations are on the mesial half of the tooth and the distal basin is absent. The p4 of *Mirusodens* also lacks the groove on the mesial end of p4; this is because there is no additional lower premolar mesial to p4, which should be regarded as an euharamiyidan feature.

As discussed above, the upper premolar of *Sineleutherus uyguricus* is unique (Martin *et al.* 2010). Several teeth identified as the lower premolars in the same species are also interesting. Among those teeth, SGP 2004/6, identified as a left ultimate lower premolar, is similar to type In p4 of euharamiyidans. We concur with this identification except that the tooth is most likely a right p4. Of the other three teeth, SGP 2004/15 has only one row of three cusps, whereas SGP 2004/16 and SGP 2004/17 bear some small cuspules on the distolingual base. A common feature shared by the three teeth is a large flat wear facet on the buccal side of the crown (Martin *et al.* 2010: fig. 3), which matches or is similar to that on the lingual side of the tooth identified as the upper premolar (SGP 2005/3). Several implications can be made based on these teeth: First, because SGP 2004/6 was considered as an ultimate lower premolar, then the other three premolars with simpler cusp morphologies may be mesial premolars, as inferred by Martin *et al.* (2010): 'it [SGP 2004/15] may derive from a more anterior position in the tooth row'. Also, the authors noted 'a prominent projection at the base of the crown for the interlock with the following tooth' on SGP 2004/16-17. This means that *S. uyguricus* has more than one lower premolar. Second, because the type I SGP 2004/6, identified as the ultimate lower premolar, does not have a large flat wear facet to match that on SGP 2005/3, then the latter is unlikely to be the ultimate upper premolar; this suggests that there

is more than one upper premolar. Third, given the identification of the large wear facet on the lingual side of the upper premolar (SGP 2005/3) and buccal side of the lower premolars (SGP 2004/15-17), it could be inferred that the wear facets were created by shearing contact between these presumably mesial lower and upper premolars. However, because of the cusp orientation, these shearing facets would be created in an awkward way in which the tallest cusp of the upper premolar is distal, whereas the tallest cusp on the lower premolar is mesial. How such extensive wear facets could be formed remains a challenging issue to be explored. New evidence may prove *S. uyguricus* to be a unique species that has a lower molar similar to those of euharamiyidans in the almost coeval Yanliao Biota but possesses additional mesial premolars that are yet unknown in any other 'haramiyidans'.

*Lower molars:* As in the upper dentition, lower molars are relatively small compared to the enlarged p4. As in other euharamiyidans, the mesiolingual cusp (a1) is the largest and tallest, and positioned near the longitudinal axis of m1. The m2 is considerably smaller than m1 and its row b is reduced. There is a central valley on both m1 and m2. A distinct feature, however, is the presence of a distinct cusp b1 mesiobuccal to the base of a1. On the left m1, this cusp was broken but its base is still discernible, while b1 is distinct on the right m1. Presence of b1 is a common feature in Triassic 'haramiyidans' and European Middle Jurassic species (Mao *et al.* 2022). Both lower molars are single-rooted. The strong root gradually tapers distally. The root of m1 is shorter than those of p4, whereas the root of m2 is the shortest and weakest. As suggested by the crown size and shape, the root condition also indicates the functional role played by the teeth decreases from p4 to m2.

Presence of b1 on m1 in *Mirusodens* is an interesting and critical feature. On the lower molars of *Thomasia*, b1 is a distinct cusp, mesiobuccal to the base of a1, although it is lower than b2. A similar cusp was denoted in *Haramiyavia* (Hahn and Hahn 2006, Luo *et al.* 2015). This cusp condition is highly similar to that of *Mirusodens*. In other euharamiyidans, b1 was denoted in some euharamiyidans, such as *Arboroharamiya* (Meng *et al.* 2014), *Sineleutherus uyguricus*, and '*Sineleutherus*' *issedonicus* (Averianov *et al.* 2019), but it is a small cusp distobuccal to a1 and is within the row of b cusps (not lower than b2). Whether b1 in *Arboroharamiya* and *Sineleutherus* is homologous with that of *Mirusodens* and *Thomasia* is uncertain (Mao *et al.* 2022). Presence of this cusp on m1 of *Mirusodens* and European taxa is another feature that suggests possible relationship between euharamiyidans from the two areas.

*Postcranium* (Figs 1, 5)*:* The dorsal axial skeletal elements and ribs were gone or preserved as carbonized film, suggesting that these elements are less ossified or more gracile than the limb bones. Although the dorsal vertebrae are not preserved, the impressions of ribs indicate that the thoracolumbar transition is distinct, as in other euharamiyidans (Bi *et al.* 2014, Mao and Meng 2019a), which is a feature in extant mammals. The long tail consists of at least 16 caudal vertebrae. Some remains of caudal vertebrae are preserved and each caudal vertebra has a long and thin centrum. The number and length of the caudal vertebrae suggest a tail with possible prehensile ability, similar to those in other euharamiyidans.

**Figure 6.** Hair impressions of *Mirusodens caii* gen. et sp. nov. (holotype, HT-B-PM-0001) in comparison with extant mammals. A–G, correspond to red-boxed areas 1–7 in Figure 1. A, hair impressions at the outer area of the body fur; these hairs are long, fine, and somewhat curly. B, imaged area in the middle of the body fur impression; hair impressions are still visible but not so distinct compared to (A). C, imaged area near the skeleton, where the hair impression is unclear; this area may represent organic remains left by skin. D, imaged area on top of the skull, showing short, fine, and dense hair. E, imaged area around the forearm, showing long hair in comparison with the limb bones. F, sampled area along part of the caudal vertebrae; F', close-up view of the red-boxed area in (F). The hairs along the caudal vertebrae are long, thick, and straight. Numerous unidentified spherical particles are caught among the coarse hair, as pointed by the two white arrows and exemplified in the upper right corner. G, imaged area near the chest, showing carbonated films of the rib and dark areas that are possible organic remains left by skin. Note that in all these areas, there seems no evidence, such as a clear membrane edge, that suggests a patagium. However, it seems unlikely that all the dark areas represent fur. For instance, the dark area along the caudal vertebrae is much broader than the area bearing the coarse hair; such a wide area does not seem to be formed only by hair but possibly suggests presence of the patagium; H, from top to bottom: marsupial *Petraurus* (AMNH 196914), gliding; *Marmosa* (AMNH 266428), arboreal; and *Monodelphis* (AMNH 263547), terrestrial; I, placental *Glaucomys* (AMNH 188250), gliding; these show extension of the pelage in the body and tail morphology of gliding species in contrast to non-gliding species.

Most of the limb elements are preserved but in split condition (Fig. 1). The hindlimbs are splayed out and forelimbs are overlapped in preservation, but it is clear that the former are longer than the latter. For the hindlimb, the femur is shorter than the tibia and fibula. Where the bones are present, they largely remain in original articulation, except for the right pes and both manus that are displaced or partly missing. As in other euharamiyidans reported from the Yanliao Biota, the limb skeleton is gracile with elongated elements, displaying features characteristic of arboreal and even gliding locomotion. For instance, the ulna is proportionally long but the olecranon process is extremely short. The digits of both the pes and manus are slender and long; in lateral view they are curved and dorsoventrally thickened (the depth is greater than the width of each phalanx). Digit III appears to be the longest, whereas digit I is the shortest of the five, as best shown in the well-preserved left pes. Pedal digit I (dI) is the shortest; dII, dIII, and dIV are long and subequal in length, with dIII slightly longer than the other two. The dV is the second shortest digit. The ankle is compact (proximodistally short), as in mammals, such as *Jueconodon*, but different from the mammaliamorphs, such as *Fossiomanus* (Mao *et al.* 2021); both *Jueconodon* and *Fossiomanus* are from the Early Cretaceous Jehol Biota (Mao *et al.* 2021).

While the general skeletal morphology is similar to other euharamiyidans, the left pes displays some additional features. Viewing the pes as a whole with the fur impressions on it the toes are proportionally long, whereas the sole is relatively short; this reflects the osteological structures (Fig. 5). The five long and well-developed pedal digits are all separate and more or less evenly spaced; it does not show the opposite arrangement of digit I, as in some arboreal marsupials (Fig. 5G, H). However, for arboreal or gliding small mammals, the digit arrangements may not be so different compared to those of terrestrial species (Fig. 5I–L).

It is also clear that, as in other euharamiyidans, the proximal or intermediate phalanges are subequal to, or longer than, the metatarsals and metacarpals. Thus, the length of each finger or toe is much longer than the corresponding metapodial (Fig. 5E, F). This feature differs from those of small mammals (Fig. 5G–M), which is best illustrated in the bone elements of the arboreal *Glaucomy* (Fig. 5M). The elongated digits, along with the sharp and curved claw sheath, suggest capability of manual and pedal prehension, consistent with the interpretation that euharamiyidans are primarily arboreal animals (Zheng *et al.* 2013, Bi *et al.* 2014, Luo *et al.* 2015, Meng *et al.* 2015, Han *et al.* 2017, Mao and Meng 2019a, Wang *et al.* 2021).

The long fingers and toes could provide the capability for holding small tree branches. However, as tree branch or trunk gets thicker, the manus and pes of these small animals cannot reach around to grip by prehension of digits. Also, the toes (fingers may well be the same) of *Mirusodens* do not have expanded plantar pads to provide sufficient pad friction to keep the animal from falling. It is the claws that contribute to the ability for *Mirusodens* to cling to structures that have a sizable diameter, as in extant squirrels (Cartmill 1974). The long and sharp manual and pedal claws extend well beyond the apical pads of each toes, allowing the animal to cling on to tree trunks in different orientations, even vertical, by digging the claws into the substrate as anchor points; this would increase vertical agility of the animal

on tree trunks and allow the animal to move in all directions or at an angle across the climbing surface. Because of the divergent toes and fingers, as well as the long limbs, the claws can be spread out and positioned at relevant places so that the body (centre of gravity) is kept close to the tree and secure the body mass being evenly distributed across tree trunk and branches against the gravity, preventing the animal from falling.

*Soft tissues* (Figs 1, 5, 6): Soft tissues refer to impressions or potential remains of the integumentary system (fur impressions, keratin sheath, pads of the digits, and carbonized skin and hair) (Figs 1, 5, 6). It should be pointed out that the specimen is split into part and counterpart, and the breakage goes through the body of the animal such that the fur on the body surfaces would be preserved in the matrix of each split part (blocked by the skeleton, organic residues of the body, and potential stomach remains); thus, only those on the periphery of the body are better exposed. Although fur impressions of mammaliaforms from the Yanliao Biota have been reported from previous studies (Ji *et al.* 2006, Meng *et al.* 2006), the exquisitely preserved fur impressions of *Mirusodens* display some new details of fossilized integumentary system. The entire body of the small animal was insulated by dense fur, a good indicator of endothermy. Hair has differentiated into the guard hairs and under hairs with a diversity of length and density. At different areas of the body, hair varies in length and thickness, and density. The guard hairs are long, sparse, and coarse; they extend outward in the preserved impressions. The under hairs are short, fine, and dense; they are concentrated close to the body, such as the back of the skeleton, as expected. In the body area, the carbonized layer of organic remains, potentially the hair and perhaps skin, become thicker and darker. Hairs around the limbs are straight and long relative to the length of limb bones; some hairs measure up to 20 mm. By the preserved condition, these long hairs are on the ventral side of the body. This is similar to the condition displayed in the extant gliding mammals, such as the marsupial *Petaurus* and the placental *Glaucomys*, where hairs on the ventral side of the body, especially around the limbs, are long. In contrast, those on the toes are fine and short. The thickest hairs are along the caudal vertebra of the tail. The thickness for the short and fine hair ranges from 6 μm to 20 μm and can be as thick as up to 90 μm in those of the tail.

Unlike some gliding euharamiyidans (Han *et al.* 2017, Meng *et al.* 2017) and *Volaticotherium* (Meng *et al.* 2006), the impressions of the integumentary system on the holotype of *Mirusodens* do not show a clear sign of a patagium (the gliding membrane). Usually, the patagium can be recognized by its well-defined edge and the dark area (in contrast to the matrix) that bears fine impressions of hairs between body parts. However, in extant gliding mammals, either marsupials or placentals, the edge of the patagium is not sharply defined by skin but by hair, although the hair along the edge of the patagium is relatively short and even in length (Fig. 2H, I). If the gliding membrane is not fully stretched, the edge of the membrane is invisible. Nonetheless, the fur outline in gliding mammals is broader than those of nongliding ones. In the holotype of *Mirusodens*, the distributions of the fur impressions and the dark area that is apparently derived from the animal body are broad, extending between the head and forearms, between limbs, between hindlimbs and the tail,

and along the tail. Such a distributional pattern does not seem to be left only by hairs from a non-gliding animal. Compared to the extant gliding mammals and other gliding species of euharamiyidans from the Yanliao Biota (Han *et al.* 2017, Luo *et al.* 2017, Meng *et al.* 2017), we interpret that the dark areas are left by skin membrane and hair. Thus, *Mirusodens* represents another gliding species in the Yanliao Biota.

The left pes has been preserved in such an exceptional condition that the fur and pedal skin impressions of the toes, in association with the bones, are visible, representing an unprecedented example of pes morphology in Mesozoic mammals. Hairs are short, fine, and dense on the ankle and instep, and gradually reduce in density toward the toe tips. Some hairs extend to pass the apical pedal tip and reach to one-third or halfway along the claw. The hairs on the pes of *Mirusodens* are similar in length and distribution to those of extant small mammals (Fig. 5G–L). Impressions of the pedal skin or digital pads are visible, which have well-defined edges in contrast to the hair impressions overlapping it. They show that each toe ends distally at the proximal base of the distal phalanx. The skin impression outlines the shape of the long and separated toes. A slight curvature is present at the joint of the proximal and intermediate phalanges of digit II. The plantar pads do not show any expansion so that the toe gradually tapers toward the claw. The relationship of the hair and pedal skin suggests that the dorsal side, instep, of the pes is exposed because there is no sign of the foot pad, which should be on the plantar side of the pes; this orientation is consistent with the curvature of the phalanges. Lack of the digital pads differs from the pes of extant mammals (Voss and Jansa 2009, 2021).

As shown by the impressions or moulds, the manual and pedal digits bear well-developed claw sheaths that are sharp, transversely compressed, and dorsoventrally recurved. Possible remains of the keratin sheath are present in some digits. The horny claw sheath extends from the proximal base of the distal phalanx beyond the apical pads of each toe. The length of the sheath is about twice that of the distal phalanx length; it increases the length, sharpness, and curvature of the claw, which allows the capability of climbing on thick tree trunks (see below). Previous studies have recognized the arboreal limb structures of euharamiyidans, particularly the long digits relative to the metacarpals and metatarsals (Zheng *et al.* 2013, Bi *et al.* 2014, Luo *et al.* 2015, Meng *et al.* 2015, Han *et al.* 2017, Mao and Meng 2019a, Wang *et al.* 2021). The new morphologies of the pes reinforce the arboreality of these euharamiyidans and furnish additional arboreal features. These pedal morphologies reported here are unknown in any non-mammalian tetrapod but highly similar to those of extant mammals, such as squirrels (Cartmill 1974) or arboreal marsupials (Voss and Jansa 2009, 2021) (Fig. 5G–L).

### Phylogenetic analyses

With the new species and morphological features, we conducted a phylogenetic analysis based on a data matrix with 131 taxa and 573 characters (see Material and Methods and Supporting Information, File S1, S7). The euharamiyidan data have been refined to reflect revision of some allotherian species and their dental morphologies. In particular, teeth previously assigned to four Jurassic genera of 'haramiyidans' and multituberculates have been reinterpreted as from different tooth loci of the same euharamiyidan species, *Kermackodon oxfordensis* (Mao *et al.* 2022). The resulted consensus tree of the analyses is illustrated in Figures 7, 8. In the phylogeny, *Mirusodens* is grouped closely with arboroharamiyids from the early Late Jurassic Linglongta phase of the Yanliao Biota and the European Jurassic species (Kermack *et al.* 1998, Butler and Hooker 2005, Mao *et al.* 2022), to which shenshouids from the Yanliao Biota and Siberia form the outgroup. This is consistent with the view that 'haramiyidans' diversified and had cosmopolitan distributions in the Middle Jurassic. Our analysis places Euharamiyida (see below for definition) as the sister-group of gondwanatherians with *Cifelliodon* and *Thomasia* being the successive outgroups; this clade further pairs with multituberculates to form a sister-group that has *Haramiyavia* and *Theroteinus* as the outgroups. The Allotheria as a clade is deeply nested within Mammalia and forms the sister-group of the clade leading to therians, which is largely similar to the results of other studies (Krause *et al.* 2014, 2020a, Hoffman *et al.* 2020, Wang *et al.* 2021). 'Symmetrodontans' and eutriconodontans are the successive outgroup taxa of this allotherian–therian clade.

Our analysis reinforces the view that multituberculates, 'haramiyidans', and gondwanatherians constitute the clade Allotheria within Mammalia, which has long been recognized (Butler 2000, Kielan-Jaworowska *et al.* 2004, Hahn and Hahn 2006) and has been supported by recent phylogenetic analyses (Luo *et al.* 2007, Zheng *et al.* 2013, Bi *et al.* 2014, Krause *et al.* 2014, 2020a, Han *et al.* 2017, Hoffmann *et al.* 2020, Mao *et al.* 2020, 2021, Wang *et al.* 2021), although competing hypotheses exist (Luo *et al.* 2015, 2017, Huttenlocker *et al.* 2018). Given the preferred phylogeny and the morphological evidence, it is most probable that the Late Triassic *Haramiyavia* and *Theroteinus* represent the primitive morphotypes of allotherians that gave rise to the Jurassic euharamiyidans and multituberculates, a view previously put forward by others (Van Valen 1976, Hahn *et al.* 1989, Butler 2000, Butler and Hooker 2005, Hahn and Hahn 2006) and supported by several phylogenetic analyses (Bi *et al.* 2014, Krause *et al.* 2014, Han *et al.* 2017, Mao *et al.* 2021, Wang *et al.* 2021), and that mammals originated in the Late Triassic (Bi *et al.* 2014, Mao *et al.* 2021).

### Phylogenetic definition of Allotheria

A phylogenetic definition for Allotheria was given by Sereno (2006: 319) as: 'the most inclusive clade including *Taeniolabis taoensis* Cope 1882, but not *Mus musculus* Linnaeus 1758'. This definition has been adopted by Wang *et al.* (2021). However, the phylogenetic relationships of allotherians and other extinct groups have been unstable, and an ideal phylogenetic definition remains challenging. For instance, the above definition fits well to the phylogeny of Krause *et al.* (2020a) but not necessarily so for others, such as Krause *et al.* (2014), Luo *et al.* (2015), Wang *et al.* (2021: extended data figs 8, 9), and this study because the definition does not sufficiently accommodate taxa that do not belong to the inclusive clade including *Taeniolabis taoensis*, nor are they closely related to the clade containing *Mus musculus* or *Ornithorhynchus anatinus*. In our phylogeny (Figs 7, 8), for instance, such taxa include 'symmetrodontans', eutriconodontans, *Tinodon*, and *Fruitafossor*. Employing species such as *Taeniolabis taoensis* as the anchor point to formulate the definition could
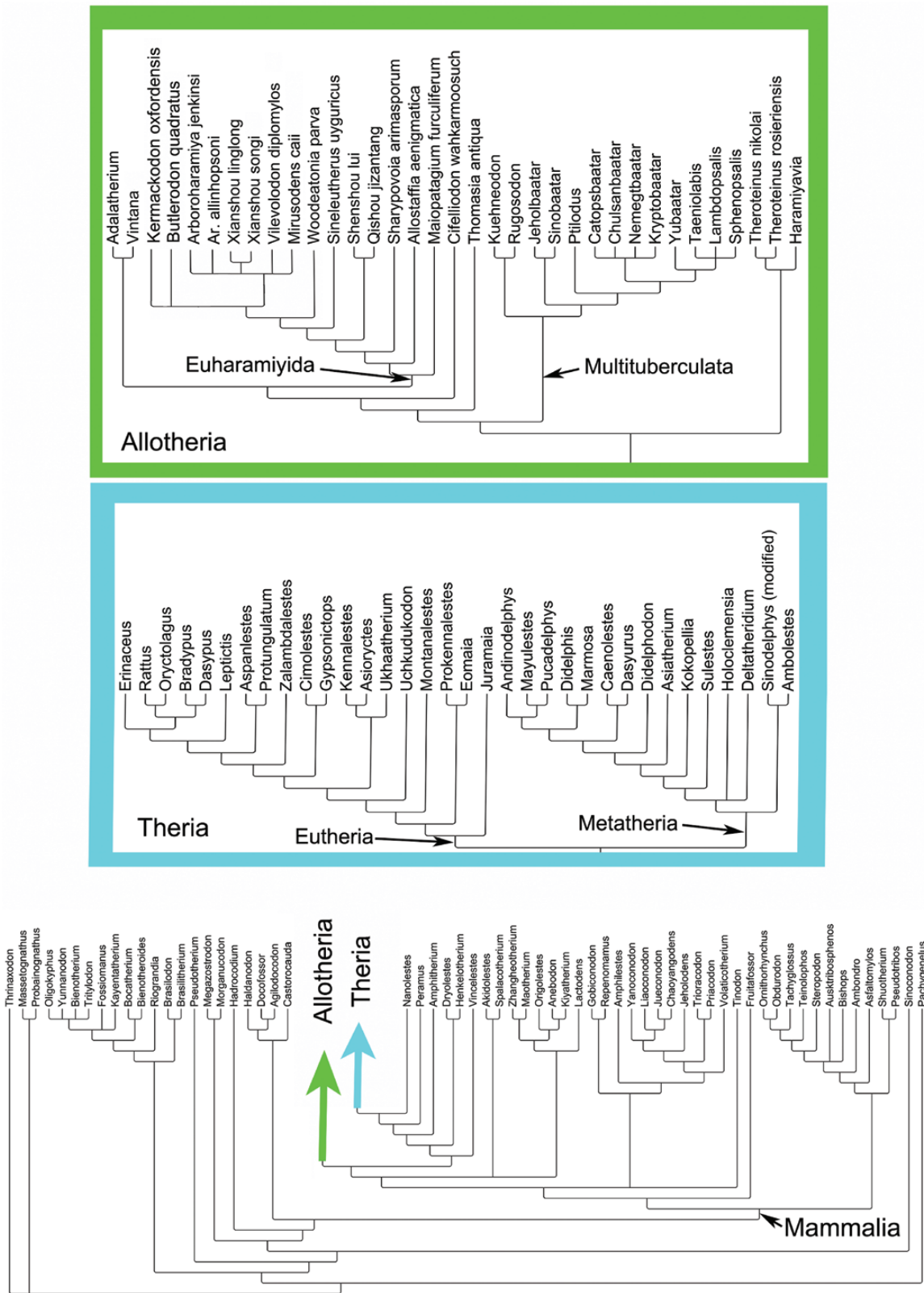
**Figure 7.** Strict consensus tree of 990 trees retained in heuristic search using (PAUP*, v.4.0) (Swofford 2002). Tree length = 2968; consistency index (CI) = 0.3245; homoplasy index (HI) = 0.6755. See Material and Methods and Supporting Information, File S1.

promote stability of the definition (Sereno 2006), compared to that using higher-level taxa to formulate the definition (Rowe 1988), but this may also be problematic for practical reasons. For instance, in some studies of early mammaliamorphs, the terminal taxa used for the phylogenetic analysis are primarily fossils, such as Krause *et al.* (2014), that do not include *Mus musculus*, and in others the terminal taxa are at the generic or higher taxonomical rank, such as cimolodontans in Luo *et al.* (2015), which
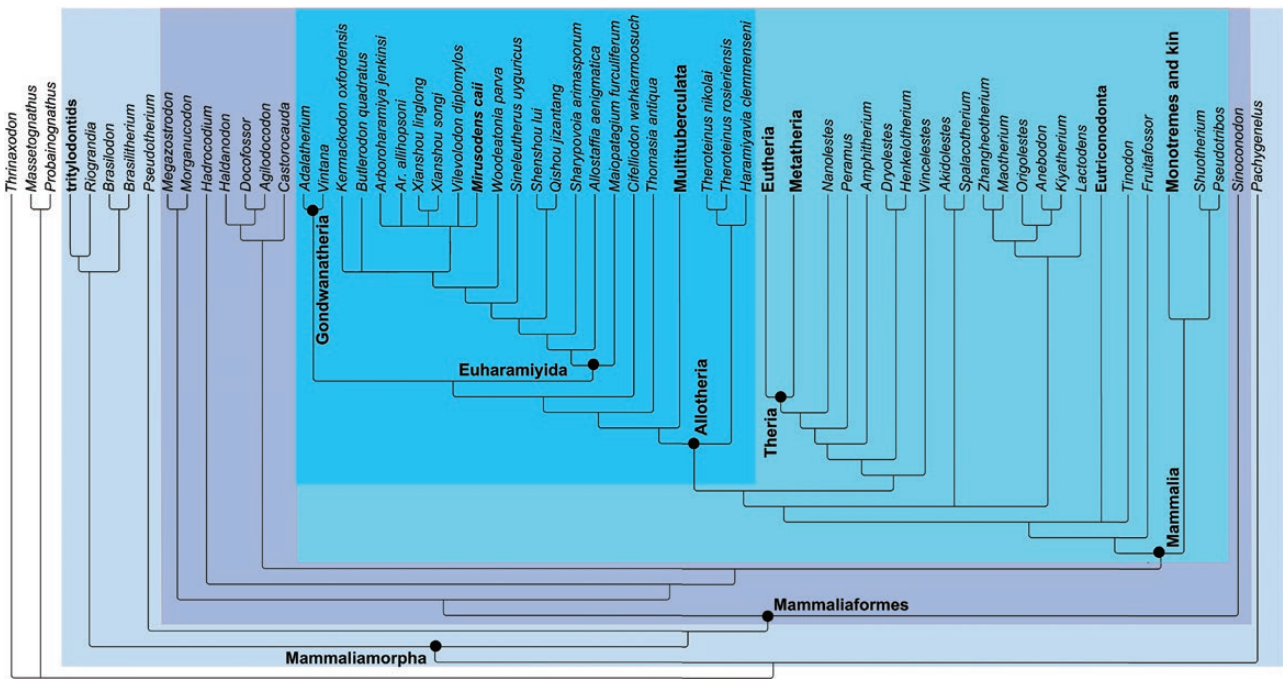
**Figure 8.** Key phylogenetic nodes and clades within mammaliamorphs. The phylogeny is condensed from the strict consensus tree Supporting Information, File S1, showing the placement of *Mirusodens caii* within Euharamiyida, Allotheria and Mammalia. The phylogenetic frame form the basis for the definitions of Euharamiyida and Allotheria (see text).

makes the definition per se semantically unclear if contrasting to those phylogenies. Considering these factors, we propose an alternative phylogenetic definition: Allotheria is the most inclusive clade containing taxa of Multituberculata (*sensu* McKenna and Bell 1997) but not those belonging to the clades of therians, monotremes, or any falling between the latter two clades. In this definition, 'taxa' implies any number of taxa at either the species, generic, family, or even higher level. Given that the allotherian phylogenies are still unstable, the definition hopefully offers the flexibility that could fit to phylogenetic analyses regardless how many terminal taxa and at which ranks are used.

## Phylogenetic definition of 'Haramiyida'

Wang *et al.* (2021: their supporting information) proposed a phylogenetic definition for 'Haramiyida': 'The most inclusive clade including *Thomasia antiqua* Plieninger 1847, but not *Cifelliodon wahkermoosuch* Huttenlocker *et al.* 2018, *Taeniolabis taoensis* Cope 1882, or *Adalatherium hui* Krause *et al.*, 2020'. The intention of this definition was perhaps to include *Thomasia* as the anchor taxon in the group because it is the typical 'haramiyidan' in the conventional view. However, this definition excludes *Haramiyavia*, another key member in the conventional taxonomy of 'haramiyidans'. The most problematic aspect of this definition is its being narrowly phylogeny-specific. This definition is based on, and thus reflects, the phylogeny reconstructed by Wang *et al.* (2021); it is hardly applied to many other phylogenies proposed in recent studies or, if applied, it would result in a distortion of what 'haramiyidans' mean in a broadly accepted sense. For instance, in the phylogeny obtained by Huttenlocker *et al.* (2018: fig. 4), 'Haramiyida' as defined by Wang *et al.* (2021) contains only the clade of *Haramiyavia* and *Thomasia* that forms the sister-group of the clade of Eleutherodontida. However, all

eleutherodontidans are not 'haramiyidans' by definition because the Eleutherodontida contains *Cifelliodon*, a taxon that is excluded from 'Haramiyida' by the definition. In the phylogeny of Krause *et al.* (2020a), for instance again, the pair of *Haramiyavia–Thomasia* was clustered with tritylodontids and placed outside of mammaliaforms; thus, by the definition of Wang *et al.* (2021) tritylodontids are 'haramiyidans' but all euharamiyidans are not. Similarly, the definition of Wang *et al.* (2021) cannot apply to the phylogeny we have here, because *Thomasia* is the outgroup of the clade that contains *Cifelliodon*, gondwanatherians, and euharamiyidans; again, the clade that contains *Thomasia antiqua* also contains taxa that are excluded by the definition of Wang *et al.* (2021). All these cases result from the fact that *Thomasia* is generally primitive in dental morphology and represented by poor specimens; thus its phylogenetic position is unstable. Therefore, the definition of Wang *et al.* (2021) for 'Haramiyida' creates instability in the phylogeny and taxonomy of 'haramiyidans'. There seems no meaningful phylogenetic definition of the potentially paraphyletic 'haramiyidans' (in the conventional sense) based on available evidence. For the sake of histological and practical reason, however, we think it is still useful to keep the widely used term 'Haramiyida' ('haramiyidans'), placed in quotation marks. This usage is more or less similar to 'Triconodonta' ('triconodontans') vs. Eutriconodonta (eutriconodotans).

## Phylogenetic definition of Euharamiyida

It is possible to reach a practical and stable definition of Euharamiyida for the reason that this group is supported by mounting derived features and thus becomes increasingly stable phylogenetically. Based on our phylogeny (Figs 7, 8) and other recent phylogenies (Huttenlocker *et al.* 2018, Krause *et al.* 2020a, Wang *et al.* 2021), we propose the following phylogenetic
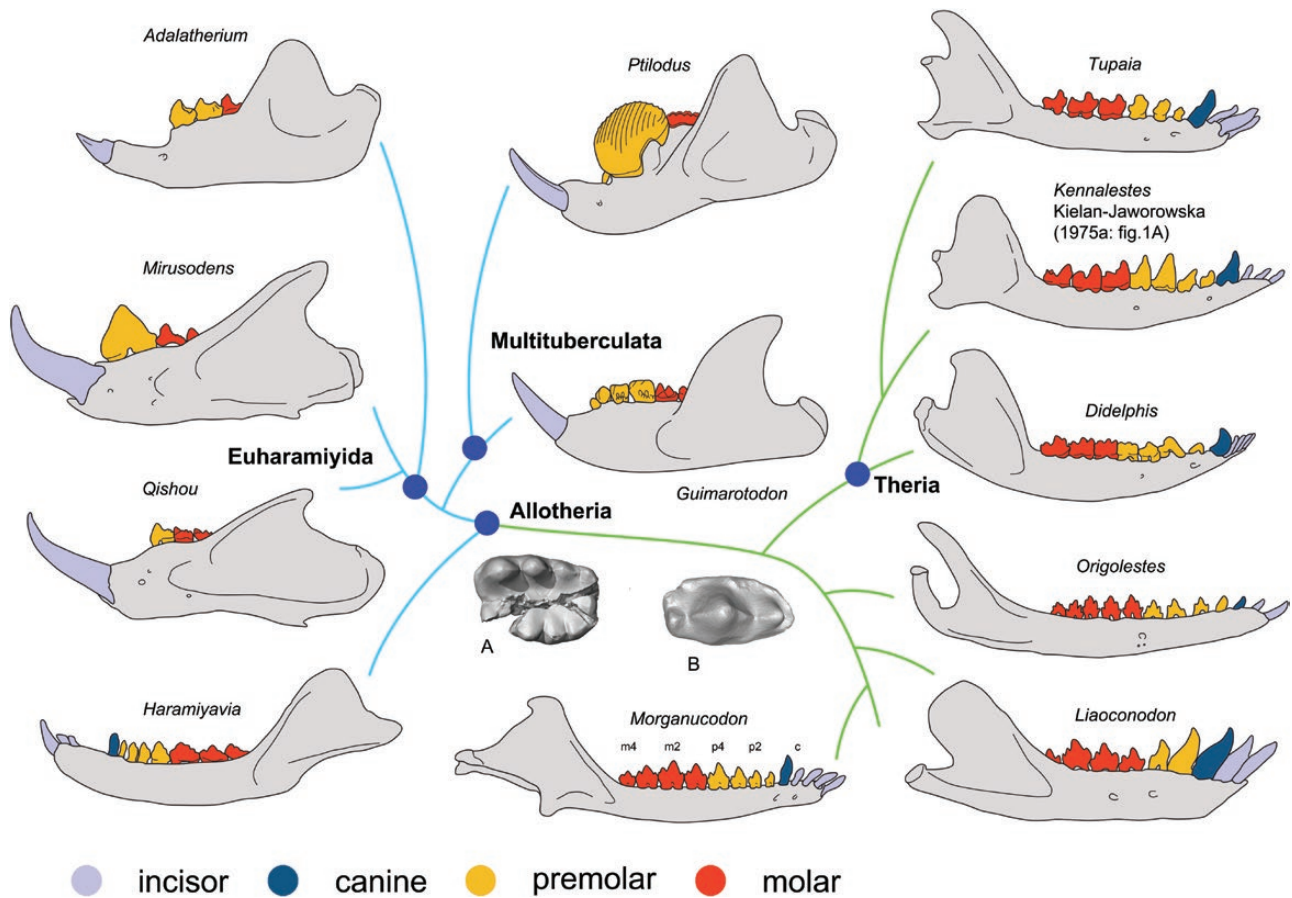
**Figure 9.** Mandibular–dental morphologies of allotherians in contrast with those leading to therians within a simplified phylogeny of Mammalia. Selected representative mammaliaform taxa contrasting the mandibular and dental features from allotherians and therians and kin. Allotherians are characterized by the molar pattern with two rows of multiple cusps (I, *Haramiyavia clemmenseni*); it differs from the triconodont molar that has three main cusps aligned in a row (II, an undescribed *Morganucodon* molar), as in *Morganucodon* and euriconodontans, which presumably gave to other dental patterns with the lineage toward therians. The branching pattern is simplified from Figure 8. Figures modified from other studies include *Guimarotodon* (Hahn and Hahn 1998), *Morganucodon* (Kermack *et al.* 1973), *Kennalestes* (Kielan-Jaworowska 1975), *Liaoconodon* (Meng *et al.* 2011), *Haramiyavia* (Luo *et al.* 2015), *Ptilodus* and *Adalatherium* (Krause *et al.* 2020b); *Qishou* (Mao *et al.* 2019a), and *Origolestes* (Mao *et al.* 2020).

definition: Euharamiyida is the most inclusive clade including taxa of arboroharamiyids (*Arboroharamiyida*, *Xianshou*, and *Vilevolodon*) but not those belonging to the clades of multituberculates, gondwanatherians, monotremes, therians, or any clade falling between the named clades. Again, in this definition, 'taxa' implies any number of taxa at the species, generic, family, or even higher level, from a clade that are used for reconstructing the phylogeny.

## DISCUSSION

### Competing phylogenies

The phylogenetic relationships of allotherians have remained as a lasting and the most controversial subject in the study of early mammal evolution. The earliest reported allotherian is *Thomasia* ['*Microlestes*', this name was pre-occupied and replaced by *Thomasia* (Poche 1908)] *antiquus* Plieninger 1847. Ten years later, the first multituberculate, *Plagiaulax becklesii*, was reported by Falconer (1857). While Falconer recognized the molar similarity between the two species, his view was countered by Owen (1871) who argued that the affinity of *Plagiaulax* was better based on 'dental system' rather than similarity of isolated teeth, for *Thomasia* was known only from isolated teeth at the time. Owen considered *Plagiaulax* to be more similar to some carnivorous marsupials based on its dental and lower jaw morphologies and placed *Plagiaulax* in Marsupialia.

With more discoveries of multituberculates and other Mesozoic mammal fossils, Marsh (1880) was convinced that these Mesozoic mammals could not be satisfactorily placed in any orders of extant mammals. Based on *Plagiaulax*, *Ctenacodon*, and possibly one or two other genera, Marsh (1880) proposed a new order, Allotheria, that is characterized by five dental and mandibular features. Marsh also noted that these characters alone could not sufficiently separate *Plagiaulax* from some of the marsupials and expected that future discoveries may prove multituberculates to be a suborder of marsupials. The concept of Allotheria has since remained somewhat equivalent to Multituberculata, and their relationship to other mammaliaforms remains uncertain, as Simpson (1945: 168) wrote: 'The multituberculate structure was so radically distinctive throughout their history that it seems hardly possible that they are related to other mammals except by a common origin at, or even before,

the appearance of the class as such, a conclusion that necessitates placing them in a separate subclass as well as order.'

More than a century later since the proposal of Allotheria, 'haramiyidans' were added to Allotheria based on additional tooth specimens (Hahn *et al.* 1989). A brief history of the early discoveries of 'haramiyidans' was introduced by Butler and MacIntyre (1994). Among those discoveries, a large sample of haramiyidan teeth was made from the Saint-Nicolas-de-Port quarry (Rhaetian, France) (Sigogneau-Russell 1989). This collection showed a great diversity of the dental morphologies of 'haramiyidans' and triggered many discussions on 'haramiyidans' thereafter. A critical advance made in the study of haramiyidan teeth was the recognition that specimens assigned to '*Haramiya*' and *Thomasia* represent the upper and lower teeth, respectively (Butler and MacIntyre 1994). 'Haramiyidans' have been considered either as the earliest multituberculates (a sub-order within Multituberculata) (Hahn 1973, Sigogneau-Russell 1989), a sister-group of the multituberculates (Butler and MacIntyre 1994, Gambaryan and Kielan-Jaworowska 1995), or a paraphyletic group that gave rise to multituberculates (Van Valen 1976, Hahn *et al.* 1989, Butler 2000, Butler and Hooker 2005, Hahn and Hahn 2006). A close relationship of 'haramiyidans' and multituberculates was clearly proposed by Hahn (1973: 2):

> By the discussed results of 1) the morphological comparison of the teeth, 2) the similarity in the use of the teeth as stated by their traces of wear and 3) the impossibility to combine the haramiyids with the traversodonts, it follows that with great probability the haramiyids are members of the multituberculate stock. Perhaps they are the direct ancestors of younger multituberculates (the lowering of the anterior cusps and the grooving of the enamel may have evolved from Rhaetic to Kimmeridgian time), perhaps they are an early side branch - in each case they show as the only group in Rhaetic times clearly many of the tendencies which one must expect in the ancestors of the Multituberculata. Pointing out this fact in the systematic arrangement, the Haramiyidae are grouped now as a new suborder - Haramiyoidea - within the multituberculates, being the oldest known members among them.

Butler (2000: 317) held a similar view in stating: 'Dental resemblances support the hypothesis that the Multituberculata originated within the Haramiyida, in which case the Haramiyida would be paraphyletic.'

The non-therian affinities of gondwanatherians, specifically in association with multituberculates, became popular in the 1990s (Krause and Bonaparte 1990, 1993, Sigogneau-Russell *et al.* 1991, Krause *et al.* 1992). Gondwanatheria was added to Allotheria as a sister-group to Multituberculata by Pascual and Ortiz-Jaureguizar (2007), which was supported by phylogenetic analysis (Gurovich and Beck 2009), but this phylogeny placed Allotheria as a clade outside of Mammalia. Recent studies with better fossil material placed gondwanatherians, along with multituberculates and euharamiyidans, in a monophyletic Allotheria within Mammalia (Krause *et al.* 2014, 2020a). Thus, Allotheria becomes a tripartite taxon, comprised of 'haramiyidans', multituberculates, and gondwanatherians.

Moreover, new gondwanatherians also greatly extended our knowledge of this southern group and its affinity with the allotherians (Krause *et al.* 2014, 2020a). Based on the tree topology, gondwanatherians would have originated by the Middle Jurassic, as already noted by Hoffmann *et al.* (2020). The high-crowned and multiple enamel-ridged tooth patterns in many gondwanatherians (Krause *et al.* 2014, 2021, Rougier *et al.* 2021) are more reflective of the allotherian tooth pattern than the triconodontan, symmetrodontan, or tribosphenic pattern. The unique molar morphologies of gondwanatherians may be interpreted as a specialization of the groups in the southern continents, and much of the morphological diversity is yet to be discovered (Hoffmann *et al.* 2020).

Again, this tripartite Allotheria as a mammalian group has been supported by many phylogenetic analyses (Luo *et al.* 2007, Zheng *et al.* 2013, Bi *et al.* 2014, Krause *et al.* 2014, 2020a, Hoffmann *et al.* 2020, Mao *et al.* 2020, 2021) and reinforced by this study. Differences exist among these phylogenetic relationships owing to different taxa and characters sampled. For instance, the recent phylogenetic analysis of Krause *et al.* (2020a) recognized the tripartite Allotheria within Mammalia, but removed *Megaconus*, *Thomasia*, and *Haramiyavia* outside of Mammalia. In the same phylogeny, *Megaconus* was identified as a stem tritylodontid and *Thomasia* and *Haramiyavia* form the sister-group of the clade consisting of *Megaconus* and tritylodontids. In another study (Wang *et al.* 2021), gondwanatherians, as represented by *Vintana* and *Adalatherium*, either form a sister-group of multituberculates (ibid., extended data Fig. 8) or a sister-group of cimolodontans within multituberculates (ibid., extended data Fig. 9). Nonetheless, the consensus of these studies is that Allotheria, as defined in this study, is a mammalian clade that includes euharamiyidans, multituberculates, and gondwanatherians. A competing hypothesis has placed all 'haramiyidans' outside of Mammalia but retained multituberculates as mammals (Zhou *et al.* 2013, Luo *et al.* 2015, Huttenlocker *et al.* 2018). These studies were based on datasets derived from Zhou *et al.* (2013), with modifications in later versions. As pointed out by Han *et al.* (2017: supporting information): 'If haramiyidans are placed outside of mammals, then numerous similar characters in cranium, mandible, dentition and post cranium, along with the DMME, must have evolved independently in haramiyidans and multituberculates'. Many such characters shared by allotherians are summarized in the discussion below. On the other hand, what characters that counter these shared characters and place 'haramiyidans' outside of Mammalia remain to be seen.

## The evidence then

Since 1847 when *Thomasia* was reported (Plieninger 1847), 'haramiyidans' were known by isolated teeth until the report of *Haramiyavia* was represented by some jaw and dental material (Jenkins *et al.* 1997). For many decades, the evidence to consider 'haramiyidans' as mammals was primarily their multicuspid molars with divided roots (Simpson 1928, Butler 2000). Butler and MacIntyre (1994) pointed out that these characters are present in Tritylodontidae, but we think the root condition and tooth crown morphology of tritylodontids are different from those of 'haramiyidans'. In addition, the preprismatic enamel structure (Frank *et al.* 1984) and small body size (Clemens and Kielan-Jaworowska 1979) were also used to support their mammalian affinity, but these features are probably plesiomorphic for mammaliaforms and present in non-mammalian cynodonts,

such as *Morganucodon.* The evidence uniting 'haramiyidans' and multituberculates as allotherians is the gross similarity of the two rows of multiple cusps on their molars (Butler 2000). On the other hand, Butler and MacIntyre (1994) noted that 'haramiyidans' differ from the Jurassic and later multituberculates in having the basined molars, the reversed symmetry of upper and lower molars, and the similar occlusal relations of M1 and M2, so that these differences seem sufficient to justify separation of 'haramiyidans' from multituberculates. Comparing the upper molar of the earliest unequivocal multituberculates with those of 'haramiyidans', Mao *et al.* (2022: 19) summarized: 'the upper molars of the Middle Jurassic multituberculates and euharamiyidans are different in cusp shape, cusp size variation, basin shape, M1–M2 contact relation, tooth root, and enamel microstructures'. It should be noted that primitive columnar enamel and the preprismatic enamel (Frank *et al.* 1984) or incipient prism-like enamel (Mao *et al.* 2017) exist in both 'haramiyidans' and multituberculates (Mao *et al.* 2017); true prisms are present in multituberculates, but not in 'haramiyidans'.

Furthermore, Kielan-Jaworowska *et al.* (2004: 524) noted: 'Based on molar characteristics alone, multituberculates are certainly more comparable to haramiyidans. However, multituberculates are far more derived than haramiyidans and tritylodontids in mandibular characters, and in these characters they are more closely comparable to the more derived mammalian clades in the mammalian crown group.' This statement was made when the mandible structure of 'haramiyidans' was known only from the Late Triassic *Haramiyavia* (Jenkins *et al.* 1997) for which presence of the postdentary trough has been on debate (Averianov *et al.* 2011, Bi *et al.* 2014, Luo *et al.* 2015; personal observation of the holotype specimens by F.M. and J.M.). The mandibles of euharamiyidans, as reported in several studies on the Yanliao species, are highly similar to those of multituberculates (see below).

Despite all the differences noted above, 'haramiyidans', especially euharamiyidans as defined in this study, and multituberculates still share more derived similarities than either of them to any other group of mammaliamorphs. In addition to the two rows of cusps, the MM2 occlusion (Meng *et al.* 2014, Mao and Meng 2019b) and the labial cusps on the M2 of both groups being larger than the lingual cusps (Hahn 1971, Butler and Hooker 2005, Yuan *et al.* 2013, Averianov *et al.* 2020, Mao *et al.* 2022) are also dental features shared by 'haramiyidans' and multituberculates. The discoveries of several species of euharamiyidans represented by skeletal material from the Jurassic of China have demonstrated that the mandibular characters are no longer features separating multituberculates and euharamiyidans; in fact, they strongly suggest a close relationship of the two groups. In addition to the dental characters mentioned above, we summarize other characters shared by allotherians in the next section. It should be kept in mind that 'haramiyidans' are probably paraphyletic and taxa placed in this group in early studies include the Late Triassic forms, such as *Haramiyavia*, and Jurassic forms, such as *Kermackodon* ('*Eleutherodon*') (see: Mao *et al.* 2022). The Jurassic forms have been placed in euharamiyidans and a monophyletic Euharamiyida, as defined in this study, has been recognized by most recent studies that independently reached a similar conclusion (Krause *et al.* 2020a, Mao *et al.* 2020, 2021, Wang *et al.* 2021; this study).

## Shared features for allotherians (Fig. 9)

1.  *One pair of lower incisors (reduction of lower incisor number) with roots extending backward in the dentary.*

This may be viewed as representing at least two features. First, it is a common pattern that mammaliamorphs have more than one lower incisor, such as *Sinoconodon* and *Morganucodon* that have four lower incisors in each lower jaw (Kielan-Jaworowska *et al.* 2004); loss of incisors would be a derived feature in allotherians, although this could take place independently in different groups. For instance, the tritylodontid *Oligokyphus* has three lower incisors, but *Kayentatherium* (and others) has only one (Kühne 1956, Sues 1986). Second, the lower incisor in mammaliaforms usually has a short and nearly vertically implanted root, whereas the root of the lower incisor of allotherians is robust and long, extending posteriorly to a level below the cheek teeth. In tritylodontids that have a single and enlarged lower incisor, the root is not so deeply extended (Hoffman and Rowe 2018, Mao *et al.* 2021). Moreover, the enlarged lower incisor of euharamiyidans is diphyodont (Mao *et al.* 2019), a typical mammalian feature, and is similar in shape and pattern to those of multituberculates (Greenwald 1988, Wible *et al.* 2019). In known 'haramiyidans', *Haramiyavia* is the only one that has three lower incisors (Luo *et al.* 2015) (originally four; Jenkins *et al.* 1997), which is probably a plesiomorphic condition.

2.  *Enlargement of the upper and lower incisors.*

The upper and lower incisors are small in most mammaliamorphs, except for some tritylodontids, so that this should be a derived feature. In tritylodontids, as well as the marsupial *Dactylopsila trivirgata* and *Petaurus breviceps*, the enlarged upper and lower incisors are more or less similar in shape with a single tip that continues toward the root, whereas in allotherians, the enlargement of the upper incisor, varying at the degree of enlargement in various species, is different from the lower one. The crown of the upper incisor is enlarged, relative to other teeth, but the crown and the root are delimited by a neck and the enamel-covered crown does not extend into the jawbone, which differs from the lower incisor. *Haramiyavia* does not show incisor enlargement, which is a primitive feature for 'haramiyidans'.

3.  *Two or more cusps on the enlarged upper incisor.*

There are commonly two cusps, a mesial one and a distal one, on the enlarged upper incisor, presumably I2 (Hahn 1971, Hahn and Hahn 2006, Averianov *et al.* 2020). In more advanced Jurassic forms, the enlarged upper incisor bears more cusps, of which *Mirusodens* represents the extreme condition. This condition is similar to some Cenozoic mammals, such as the plesiadapid *Pronothodectes* (Boyer *et al.* 2012); in the latter, the cusps do not bear enamel flutings. A multicuspid upper incisor and a pointed lower incisor form a food-picking device that is unique for allotherians, differing from those of tritylodontids or Glires, although such a device may be modified in later and more advanced forms, such as the Late Cretaceous gondwanatherian *Adalatherium* (Krause *et al.* 2021) and Cenozoic multituberculate *Lambdopsalis* (Miao 1986). Bicuspid upper incisors are shared by 'haramiyidans' and multituberculates (Gambaryan

and Kielan-Jaworowska 1995) and present in some eutherian mammals; along with the pointed, procumbent lower they form an efficient grasping mechanism used by shrews for picking up and killing insects (Gambaryan and Kielan-Jaworowska 1995). In *Haramiyavia* the incisors are single-cusped and not enlarged, representing the primitive condition for allotherians.

4. *Absence (loss) of the lower canine.*

Although the upper canine is present in some Jurassic multituberculates, such as *Kuehneodon* Hahn 1969, *Pseudobolodon* Hahn 1977, and *Rugosodon* Yuan et al. 2013, the lower canine is absent in all known multituberculates, euharamiyidans, and gondwanatherians where the lower dentition is known. In mammaliamorphs, the lower canine is generally present except for tritylodontids (Kühne 1956, Sues 1986); however, tritylodontids do not have cheek teeth differentiated, which is a non-mammaliaform feature. *Haramiyavia* has the lower canine. Tooth reduction is not uncommon in early mammaliaforms, such as *Sinoconodon* (Crompton and Luo 1993), but it is the premolars, not the canine, that is usually lost.

5. *Two molars in each jaw quadrant.*

Differentiation of the cheek teeth into premolars and molars is a mammaliaform condition, differing from the non-differentiated cheek teeth of tritylodontids and other non-mammalian cynodonts. In the conventional view, euharamiyidans and multituberculates share a derived feature in having two molars in each jaw quadrant. In gondwanatherians, there are four molariforms (Krause *et al.* 2014) or postcanines (Krause *et al.* 2020a) that display unique tooth morphologies different from those of Mesozoic mammals from the northern continents, which may be interpreted as a specialization of the groups in the southern continents and much of the morphological diversity is yet to be discovered (Hoffmann *et al.* 2020). However, it has also been hypothesized that the anterior molariforms of gondwanatherians evolved from blade-like precursors similar to the p4 of *Ferugliotherium*, possibly in response to the appearance of grasses in Gondwana during the Cretaceous (Gurovich and Beck 2009). These highly derived tooth morphologies do not form an obstacle for the interpretation that allotherians have two molars.

*Haramiyavia* has three molars, at least judging by the shape, in each lower and upper jaw (Jenkins *et al.* 1997, Luo *et al.* 2015); this is probably the plesiomorphic condition for allotherians. The number of molars is unknown in *Thomasia* for which various possible reconstruction of its dentition have been proposed (Butler and MacIntyre 1994, Debuysschere 2015). Given that *Haramiyavia* has three molars, it is probable that *Thomasia* had a maximum of three molars in each jaw quadrant. With that assumption, and the possibility that the teeth grouped as '*Thomasia* II' (Sigogneau-Russell 1989) are either m1 (Butler 2000) or lower premolar (Debuysschere 2015), the distal three teeth of *Thomasia* are probably similar to those of *Qishou* (Mao and Meng 2019a). This is because *Thomasia* II teeth are highly comparable to p4 of *Qishou*, where a1 is enlarged but cusp row b is still distinct (Mao *et al.* 2022: fig. 17A3, A4, D). On the other hand, *Mirusodens* shows an extreme condition within

'haramiyidans' by displaying the highly specialized ultimate premolars. This morphocline of ultimate premolars from *Qishou* to *Mirusodens* is similar to that in multituberculates. For both multituberculates and euharamiyidans, the ultimate premolars evolved from a molariform tooth to an enlarged and blade-like one; the molars became relatively minor in size and function. This shows that the two groups share similar developmental plasticity that could produce the similar phenotypes of the antepenultimate teeth for a similar functional role.

There exists the view that the ultimate premolar of multituberculates could be a molar, which was suggested long ago (e.g. Patterson 1956) and has been occasionally raised in recent studies [A. Weil in Wible and Rougier (2000), Meng (2014)]. Nonetheless, even if the antepenultimate cheek tooth is proved to be a molar, its high specialization, as a plagiaulacoid tooth (Simpson 1933), would still be a derived feature shared by euharamiyidans and multituberculates. Although the plagiaulacoid dentitions are present in various therians (Simpson 1933, Clemens and Kielan-Jaworowska 1979, Gambaryan and Kielan-Jaworowska 1995), those teeth are on different tooth loci in 'haramiyidans' and the chewing movement is different.

6. *Reduction of lower tooth number.*

As a general feature, the total number of lower teeth is less than the upper ones in allotherians. A potential functional explanation is that this is an adaptation for palinal chewing. If the chewing is unilateral and has a transverse component, as in 'triconodontans' and their derivatives (Crompton and Hiiemae 1970, Crompton and Sita-Lumsden 1970, Crompton 1971, 1974), the upper and lower dentitions with subequal length would function efficiently within the available oral space. For a palinal chewing movement, however, if the upper and lower dentitions have full dentitions (e.g. the premolars and canines are present) and their lengths are subequal, then there could be a problem for palinal jaw movement. In all allotherians known (best known in multituberculates), the lower dentition is shorter than the upper so that the lower teeth work against a longer pad of the upper dentition and could always engage in contact with the upper teeth during chewing. This has been convincingly shown by Gambaryan and Kielan-Jaworowska (1995). For rodents that are capable of propalinal jaw movement, the upper and lower dentitions are subequal in length, but similar to allotherians, their canines and premolars are lost.

The lower dentition shorter than the upper is achieved by reducing the tooth number in most allotherians. In the earliest known multituberculates, where the lower and upper teeth are not specialized, the maximum number of lower cheek teeth is six, whereas the uppers have at least one more tooth (Kielan-Jaworoska *et al.* 2004). In addition, the lower cheek teeth are tightly compacted, which contributes to length reduction of the cheek tooth row. In species with enlarged (elongated) p4, such as *Ptilodus*, the lower cheek teeth are reduced to four with p3 becoming a tiny and non-functional cusp-like tooth, whereas the upper teeth retain a more or less normal dental formula and shape. In taeniolabidoids, where p4 and P4 are simplified and reduced in size and the cheek tooth number is the same, the upper molars are enlarged (elongated) to a greater degree than the lower ones so that the lower dentition is still shorter than

the uppers [see samples of *Taeniolabis* and *Lambdopsalis* in Mao *et al.* (2016)]. This lower molar reduction in tooth number and length is unique for allotherians in Mesozoic mammaliamorphs. In tritylodontids, the lower dentition is as long as the upper (Sues 1986). *Haramiyavia* has a lower dentition with a full set of teeth, similar to other mammaliaforms (Fig. 4A), which should be a plesiomorphic feature for allotherians.

7.    *Lower molar mesiolingual cusp large.*

As mentioned above and summarized by Mao *et al.* (2022), a shared feature for known 'haramiyidans' is that the mesiolingual cusp of the lower molar is the largest and this feature is shared by early multituberculates. Kielan-Jaworowska *et al.* (2004) considered that paulchoffatiids and some pinheirodontids, differing from other multituberculates, have molars with cusps of different heights, similar to that of 'haramiyidans' and this was considered as a plesiomorphic feature, compared to the even-sized cusps in later multituberculates. In our view this feature may be plesiomorphic for multituberculates, but could well be a shared derived feature for allotherians. This is because in mammaliamorphs that have multiple cusps in one row, such as *Sinoconodon* and *Morganucodon*, the middle one, cusp a, is the largest. In tritylodontids that have two cusp rows, the cusps are subequal or the mesial cusps tend to be smaller; these cusps are also crested in shape. In 'haramiyidans' and early multituberculates, the mesiolingual cusp is usually conical and the largest one on the lower molar (Hahn 1971, Yuan *et al.* 2013), similar to that of Late Triassic 'haramiyidans', such as *Haramiyavia* and *Thomasia*, as compared by Mao *et al.* (2022). In association to this lower molar feature, the upper molars of 'haramiyidans' have labial cusps that are larger than the lingual ones, which is also true at least in M2 of multituberculates.

8.    *Lingual cusp row of m2 occluding in the central valley of M2.*

In the conventional view about multituberculate occlusion, the m1–M1 occlusal relationship (MM1 occlusal mode; Mao and Meng 2019b) has attracted attention (Kielan-Jaworowska *et al.* 2004). In the MM1 mode, the buccal cusps of m1 bite in the central valley of M1. However, Meng *et al.* (2014) (see also: Mao and Meng 2019b) has argued that the m2–M2 occlusal pattern (MM2 mode; Mao and Meng 2019b) is a shared derived character between euharamiyidans and multituberculates. In the MM2 mode, the lingual cusps of m2 bite in the central valley of M2. The MM1 mode is probably a primitive feature, whereas the MM2 mode is derived and unique so that it bears more phylogenetic information for reconstructing phylogenetic relationships within mammaliamorphs.

It is known that in all euharamiyidans the molars have the MM2 occlusal mode (Zheng *et al.* 2013, Bi *et al.* 2014, Han *et al.* 2017, Luo *et al.* 2017, Mao and Meng 2019a), with the exception of *Maiopatagium furculiferum* (Meng *et al.* 2017). However, the occlusal pattern of *M. furculiferum* contradicts that of *M. sibiricum* (Averianov *et al.* 2019), because it shows an MM2 occlusal mode, as in other euharamiyidans (Mao *et al.* 2022). The molar occlusal pattern in *Haramiyavia* remains uncertain. Although an MM1 mode was proposed for *Haramiyavia* (Jenkins *et al.* 1997, Luo *et al.* 2015), this interpretation has not been supported by unequivocal evidence, as discussed elsewhere (Meng *et al.* 2014, Mao and Meng 2019b, Mao *et al.* 2022). If *Haramiyavia* has the MM1 occlusal mode, then there must be a chewing function 'jump' from MM1 to MM2 mode during the evolution of 'haramiyidans' (Mao and Meng 2019b); this, if true, would conflict with the view that 'the teeth must continue to function throughout the evolutionary transformations of the body as a whole' (Butler 2000: 339).

In addition to several reasons already pointed out to favour the MM2 occlusal mode in 'haramiyidans' (Meng *et al.* 2014, Mao and Meng 2019b), Mao *et al.* (2022: fig. 17A3, A4, D) also showed that p4 of *Thomasia* is highly similar to that of *Qishou* (Mao and Meng 2019a) in which the enlarged cusp a1 must be the functional cusp, judging from its size, shape, position, and wear, that bites in the basin of P4 as in *Qishou*. Thus, in *Thomasia* the molars following p4 should have an MM2 occlusal mode so that the dentition forms a consistent functional unit. If the molars occlude in the MM1 mode in *Thomasia*, as assumed for *Haramiyavia* (Jenkins *et al.* 1997, Luo *et al.* 2015), then it would be difficult to explain why cusp a1 of p4 is the primary functional cusp but in the following molars the functional cusp rows switched to row b. *Thomasia* appears to have the MM2 occlusal mode and, if so, it would be difficult phylogenetically to interpret *Haramiyavia* as having the MM1 occlusal mode.

9.    *Mandible deep but short.*

The mandibles of euharamiyidans and multituberculates are proportionally short but deep compared to those of other mammaliamorphs in which the mandible is slender and long, as shown in Figure 9. This morphology is probably related to the reduction of lower teeth and the enlargement and distal extension of the lower incisor. The jaw morphology is highly similar to that of the marsupial *Dactylopsila trivirgata*, and, as discussed above, these similarly must have evolved independently for similar jaw function and perhaps a similar dietary for animals living in forest environments. In contrast, *Haramiyavia* has a long and slender mandible, resembling that of other primitive mammals, such as *Morganucodon* and *Kuehneotherium* (Butler 2000; Fig. 9).

10.    *Anterior extension of the masseteric fossa.*

Gambaryan and Kielan-Jaworowska (1995: 45) noted that 'The backward chewing stroke in multituberculates (unique for mammals) resulted in a more anterior insertion of the masticatory muscles than in any other mammal group, including rodents.' Butler (2000) further noted that it is possible that specialization of the masseter had some relation to the evolution of the sectorial premolars. These interpretations can also be applied to euharamiyidans, given that the masseteric fossa is anteriorly extended (Fig. 9). As a related feature, the coronoid process usually extends anteriorly on the labial side of the distal lower molars and in lateral view the ultimate lower molar is usually hidden by the process. In *Adalatherium* (Krause *et al.* 2020a; Fig. 9), the masseteric fossa does not seem extended so anteriorly as in euharamiyidans and multituberculates, which may be interpreted as a primitive retention; however, as in multituberculates and euharamiyidans, the coronoid process extended anteriorly

to the labial side of the ultimate molar and part of the penultimate molar.

### 11. *Mental foramen position.*

There is one, presumably the posterior, mental foramen that is present at the lateral side of the diastema between the incisor and premolar; this is unique in mammaliamorphs. Even in triconodontids, the same foramen is more posteriorly located (Sues 1986). In other mammaliamorphs, this foramen is even more posteriorly positioned on the lateral side of the dentary. In *Haramiyavia* the mental foramen is more distally located.

### 12. *Mandibular condyle vertically (posteriorly) extended.*

A fully developed dentary (mandibular) condyle is a mammalian feature. In non-mammalian mammaliamorphs, the jaw joint is exclusively between the articular and quadrate, as in tritylodontids, so that a dentary condyle is absent. Dual joints between articular–dentary and quadrate–squamosal, as in *Morganucodon*, would imply a partial dentary condyle (Kermack *et al.* 1981).

It is known that in most multituberculates, except for specialized forms, such as some taeniolabidids and sloanbaatarids, the condylar process slopes posteriorly and contributes to the posterior margin of the lower jaw (Gambaryan and Kielan-Jaworowska 1995). More specifically, in multituberculates 'the condylar process is continuous with the remainder of the posterior border of the dentary which forms a semicircle' (Gambaryan and Kielan-Jaworowska 1995: 86). Unlike most therians, where the condylar process is transversely elongated, the articular facet of the condyle shows a vertical, or ventral, extension (Gambaryan and Kielan-Jaworowska 1995). In paulchoffatiids, the articular surface of the condyle faces posteriorly (Hahn 1969, 1978), whereas in later multituberculates it has a more dorsal orientation. The dentary condyle of euharamiyidans has a similar vertical extension in orientation. Along with a longitudinally orientated glenoid fossa (see below), such a transversely narrow and vertically (dorsoventrally) extended condyle allows palinal movement of the lower jaw during chewing. The dentary condyle of *Haramiyavia* is unknown but given its dentition and potential possession of the postdentary bones (Jenkins *et al.* 1997, Luo *et al.* 2015), the condyle would be similar to those of *Morganucodon* or basal therians.

### 13. *An anteroposteriorly orientated glenoid fossa without the postglenoid process.*

A fully developed glenoid fossa in the squamosal is a mammalian feature. In stem mammaliaforms, the glenoid fossa may be partly formed, such as in *Morganucodon* (Kermack *et al.* 1981). In tritylodontids the lower teeth can move horizontally and backward, judged by the tooth wear striations (Sues 1986), the jaw articulation is between the articular and the quadrate. It has been recognized that in multituberculates the longer axis of the glenoid is directed anterolateral (more longitudinally than transversely), but it is arranged transversely in most therians, monotremes, *Morganucodon* and *Sinoconodon*, or subtransversely in *Vincelestes* (Gambaryan and Kielan-Jaworowska 1995, and references therein). The glenoid fossa of 'haramiyidans' was unknown until the report of several euharamiyidans, which is longitudinally orientated without the postglenoid process, allowing for palinal jaw movement (Bi *et al.* 2014). A similar glenoid fossa was reported in gondwanatherians (Krause *et al.* 2014, 2020a). Whether there is a glenoid fossa in *Haramiyavia* is unknown. If the postdentary unit is present, as interpreted by Luo *et al.* (2015), then the glenoid, if any, should be partial. Because a palinal component is present in the chewing cycle, as inferred from the tooth shape and wear (Luo *et al.* 2015), the glenoid will not be the same as in *Morganucodon*; it would be orientated anteroposteriorly and likely without the postglenoid process.

### 14. *Palinal chewing.*

The backward chewing stroke in multituberculates (Gingerich 1977, Krause 1982) was considered unique for mammals, which is associated with an anterior insertion of the masticatory muscles (Gambaryan and Kielan-Jaworowska 1995). Butler and MacIntyre (1994) also showed that 'haramiyidans' chewed backwards without any transverse component, which existed in the Triassic haramiyidan *Thomasia* (Butler 2000) but not in *Theroteinus*; the jaw movement of the latter was interpreted as to be orthal (Sigogneau-Russell *et al.* 1986, Butler 2000, Debuysschere 2015, 2016). *Haramiyavia* was originally interpreted as having predominantly orthal jaw movement, but a short distal movement of the lower jaw, about one-third of the length of an upper molar, appears possible in the chewing stroke of *Haramiyavia* (Butler 2000, Luo *et al.* 2015). Butler (2000) also thought that the amount of distal movement in *Haramiyavia* was probably less than in *Thomasia*, as shown by tooth wear, with which we concur, based on p4 morphology of *Thomasia* that is similar to that of *Qishou* but different from *Haramiyavia*. We also concur that the distal movement of the lower jaw in *Haramiyavia* must be short if it does exist. The reason is that the lower dentition of *Haramiyavia* is long, similar to those that cannot do palinal jaw movement. Although its upper dentition is only partly known (only the incisors and molars are preserved) (Jenkins *et al.* 1997, Luo *et al.* 2015), we predict that the upper dentition should have the tooth number and length similar to those of the lower one. We have argued above that a short lower dentition, relative to the upper, is a premise for palinal jaw movement. On the other hand, there is to our knowledge, no example in mammaliamorphs in which the upper dentition is shorter than the lower one, except for *Megaconus* (Zhou *et al.* 2013, but see: Meng *et al.* 2014). If the upper and lower dentitions are subequal in tooth number and length, it stands as evidence for a very short, if any, palinal component in lower jaw movement during chewing in *Haramiyavia*.

The general molar morphology and palinal jaw movement are the main features uniting gondwanatherians (Rougier *et al.* 2021). The molar morphology of gondwanatherians is complex and peculiar, but it seems more derivable from the allotherian tooth pattern than from the triconodont molar or its derivatives. The inferred palinal jaw movement of gondwanatherians is shared with multituberculates and 'haramiyidans'. For those that do not have the lower jaw and teeth preserved, such as *Vintana*, the palinal jaw movement can be inferred from the longitudinally

orientated glenoid fossa that lacks the postglenoid process (Krause *et al.* 2014).

Tritylodontids are also capable of backward horizontal jaw movement, which differs from the allotherian palinal jaw movement, as reflected by their different dental structures. In addition to the articular–quadrate jaw articulation, their jaw joint is positioned very high above the level of the cheek teeth, as in herbivorous therian mammals; in contrast, the jaw joint is below the occlusal level in most multituberculates (Gambaryan and Kielan-Jaworowska 1995). In addition, as discussed above, the teeth of tritylodontids are not differentiated into premolars and molars, and all the teeth have similar cusp shape and height. In contrast, the teeth of allotherians, at least in multituberculates and 'haramiyidans', are heterodont in which some teeth and cusps are taller than other teeth and cusps. This indicates that there is a puncture function in allotherians in which the taller tooth, such as p4, or cusps, such as cusp a1, could function to pierce food items in an orthal component of the jaw movement. Moreover, a common feature in multituberculates and 'haramiyidans' is that the occlusal surface of the upper dentition is not flat; instead, it has two arcs in multituberculates (Jin *et al.* 2022) and an en echelon pattern in 'haramiyidans' (Jenkins *et al.* 1997, Luo *et al.* 2015). Because of this, multituberculates have the need and ability to gape the mouth, as shown by the backward sloping of the condyle in multituberculates (Gambaryan and Kielan-Jaworowska 1995). A similar function is expected in euharamiyidans. These structures, thus functions, are lacking in tritylodontids, as well as in rodents, in which the occlusal surface of the dentition is flat. Along with other features, such as the shorter lower dentition in relation to the upper, the palinal jaw movement or chewing in allotherians differs from that of tritylodontids.

## Discussion

One-hundred and seventy-five years after the report of the first haramiyidan *Thomasia* ('*Microlestes*') (Plieninger 1847) and 165 years since the report of the first multituberculate *Plagiaulax* (Falconer 1857), the phylogenetic relationships of 'haramiyidans' and multituberculates have remained unsettled. The molar similarity between *Plagiaulax* and *Thomasia* was recognized by Falconer (1857: 275), as he stated that the molars of the two taxa are so similar that 'had detached molars of both been met with in beds of the same formation, they might have been taken for back and front, or upper and lower teeth of the same, or of nearly allied, species'. Owen (1871: 110), however, disagreed: 'To be able to affirm of a "close alliance" between *Plagiaulax* and *Microlestes*, the palaeontologist must know, not only the degree of resemblance between certain of their teeth, but also that between the rest of their dental system. One must first learn in what numbers the small tubercular teeth of *Microlestes* were present in its jaws, and next with what other kind of teeth they may have been associated.' Owen (1871) considered the dentition of *Plagiaulax* to resemble that of *Thylacoleo*, more so than to any other marsupial; he argued that *Plagiaulax* was a carnivore and '*Plagiaulax* is to *Thylacoleo* what the Weasel is to the Lion'. (Owen 1871: 113). As time went on, a carnivorous mode of life for multituberculates became unacceptable (Gidley 1909), and Granger (1915), in a short abstract, argued

that multituberculates are neither marsupials nor monotremes but belong to a separate group of mammals (Kielan-Jaworowska *et al.* 2004), a view universally accepted today. The dental system of *Thomasia* still remains unknown today, but the information about 'haramiyidans' from discoveries during the last one-and-a-half centuries has been greatly enriched. While multituberculates have long been separated from marsupials, the 'close alliance' of 'haramiyidans' and multituberculates has gained increasing support by morphological evidence from the dental system, as we outline in this study.

Given our phylogeny, allotherians had already departed from other mammaliamorph groups in the Late Triassic, which witnessed the emergence of the mammalian physiology and bauplan (Araújo *et al.* 2022). In addition to divided tooth roots (Simpson 1928), the heterodont dentition of *Haramiyavia* with three molars, as an example, are highly mammalian. Combining with a relatively long and shallow mandible, the dentition of *Haramiyavia* probably represents the primitive morphotype for euharamiyidans and multituberculates. The aforementioned allotherian features form a convincing set of evidence to argue for Allotheria as a monophyletic tripartite group of mammals. Within allotherians, basal 'haramiyidans', including *Haramiyavia*, *Theroteinus* and *Thomasia*, are known from the Late Triassic (Hahn and Hahn 2006, Debuysschere 2015, Mao *et al.* 2022), whereas the earliest known euharamiyidans are from the Middle Jurassic, although they may have occurred earlier as predicted by the tip-dating analysis (Mao *et al.* 2021). The earliest unequivocal multituberculates are from the Middle Jurassic and co-exist with euharamiyidans, at least in Europe, Siberia, and East Asia (Butler and Hooker 2005, Yuan *et al.* 2013, Averianov *et al.* 2019, 2020, Mao *et al.* 2022). In these sites, species diversity and specimen abundance of multituberculates are lower than those of euharamiyidans. Thus, paleogeographic, chronological, and diversity data appear consistent with the hypothesis 'haramiyidans' as a paraphyletic group that gave rise to multituberculates (Van Valen 1976, Hahn *et al.* 1989, Butler 2000, Butler and Hooker 2005, Hahn and Hahn 2006), which is also supported by most phylogenetic studies (Luo *et al.* 2007, Zheng *et al.* 2013, Bi *et al.* 2014, Krause *et al.* 2014, 2020a, Hoffmann *et al.* 2020, Mao *et al.* 2020, 2021, Wang *et al.* 2021, this study).

Gondwanatherians would have originated by the Middle Jurassic, as depicted by Hoffmann *et al.* (2020). The high-crowned and multiple-ridged tooth patterns in many gondwanatherians (Krause *et al.* 2014, 2020a, Rougier *et al.* 2021) are more reflective of the allotherian tooth pattern than the triconodont, symmetrodont, or tribosphenic pattern. The unique molar morphologies of gondwanatherians may be interpreted as specialization of the groups in the southern continents and much of the morphological diversity is yet to be discovered (Hoffmann *et al.* 2020).

The allotherian dental features and palinal chewing differ radically from those of therians and kin, such as 'triconodontans' and docodonts, in which there is a transverse component in the lower jaw movements (Crompton and Hiiemae 1970, Crompton and Sita-Lumsden 1970, Crompton 1971, 1974) (Fig. 9). The palinal chewing does not have the transverse component in multituberculates (Krause 1982) and 'haramiyidans' (Butler and MacIntyre 1994); this is probably true for gondwanatherians, as indicated by the longitudinal glenoid fossa (Krause *et al.* 2014, 2020a). The

palinal jaw movement has been considered as an obstacle to derive allotherian tooth pattern from those with the transverse jaw movements in chewing (Butler 2000). Butler (2000: 338, 2001) postulated that the palinal jaw movement of allotherians 'seems to have evolved from an orthal, crushing type of occlusion in which cusps bit into longitudinal valleys on opposing teeth'. Gambaryan and Kielan-Jaworowska (1995: 101) wrote: 'However, given that in rodents the forward power stroke (with only a limited transverse component) developed from forms with a transversely directed power stroke, the origin of multituberculate backward power stroke from a transversely directed power stroke of triconodonts may be possible.' In 'haramiyidans', *Haramiyavia* was considered as having the orthal occlusion (Jenkins *et al.* 1997) but a palinal component has been recognized in a more recent study (Luo *et al.* 2015). The chewing movement of *Theroteinus* was interpreted as being orthal (Sigogneau-Russell *et al.* 1986, Butler 2000, Debuysschere 2015, 2016) and the orthal tip-to-tip tooth contact, primarily for crushing, in *Theroteinus* may represent a transitional condition (Mao *et al.* 2022), a hypothesis that calls for testing with better specimens.

The molar morphology and palinal jaw movement of allotherians indicate an omnivorous diet, as already recognized by others (Clemens and Kielan-Jaworowska 1979, Krause 1982, Butler and MacIntyre 1994, Gambaryan and Kielan-Jaworowska 1995, Butler 2000, Kielan-Jaworoska *et al.* 2004, Wilson *et al.* 2012), which sharply contrasts to the triconodont tooth pattern and its derivatives (Fig. 9). Those with the latter tooth patterns are primarily insectivorous, given their small body size, sharp tooth cusps, and slender mandible, as represented by *Morganucodon* and *Kuehneotherium*, which have been thought to be generalized insectivores (Kielan-Jaworoska *et al.* 2004). For *Morganucodon* and *Kuehneotherium*, their diet has differentiated into consuming harder prey, such as coleopterans in *Morganucodon*, and soft prey, such as lepidopterans, in *Kuehneotherium*, which suggests deep lineage splitting of mammals associated with ecomorphological specialization and niche partitioning (Gill *et al.* 2014). In comparison, the dental morphologies, the palinal jaw movement, and the inferred omnivorous diet of the Late Triassic 'haramiyidans', which co-existed with *Morganucodon* and *Kuehneotherium*, must represent an even more divergent lifestyle in terms of ecomorphological specializations and niche partitioning during the earliest stages of mammalian evolution.

## CONCLUSION

We name a new genus and species of euharamiyidans, *Mirusodens caii*, based on a skeletal specimen from the late Middle Jurassic Yanliao Biota. The superbly preserved specimen furnishes new data on osteological and integumentary morphologies of euharamiyidans. Using a set of imaging methods, we are able to document the anatomical features of dentitions, skeleton, and integumentary system and demonstrate again that 'haramiyidans' were a group with diverse morphologies. These data broaden and deepen our knowledge of the euharamiyidan biology and evolution and are important to understand early evolution of mammals.

Our phylogenetic analyses identify, again, that multituberculates, euharamiyidans, and gondwanatherians form a tripartite monophyletic clade of Allotheria within Mammalia. The Late Triassic taxa, including *Haramiyavia* and *Theroteinus*, are

stem allotherians. Our study and other recent discoveries have revealed many shared derived characters uniting allotherians, particularly euharamiyidans and multituberculates. We tabulated and briefly discussed these features in our study, which include, but are not limited to, the following: one pair of lower incisors (reduction of lower incisor number) whose roots extend backward in the dentary, enlargement of the upper and lower incisors, two or more cusps on the large upper incisor, absence (lost) of the lower canine, two molars in each jaw quadrant, lower number of teeth, lower molar mesiolingual cusp large, the lingual cusp row of the ultimate lower molar occluding in the central valley of M2 (as shown by wear facets on the lingual side of lingual cusp row of m2), a deep but relatively short mandible, anterior extension of the masseteric fossa, the posterior mental foramen at the lateral side of the diastema between the incisor and premolar, mandibular condyle vertically (posteriorly) extended, and an anteroposteriorly orientated glenoid fossa lacking the postglenoid process. These features constitute what Owen (1871) called the 'dental system' that forms much more robust evidence than only the overall molar similarity to diagnose multituberculates, euharamiyidans, and gondwanatherians as a tripartite clade of Allotheria within Mammalia.

The phylogenetic and morphological evidence favour the view that the traditional 'Haramiyida' is a paraphyletic group and multituberculates were probably derived from the Triassic 'haramiyidans'. This view is consistent with the paleogeographic, chronological, and diversity data of allotherians. The dental system of allotherians is suggestive of an omnivorous/herbivorous diet, and the division of the dental systems between allotherians and therians represents ecomorphological adaptations in different directions and reflects a profound niche-partitioning among early mammals.

## SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

**File S1.** A new euharamiyidan, *Mirusodens caii* (Mammalia: Euharamiyida), from the Jurassic Yanliao Biota and evolution of allotherian mammals/Character list/Phylogenetic analysis/Input data matrix/Heuristic search settings/Strict Consensus tree/Apomorphy list.

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## DATA AVAILABILITY

The data underlying this article are available in the article and in its online supplementary material.

## CONFLICT OF INTEREST

The authors declare no conflict of interests.

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